CHALLENGES AND INNOVATIVE SOLUTIONS IN RIVER SCIENCES

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CHALLENGES AND INNOVATIVE SOLUTIONS IN RIVER SCIENCES

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EDITORIAL
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Editorial: Challenges and Innovative Solutions in River Sciences

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Editorial on the Research Topic

Challenges and Innovative Solutions in River Sciences

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INTRODUCTION

The Anthropocence describes the time period when humans have become significant modifiers of the Earth's ecosystems (Waters et al., 2016), with dramatic consequences for riverine landscapes. Worldwide, rivers and their associated floodplains have undergone substantial transformations, leading to dramatic reductions of their integrity, natural multi-functionality and the diversity of ecosystem services they provide (Erös and Bányai, 2020). Parallel to this development, the complexity of social, economic, and ecological demands has increased, exercising multiple and often interlinked stressors on river-floodplain systems at different spatial and temporal scales (Birk et al., 2020). River managers have to perceive riverine landscapes as socio-ecological systems, in which human demands, attitudes and perceptions as well as ecological requirements must be collectively considered. This requires new approaches and innovative tools and solutions in river management to harmonize the ecosystem and human needs and to protect riverine landscapes from further degradation, while also considering their critical role for support of aquatic biodiversity (van Rees et al., 2020; Bonar, 2021).

This Research Topic presents selected original research articles from the sixth Biennial Symposium of the International Society for River Science hosted by the Institute of Hydrobiology and Aquatic Ecosystem Management at the University of Natural Resources and Life Sciences, Vienna (BOKU) Austria, from 8–13 September 2019. According to the conference theme "*Riverine landscapes as coupled socio-ecological systems*," the symposium emphasized integrative research on the sustainable use, management, and protection of riverine landscapes and societal implications (Weigelhofer et al., 2021). This special issue focuses on new insights in changes of ecosystem functions and biodiversity and approaches and tools leading to innovative solutions for river management presented at the conference which help to deal with current and future challenges in river research and management.

This special issue covers the following themes:

- Effects of changes to river ecosystems at landscape and global scales
- Innovative solutions to assess these changes
- Long-term strategic and integrative approaches in coupled socio-ecological systems

EFFECTS OF CHANGES TO RIVER ECOSYSTEMS AT LANDSCAPE AND GLOBAL SCALES

Changes of human behavior and interventions at landscape and global scales have multiple consequences for riverine ecosystems, such as altered discharge, temperature and biogeochemical characteristics. Reduced hydrological connectivity of floodplains may impact the phosphorous buffering capacity of floodplain sediments, thus altering the total riverine phosphorous cycle (Preiner et al.). Furthermore, climate change affects aquatic organisms in multiple ways and may intensify prevailing human stressors. Salmonids of alpine rivers showed increased physiological stress and diseases (Borgwardt et al.), while macrophytes responded negatively to simulated climate induced changes of the interplay between flow velocity, DOC and CO_2 (Reitsema et al.).

INNOVATIVE SOLUTIONS TO ASSESS THESE CHANGES

Addressing changes in river systems requires the continuous development of new concepts and tools to tackle specific- and multiple stressors, their altered patterns and effects on ecosystem services in these modified systems more accurately. The morphological structure of riverine landscapes has been largely altered, and human uses have changed them massively at least during the past 150 years, leading to a further change in interactions between humans and river systems (Haidvogl, 2018). Fisheries are a globally important, socially, ecologically and economic relevant ecosystem service. To study and manage social-ecological linkages occurring in salmonid fisheries, the metacoupling framework offers an innovative solution from the United States (Carlson et al.), by assessing and managing socioeconomic and environmental interactions within and between coupled human and natural systems at local, regional, and global scale. Secondary development of decoupled floodplains and conflicting policies present challenges to restoration planning of these systems. By combining single- and multiple-species approaches in an Austrian floodplain, Weigelhofer et al. provides insights into the potential of different restoration measures and trade-offs between different ecological aims. Likewise, a comparison of modeling approaches to estimate nutrient retention in decoupled and reconnected floodplain sections provides evidence of the strengths and weaknesses of the different approaches and the effects of potential restoration measures in Danube floodplains (Natho et al.). Regarding the management of nutrient dynamics, Teubner demonstrated that water transparency thresholds are a useful socio-ecological indicator for macrophyte and algal growth and hence recreational opportunities in an old, urban oxbow lake along the Austrian Danube.

Rivers transport enormous amounts of plastic debris, leading to massive accumulations in the sea (Lechner et al., 2014). This problem calls for new collection methods, as shown for Asian rivers (Owens and Kamil). Future changes in temperature regimes need new equipment to identify cold-water patches as critical refugia for endangered species, as shown by a combination of novel techniques (Casas-Mulet et al.). Invasive plant species are a significant global issue affecting riverine landscapes (Hofstra et al., 2020) and accurate measurements of tissue H_2O_2 concentrations provide a new approach to analyze stress intensity and identify stressors for plant growth as shown for *Egeria densa* in Japanese rivers (Asaeda et al.).

LONG-TERM STRATEGIC- AND INTEGRATIVE APPROACHES IN COUPLED SOCIO-ECOLOGICAL SYSTEMS

The critical situation of stressed and degraded river systems requires not only immediate actions, it also calls for long-term strategic and especially novel integrative approaches to address (river basin) management options at larger scales. Sievert et al. provided such an approach by considering established conservation networks in stream systems in Missouri, which can be an efficient tool to prioritize fish conservation sites throughout river networks. Further, interdisciplinary educational programmes can be a key element to face future challenges while supporting interdisciplinary and management-orientated science at an international scale, as shown for the SMART (Science for MAnagement of Rivers and their Tidal Systems) program (Serlet et al.).

OUTLOOK

These selected examples highlight current progress in freshwater conservation science and river basin management planning and emphasize that more efforts are needed to fully consider riverine landscapes as socio-ecological systems under the view of accelerated changes in the near future. In order to offer holistic solutions for these challenges, a new socio-ecologically driven research agenda is a promising approach. Thus, the following aspects need further attention to support new management schemes in riverine landscapes:

Considering riverine landscapes conceptually as socio-ecological systems would need the incorporation of socio-ecological concepts such as colonization of natural systems (Fischer-Kowalski and Erb, 2016) and social metabolism (Schmid, 2016) to address the coupling between ecological and societal systems. The integration of these concepts would allow to analyze the changing role of rivinere landscapes in the societal metabolism and the elements of the transformation of riverine landscapes.

There is a need to tackle problems and develop indicators more integratively to depict ecological and societal dimensions. New techniques, as for example in optical or acoustic imagery, and interdisciplinary approaches, as well as seeing rivers with their wetlands and surrounding landscape in a holistic way will support this.

The complex setup of stressors acting on our river ecosystems calls for an intensified development of tool-sets, considering future drivers of change and related direct and indirect effects. This will support efforts to tackle conflicting goals of laws and directives and to diagnose more accurately consequences and more tailored management actions at appropriate scales.

More interdisciplinary doctoral programmes need to be developed to address the multi-dimensional nature of these coupled systems and educate a new generation of scientists facilitating the knowledge transfer to application.

Meetings that bring together inter- and transdisciplinary scientists and other actors from across the globe are a critical mechansim to develop strategies for conserving riverine landscapes as coupled socio-ecological systems; participation to jointly define key issues and novel solutions should be encouraged.

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All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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METHODS
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Adapting Coastal Collection Methods for River Assessment to Increase Data on Global Plastic Pollution: Examples From India and Indonesia

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Marine debris often begins as litter or waste on land. Rivers play an important role in transporting this debris from communities to ocean systems, and yet we lack data on debris in freshwater systems. This work promotes eliminating the gap in knowledge between debris in marine and freshwater systems through use of a consistent, replicable methodology that can be used to improve data on freshwater shoreline debris. Expansion in the application of this method globally can allow researchers to ground-truth estimates of the debris entering the world's oceans via rivers. Widespread use of this method would provide data on the litter degrading in the world's riverine systems, an important ecological problem in its own right often sidelined in work on marine debris. Improved ground-truthing will also shed light on the missing plastics question: the disparity between input estimates and measurement of plastic waste in the world's oceans. Cataloging the way debris moves through, and remains a part of, freshwater systems is imperative to addressing the global plastic waste problem. Here we share examples of how the method has been applied in the Tukad Badung river in Indonesia and the Karamana river in India.

Keywords: litter, debris, freshwater, river, plastic pollution, methods, missing plastic

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INTRODUCTION

Rivers of Plastic

Evidence indicates that litter and plastic pollution is not only a problem in the world's oceans but also in global riverways (Rech et al., 2014; Jambeck et al., 2015; Lebreton et al., 2017; Schmidt et al., 2017; Blettler and Wantzen, 2019). Many researchers point to rivers as an important pathway for debris from clusters of human population to ocean systems (Nollkaemper, 1994; Islam and Tanaka, 2004; Lechner et al., 2014; Jambeck et al., 2015; Lebreton et al., 2017; Schmidt et al., 2017; Blettler and Wantzen, 2019). Whether a study from Europe describing how floating macro-plastics from the Rhone reach the Mediterranean (Castro-Jiménez et al., 2019) or research from Indonesia suggesting how rivers transport land-based plastic to the ocean (van Emmerik et al., 2019), the literature is replete with examples. In a comprehensive study testing hypotheses for how debris reaches oceanic systems, Willis et al. (2017) find that most debris comes from local sources. The *Stemming the Tide* report confirms that rivers bring debris from upstream communities to coastal areas (Ocean Conservancy, 2015). It also states that while researchers estimate that 80% of debris comes from land-based sources, their work on the ground in China and the Philippines indicates this number is likely much higher (Ocean Conservancy, 2015). In developing countries, uncollected waste "is directly deposited into and around rivers and other water bodies that present direct pathways into the marine ecosystem" (Ocean Conservancy, 2015, p. 14). As noted by van Emmerik et al. (2019) while rivers in South East Asia are seen as primary channels for plastic waste, without better observations "the origin and fate" of this waste remains unclear (p. 2). The most recent IPBES report (Díaz et al., 2019) notes that oceanic plastic pollution "has increased ten-fold" since 1980 (p. 28). Improving data on the way debris moves through, or remains a part of, freshwater systems is imperative to better understanding the global plastic waste problem. Here we share a consistent, replicable methodology—a modification of the NOAA Marine Debris Shoreline Field Guide methods (Opfer et al., 2012)—that can be applied to improve data on freshwater shoreline debris globally. This is not a new methodology, but instead a call to expand the application of this methodology globally to improve empirical evidence of debris in river systems. Expansion in the application of this method worldwide can allow researchers to ground-truth estimates on the debris entering the world's oceans and degrading in riverine systems, both of which can inform the "missing plastic" question.

BACKGROUND

Understanding Freshwater Litter

While there are fewer assessments of freshwater debris than that of oceanic or coastal, freshwater research has grown in the last two decades. The published research favors collection from river water or sediment over that of riverbank assessments and more often than not focuses on the developed world. That said, the literature includes a range of studies of varying scope, many of which emphasize the potential of rivers to deliver waste—most often plastic—to the world's oceans.

Many studies emphasize water-based collection. An early assessment of the Los Angeles and San Gabriel Rivers reported an average of 2.3 billion pieces of plastic over 72 h of collecting in water under multiple conditions (Moore et al., 2011). Lechner et al. (2014) conducted a multi-year driftnet study on debris in the Danube, estimating 4.2 tons of debris flow from this river to the Black Sea each day. Researching floating debris in England's Tamar Estuary, Sadri and Thompson (2014) found 82% were micro-plastics. Working on the Thames, Morritt et al. (2014) netted over 8,000 items in a 3-month period and found it to be overwhelmingly made of plastic. In a study of 29 Great Lakes tributaries, Baldwin et al. (2016) collected and cataloged floating micro- and macro-plastics, finding plastic in all of their 107 samples. The authors report finding "fragments, films, foams, and pellets/beads… at greater concentrations during runoff-event conditions" but this was not the case for fibers (Baldwin et al., 2016, p. 10377). In a study modeling the distribution and transport of debris in the Great Lakes, Cable et al. (2017) found 2 million fragments/km^2 in the Detroit River. In Vietnam, Lahens et al. (2018) evaluated both micro- and macro-plastic accumulation, determining that about 4.4 g per inhabitant per day of land-based waste entered the water system, a significant problem as their study area encompasses the megacity Ho Chi Minh. As a result of monthly observations of floating macro debris on the Rhone River, Castro-Jiménez et al. (2019) estimated that the river serves as conduit for approximately 200,000 pieces of plastic debris traveling to the Mediterranean annually. In 2019, van Emmerik et al. used field methods and modeling to discover 2,100 tons of plastic waste travels from the Jakarta area to the sea each year. Studies in freshwater consistently reveal that debris, primarily plastic, is a significant problem.

Micro-plastics are often the focus of water and shoreline assessments. Imhof et al. (2013) examined micro-plastics on the shores of the subalpine Italian lake Garda finding micro-plastic contamination in sediment at similar magnitude of that in marine systems. Studying 11 sites spanning over 800 km of the Rhine River Mani et al. (2015), measured an average of 892,777 micro-plastic particles per km^2. In the first study on micro-plastics in the Thames, Horton et al. (2017) found this type of debris at all four of their sites, recording a high abundance of debris from paint used for road marking. An assessment from the South American Paraná floodplain lakes of micro-, meso-, and macro-plastics found contamination comparable to river and marine beach collections (Blettler et al., 2017). In the first report on micro-plastics in lake or estuarine habitats in India, Sruthy and Ramasamy (2017) found a mean abundance of micro-plastic of 252.80 ± 25.76 particles/m^2, with low-density polyethylene dominating the sample. In a watershed-scale assessment from Montana encompassing 72 sites and 714 samples, Barrows et al. (2018) found micro plastics in 57% of the samples; the composition of which was predominantly fibrous, and made up of "synthetic or semi-synthetic materials" (p. 382). Comparing collections to discharge in the region, and unlike the results from the Baldwin et al. (2016) study, the authors determined storm water was not a source of micro-plastics in the Montana study area (Barrows et al., 2018). In a study of micro-plastics in five tributary basins of the Selenga River in Mongolia, Battulga et al. (2019) selected 12 sampling sites along river shorelines, collecting once during the dry season in August. They classified micro-plastic debris by subdividing it (mega-, macro-, meso-, and micro-fractions) and then typing it (foam, fragment, fiber, and film) and finally delineating polymers (polyethylene, polystyrene, polypropylene, polyvinyl chloride, polyethylene terephthalate, and polyurethane) (Battulga et al., 2019). The authors found polystyrene foam to be the most frequently appearing material, and concluded that debris was fragmenting on river shorelines (Battulga et al., 2019). Both shoreline and water-based microplastic research indicates that this is a significant environmental problem in freshwater systems.

Some studies use a range of methods, perhaps combining types (shoreline, water, or sediment) or including shorelines assessment of micro and macro plastics, or analyzing wildlife. Evaluating the Laurentian Great Lakes, Driedger et al. (2015) found that debris density in water rivaled that of ocean gyres, that shoreline litter was more than 80% plastic, and that sediments were not well studied. One comprehensive study of 15 sites in five rivers in Illinois and Indiana evaluated both riparian and benthic accumulation. They found riparian zone density in their sites was comparable to global beach averages, but that river benthic accumulation proved higher than in marine benthic environments (McCormick and Hoellein, 2016). In a shoreline study of the coastal wetland Martil in North-East Morocco, Alshawafi et al. (2017) found plastic (57%) dominated macro-debris types, and also noted its composition in micro-plastics including 26.9% foam, 7.8% fishing line, and 1.23% film. In a unique study analyzing data from the African duck, Reynolds and Ryan (2018) found that micro-fibers existed in 5% of fecal and 10% of feather samples, indicating a threat to freshwater systems and the wildlife residing there. This work provides evidence that the issue of global plastic pollution is as important in freshwater as it is in marine systems.

Several researchers focus, as we do, on river shoreline collections. Rech et al. (2014) conducted assessments along the shores of four Chilean rivers (Elqui, Maipo, Maule, and BioBio). They determined the main composition of debris found along riversides to be plastics, polystyrene, and manufactured wood, which ranged from 36 to 82% proportionally. Vincent and Hoellein (2017) collected at Pratt beach, Lake Michigan, USA, bi-weekly from March to November of 2015. They reported the highest density of litter in the fall, when compared to spring and summer; their assessment determined that direct littering as well as distribution via wind and waves led to pockets of higher accumulation (Vincent and Hoellein, 2017). Evaluating France's Adour River, Bruge et al. (2018) worked with stakeholders to collect over 120,000 items across 278 riverbank samples. While 41% of their collected debris was not identifiable due to degradation, of that which could be identified, 70% consisted of "food and beverage packaging, smoking-related items, sewage related debris, fishery and mariculture gear, and common household items" (Bruge et al., 2018, p. 1). These studies do not represent an exhaustive review of the literature on freshwater debris. And yet, collectively they provide evidence for how rivers transport debris globally, revealing the ways in which measuring debris in river systems can help inform work to understand the global problem of litter and debris.

Why Are Shoreline Studies Important?

While researchers study debris in both marine and freshwater systems, much more data exists for marine contexts. Researchers understand that river systems both retain and export debris, though rivers are often presented as only a conduit from land to oceans (McCormick and Hoellein, 2016). It should be noted that river and freshwater systems are an important component of the story of marine debris, not only due to their role as carriers of debris from land to ocean. Broadly speaking, freshwater systems contribute significantly to both human drinking water and food systems (Eerkes-Medrano et al., 2015). It is not only direct usage of freshwater that is important, but also the merits of protecting riverine ecosystems. Blettler and Wantzen (2019) promote eliminating the gap in knowledge between debris in marine and freshwater systems, emphasizing the study of macro debris from rubbish. The authors remark that studies of micro-plastics, a hot topic in the field, are far outpacing studies of macro-plastics in freshwater research perhaps to the detriment of our understanding (Blettler and Wantzen, 2019). Why is the study of macro-debris so important, particularly in the developing world? As noted by Blettler and Wantzen (2019), many studies estimate the movement of plastics from rivers to the ocean, yet often do so based not on collections but on extrapolations from population, waste infrastructure, and hydrological modeling (e.g., Jambeck et al., 2015; Lebreton et al., 2017; Schmidt et al., 2017). Few studies exist of river shoreline debris in the southeast and south Asian countries frequently named as the largest contributors to riverine to oceanic plastic (i.e., China, India, Indonesia, the Philippines, Sri Lanka, Thailand, and Vietnam) (Jambeck et al., 2015; Ocean Conservancy, 2015; Blettler et al., 2018; van Emmerik et al., 2019). Castro-Jiménez et al.'s (2019) research on the Rhone River's surface waters indicates that current estimates are not well coordinated with field observations. In addition, Blettler and Wantzen (2019) note that macro-plastics weigh more than micro-plastics, therefore removing them yields a higher reduction in inputs; that what many researchers call "mismanaged solid waste" is often pointed to as a primary source in developing countries, and can occur along waterways; and that if plastics join water systems at rivers, then both finding and collecting them there is a more economic and efficient way to prevent marine debris. Gasperi et al. (2014) recommend that the best estimates of river inputs will come from comprehensively assessing debris in "mid water and river floor… the surface and sub-surface" (p. 166). Lechner et al. (2014) emphasize the importance of quantifying river debris flows based on field studies. Blettler et al. (2018) note the particular importance of conducting studies on freshwater plastics in countries with the combined features of a lack of waste infrastructure and growing economic development, as is the case with our sites in India and Indonesia. Several researchers point out that debris in developing countries is often disposed next to freshwater bodies, in systems known to lead to excess leakage (Ocean Conservancy, 2015; Kaza et al., 2018). For all of these reasons, improving freshwater data collection is an important step in better understanding both the problem of marine debris and the problem of freshwater ecosystem degradation via pollution.

METHODOLOGY FOR RIVER COLLECTION

While researchers proposing estimates of debris moving through rivers were clearly working with the best data available, more often than not these estimates are not based on empirical data of debris along riversides. It is more often the case that studies extrapolate debris loads through estimations based on population density, waste infrastructure (or lack thereof), economic status, or hydrology (Jambeck et al., 2015; Lebreton et al., 2017). Using these data builds a composite estimate of debris in riverine systems, but to improve these estimates we need focused, scientifically replicable data to help us better understand the ways that plastic moves from rivers to oceans—and, importantly—stays in riverine systems. The focus should be broadened to include scientific collections along river shorelines (as we describe here) as well as in freshwater water columns and sediments. Our method as such is not a new method, but a call to amplify an existing method with the stated purpose of improving real data on riverine systems. Freshwater collections should expand beyond rivers to include lakes and wetlands. An emphasis on this research has the potential to solve the so-called missing plastic problem: the disconnect between material input estimates and what has been measured in the world's oceans (Cózar et al., 2014; Schmidt et al., 2017). Researchers know that a great deal of marine debris begins as river debris. As such, expanding debris collection to riversides will help us holistically understand the issue, which should more aptly be called global plastic pollution.

Many organizations, non-profits, groups, and individuals promote annual or more frequent beach and river cleanups at city, regional, national, and international scales (e.g., Afroz Shah's Versova Beach Cleanup, Bali's Biggest Cleanup, The International Coastal Cleanup, The Surfrider Foundation National Beach Cleanup, The Source to Sea Cleanup, The Great American Cleanup). While these efforts contribute to a decrease of debris in locations around the world, and may provide limited debris composition data, they do not necessarily produce scientifically replicable results that allow comparisons across sites. In their 2009 United Nations Environmental Guide, Cheshire and Adler called for more consistent, comparable methods in marine coastal cleanups. Interestingly, Cheshire and Adler (2009) write that the "only practical route" to combat the problem is through "managing discard behavior" (p. 8). This is fascinating in that it fails to recognize that creating materials for one-time use that take decades or longer to degrade—and which never biodegrade—is inherently unsustainable. They continue by noting that "popular beaches" may be cleaned, though the process is "both expensive and logistically difficult" and "almost impossible" in an oceanic setting (p. 8). In this way the authors recognize that beach cleanups are not a long-term solution for the problem of marine debris. We concur, and promote riverside cleanups not as a solution, but instead as a tool to better inform communities, policymakers, and a global audience about the debilitating concentrations of debris polluting the world.

At present, researchers studying waste along riversides use wildly different methodology. In most of the riverside collection studies we evaluated, researchers did not note the source of their methodology, making it difficult to link to other studies potentially using the same or similar methods for comparison in meta-analysis. In many cases, it appears that the researchers devised new methodologies. While this arguably allows flexibility to local conditions, it prevents connecting the results to other research. In reading descriptions of methodology for the studies included here, it was at times difficult to understand basic facts about the collection, for example the total area sampled, the length of collection time, how many individuals took part in the collection, or whether researchers used a methodical pattern of walking an area to ensure consistency, thoroughness, and allow for replication. Our proposed method alleviates these concerns.

We also noted that researchers often collect and report data on broad categories of debris (plastic, metal, cloth, etc.). Broad categorization allows researchers to understand the percentage of plastic, for example, but does not allow a deeper understanding of what kind of plastic (or metal, or cloth, etc.) is most frequently found. More detailed data is often needed when cataloging debris as it allows understanding what percentage of the found debris is, for example, food packaging or fishing gear. This depth of information can better allow linking science and policy—and provide data that can enrich recommendations to target policy change.

In some cases, researchers divide the debris into broad categories based on function (i.e., hygiene/medical; food packaging). In this way they more closely tie their data with human behavior instead of source materials (i.e., plastic, glass). While this may potentially allow more targeted outreach to local users, collecting data in this way does not allow simple comparison with results from other sites. One way to improve these results would be to count and categorize materials explicitly by type (e.g., plastic bottles, plastic bags, shoes) and then merge categories to form broad groups based on usage. When data are collected with a high level of detail, as can be the case when using the NOAA methodology, explicit categories can always be merged into groups later.

Cheshire and Adler (2009) provide methodologies for comprehensive and rapid beach litter assessments, benthic assessments, and floating litter assessments. When considering their comprehensive coastal assessment, the Cheshire and Adler (2009) methodology recommends selecting a beach site of minimum 100 m length, from 15 to 45° slope, accessible both in terms of a lack of built structures (i.e., jetties) and to researchers throughout the year. In addition they recommend selecting a site not featuring other collection activities and one on which collection activities will not harm threatened or endangered species (Cheshire and Adler, 2009). The authors note that both the Convention for the Protection of the Marine Environment of the Northeast Atlantic (OSPAR) and Northwest Pacific Action Plan (NOWPAP) recommend that collection sites should "not be within close proximity to rivers, harbors and ports" but in contrast, Cheshire and Adler recommend a stratified sample featuring "Urban coasts (i.e., mostly terrestrial inputs); Rural coasts (i.e., mostly oceanic inputs); and Within close distance to major riverine inputs" (Cheshire and Adler, 2009, p. 23). As such, they recognize that river inputs are an important part of the marine litter equation, mentioning them as one of seven potential sources (others listed are fisheries and aquaculture; ships of all types; storm water runoff; debris blowing from land; beach users/dumping; and oil rigs) (Cheshire and Adler, 2009). Throughout their methodological description, Cheshire and Adler (2009) comment on the importance of understanding how marine litter may be influenced by rivers, and yet do not recommend collecting on riversides.

In their shoreline field guide, Opfer et al. (2012) have similar recommendations of sites with characteristics such as, "Sandy beach or pebble shoreline; Clear, direct, year-round access; No breakwaters or jetties; At least 100 m in length parallel to the water; and No regular cleanup activities" (p. 2). Opfer et al. (2012) methodology includes making a note of potential land sources that might influence a marine shoreline cleanup, including distance to a nearby town or river mouth but as with Cheshire and Adler, their methodologies are written expressly for marine shoreline cleanups. Opfer et al. (2012) provide information for conducting either an accumulation or a standing stock survey; their methods form the basis for the methods we propose here.

This method is a cost-effective way to understand the global plastic waste problem, is applicable by citizen scientists and scientists, and provides local data. In this application of the methodology we encourage breadth not depth. In other words, our goal is to encourage a global application of this methodology to provide empirical evidence of riverine debris. While in these examples we provide only a one-time analysis, the method can be applied repeatedly to understand accumulation over time and seasonal variation, as has always been true for the NOAA field methodology. Other researchers could use this methodology repetitively to understand local variation and accumulation.

One could argue that a one-time collection may not provide comprehensive enough data to inform policy. This is a valid criticism, and yet our current understanding of the way plastic moves through riverine systems frequently does not include any ground-truthed evidence and therefore no information about the composition of debris. As such, these large scale assessments (see Jambeck et al., 2015; Lebreton et al., 2017) provide understanding of the problem from a systems level—a truly important aspect of how we understand the problem— but little evidence about how debris composition may vary within systems. While our proposed methodology cannot answer all questions about the problem of marine litter, it can provide important evidence that informs local policy and behavior as well as contributes to our understanding of the missing plastic question.

PROPOSED METHODOLOGY

Our proposed method is modified from the NOAA Marine Debris Shoreline Survey Field Guide (Opfer et al., 2012). Opfer et al. (2012) present two methods in their guide: that of an accumulation study and of a standing stock study. In an accumulation study, all debris is removed from "the entire length of the shoreline during each site visit" (Opfer et al., 2012, p. 1). This method is used for periodic cleanups, measuring debris deposition of one site over time; it also provides data on types and weight of debris (Opfer et al., 2012). Depending on the size of the beach, this type of survey may require a large number of volunteers. In a standing stock study, participants survey a 100 m long stretch of beach to determine debris density (Opfer et al., 2012). This assessment may require less time, but the debris is left on site during the analysis. When using a standing stock study, the researchers return periodically to the site to measure density, shedding light on how this may change over time.

Our modified method is neither of these methods, but pulls important elements from each: surveying a 100 m long, 5 m deep area along a riverside to quantify density and composition of debris. After selecting a site that ideally allows 100 m of continuous riverside collecting (i.e., avoiding walls, private property, or an impenetrable landscape) researchers measure the site and mark a 100 m length of shoreline with survey flags, starting at the river's edge. Researchers then measure 5 m depth landward from the shoreline, marking this distance with flags along the 100 m length. This produces a total collection area of 500 m^2 as shown in **Figure 1**. Researchers then walk in a systematic pattern, back and forth from the shoreline, to the edge of the 5 m deep area, and then back to the shoreline until the entire area has been covered, as shown in **Figure 1**. Researchers collect everything visible within the given area that is attributable to humans.

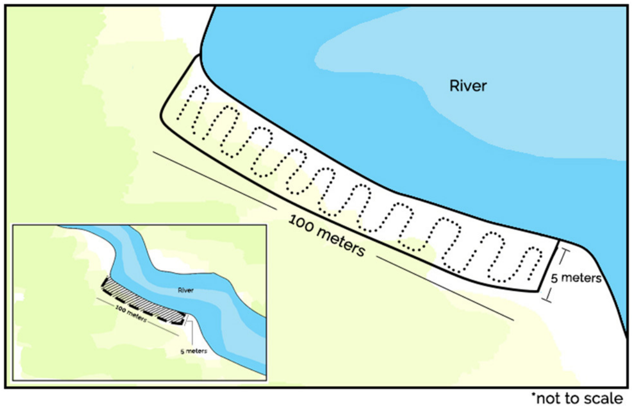


FIGURE 1 | How a collection area should be sited along a river including the recommended walking pattern adapted from Opfer et al. (2012) to a riverside collection site (Illustration by K. Owens and P. Kamil).

We recommend that researchers remove the material from the site, returning to a laboratory or classroom to analyze it systematically by counting, weighing, and cataloging the constituents in accordance with the attached appendices, which include data sheets for both site data and for cataloging debris, derived and adapted from Opfer et al. (2012). While most categories may allow for easy classification of material, in some cases researchers may wish to add more types of debris to allow for maximum depth of data. Examples of sorting categories can be seen in **Figure 2**; an example of the spreadsheet being used to tally data during a collection can be seen in **Figure 3**; "nylon foam sponge" and "child swim toy" were not categories included in the original list, but were added for this particular collection.

While we recommend weighing each subcategory, we recognize that this may not always be practical, particularly when working in remote sites. In our examples below, one researcher was able to return all material to the laboratory for individual weighing (India), while the other was able to count and catalog all pieces debris, but only weigh in broad categories (i.e., plastic, glass, metal) due to conditions (Indonesia). Clearly, sub-category weighing provides more detail but may not always be practical. In the NOAA shoreline method, researchers would be expected to visit a beach at low tide; for river collections the recommendation is to visit in the dry season, as more debris that has made its way along the river may be evident in that period. It should be noted that until researchers have made comparative studies of riverside collections in the wet and dry seasons, we could only presume how these varying conditions might affect results.

BENEFITS OF THIS METHODOLOGY

The methodology we propose is not elaborate and does not require expensive supplies or equipment. Recommended

FIGURE 2 | Examples of some distinct categories including (clockwise from top left) nylon cords and ropes, plastic bottle caps, glass bottles, hard plastic fragments, filmed plastic fragments (Photos by K. Owens).

equipment includes: GPS, 100 M measuring tape, gloves, scales (hanging scale and more precise scale for smaller items), clipboards, paper, writing instruments, collection bags, boots, sunscreen, drinking water, and insect repellant. Often, large-scale cleanups are used to educate the public about littering and debris, to collect data, or to clean rivers. This methodology does not propose to clean an entire river system, but instead to harness the work of a small team to better understand local debris. It can be completed with a small team of researchers in a few hours. It does allow for a consistent and replicable scientifically valid way of collecting material in a range of settings. This method enables:

- Collecting data on the total weight and count of debris found within a 500 m^2 riverside area
- Cataloging said debris to understand what percentage is comprised of plastic, metal, glass, paper, clothing/shoes, and other materials
- Classifying within these broad categories to understand whether the preponderance of material originates from municipal waste, shipping, commercial or recreational fishing, manufacturing, or another source
- Calculating a mean density of debris

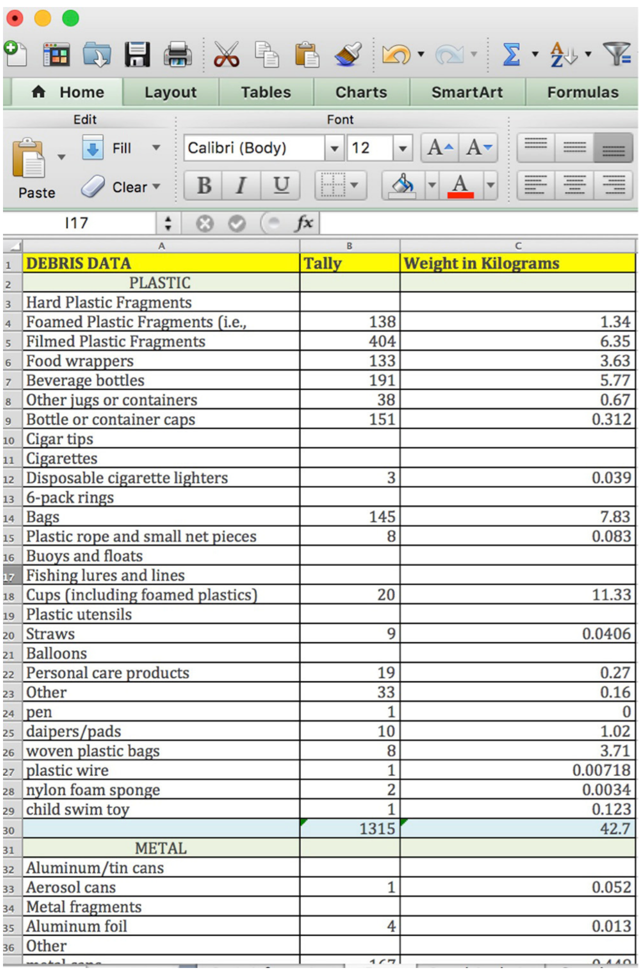
This level of detail can be used to report conditions to local policymakers, therefore linking science and policy in the local context (as is the case for the author working in India) or as a part of a comparative study to analyze human behavior (as is the case for the author working in Indonesia). Sharing methodology with other researchers allows comparative analysis in different countries, systems, and settings. We should reiterate that neither of our studies have the goal of removing all debris from an area, but instead of using sampling to better understand the composition of debris in a given area.

EXAMPLES FROM INDIA AND INDONESIA

The authors honed this methodology in a series of discussions as they planned research projects funded by the National Geographic Society—the results of those studies are a part of other publications (Kamil, under review; Conlon et al., under review). Here we describe how these methods have been applied in settings on the ground in Indonesia and India.

Indonesia: Tukad Badung River, Bali

We conducted data collections at two sites along the Tukad Badung River of Bali as a pilot for a larger study. Data collection took place on May 9, 2019, in the dry season. Sites, shown in **Figure 4**, were selected using river hydrology maps. The pilot



	A	B	C
1	DEBRIS DATA	Tally	Weight in Kilograms
2	PLASTIC		
3	Hard Plastic Fragments		
4	Foamed Plastic Fragments (i.e.,	138	1.34
5	Filmed Plastic Fragments	404	6.35
6	Food wrappers	133	3.63
7	Beverage bottles	191	5.77
8	Other jugs or containers	38	0.67
9	Bottle or container caps	151	0.312
10	Cigar tips		
11	Cigarettes		
12	Disposable cigarette lighters	3	0.039
13	6-pack rings		
14	Bags	145	7.83
15	Plastic rope and small net pieces	8	0.083
16	Buoys and floats		
17	Fishing lures and lines		
18	Cups (including foamed plastics)	20	11.33
19	Plastic utensils		
20	Straws	9	0.0406
21	Balloons		
22	Personal care products	19	0.27
23	Other	33	0.16
24	pen	1	0
25	daipers/pads	10	1.02
26	woven plastic bags	8	3.71
27	plastic wire	1	0.00718
28	nylon foam sponge	2	0.0034
29	child swim toy	1	0.123
30		1315	42.7
31	METAL		
32	Aluminum/tin cans		
33	Aerosol cans	1	0.052
34	Metal fragments		
35	Aluminum foil	4	0.013
36	Other		

FIGURE 3 | Example data shown as entered into the spreadsheet after collection.

study includes two site types (transition and floodplain) as this met the larger constraints of our study. While in one site we found 100 continuous meters for our collection, due to limited access, our second site was instead 50 m in length. At each site, we conducted the debris collection in one continuous shoreline. We picked the shoreline based on its accessibility and safety for the team members and volunteers. The rest of our procedure follows that described in the methodology section.

Tukad Badung River is a short river of 22 km in length, flowing across the capital city of Bali, Denpasar, the most densely populated city on the island. The first site was in the floodplain zone, −8.6733 N, 115.2048 E. In this site, we successfully created a block of 500 m^2. We collected a total weight of 14.84 kg, or 0.029 kg/m^2. We collected 598 pieces of debris here, averaging 1.19 pieces per m^2 with 92.8% of the found pieces being plastic. Our methodology allows assessing the composition to better understand the source of debris. The source of the material appears to be litter and human household waste (i.e., not from industry, manufacturing, commercial fishing, recreational fishing, aquaculture, or shipping). This site only has one solid riverbank on its shoreline, covered by soil and grass, surrounded by permanent settlements. At this particular site, we found three large sacks (>30 cm in dimension), used for rice, cement, and shallots.

The second site was in transition zone, −8.306 N, 115.2065 E, where we were only able to create a block of 250 m^2 due to soil contour and vegetation coverage. Big rocks and solid soil, a very limited amount of grass, and a notable amount of fig trees cover riverbanks in this area. While under the recommended ideal coverage of 500 m^2, because in this method we measure area, the density of debris can always be calculated. At this site we collected 147 pieces debris weighing 3.58 kg, averaging 0.58 pieces per m^2 or 0.014 kg/m^2. Again, most of the pieces found are plastic (88.4%). The source of the material appears to be litter and human household waste (i.e., not from industry, manufacturing, commercial fishing, recreational fishing, aquaculture, or shipping). At this site we found two relatively larger pieces of debris comprised of two rice sacks and a 90 × 150 cm carpet. Example summary debris data from Tukad Ayung is shown in **Table 1**. We originally planned to measure within the source zone, however, there is no riverbank available in the area (−8.5751 N, 115.1940 E), as a wall designated for irrigation blocks the stream. These pilot data are a part of a larger study available (Kamil, P., manuscript under review).

India: Karamana River, Kerala

The collection took place on June 12, 2019 from 8:00 a.m. to 10:45 a.m. local time and included a team of researchers from the national workshop *Experiential learning with Indian educators on marine debris and its management* sponsored by the National Geographic Society and the Fulbright Nehru Scholar program. Participants included 17 individuals: workshop attendees and trained students and faculty from the University of Kerala, Karyavattom campus, Department of Environmental Science. The collection site, shown in **Figure 5**, was on the Karamana River, upstream of the Parasurama Temple Thiruvallam just off the Kazhakootam-Kovalam Bypass Road at location 8.4425 N, 76.9544 E. The cleanup event took place at the beginning of the typical monsoon season, however monsoon rains increasingly begin later in this region. On this day the river was not flooded; little rain had yet fallen. Example summary debris data from the Karamana River is shown in **Table 1**. We collected a total of 1,630 pieces weighing 71.93 kg. In this case, the most frequently found type of debris by category was plastic (80.7% of the found pieces) and the source of the material appears to be litter and human household waste (i.e., not from industry, manufacturing, commercial fishing, recreational fishing, aquaculture, or shipping). The mean density of debris at this site was 3.26 pieces/m^2 or 0.14 kg/m^2. The full results of this study are available in (Conlon et al., under review).

These data could help scientists and policymakers better estimate debris in freshwater systems worldwide. For example, the Karamana River is 42 miles long (67.59 km) when considering both shores the river has a total shoreline length of 135.18 km. In our study we found just over 1,600 pieces along a 100 m long stretch of river. If you were to extrapolate from that, assuming that this is an average level of accumulation (which we

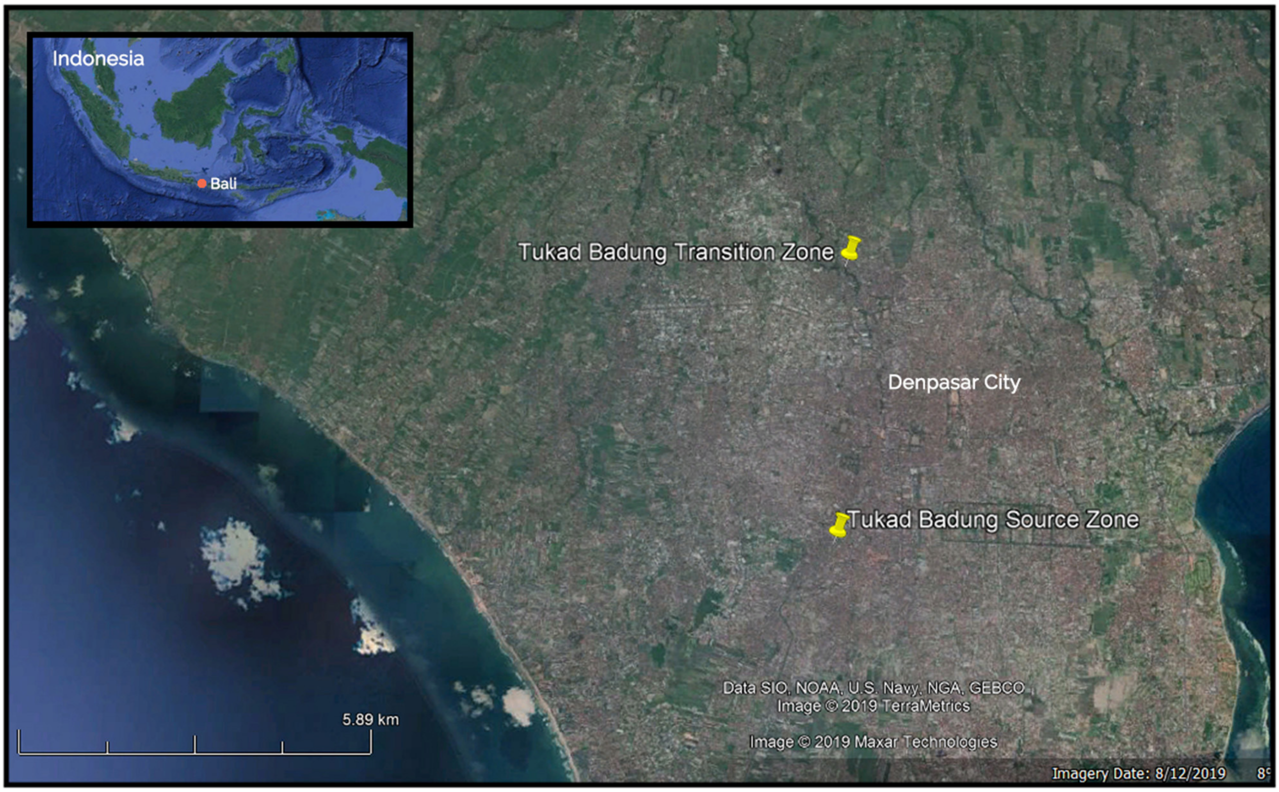


FIGURE 4 | Map of Indonesian sites (Map by P. Kamil).

TABLE 1 | Compiled results from example studies.

Location	**Tukad Badung floodplain zone Indonesia**	**Tukad Badung transition zone Indonesia**	**Karamana River India**
Date	May 9 2019	May 9 2019	June 12 2019
Length of shoreline	100	50	100
Depth of shoreline	5	5	5
Collection time	2 h	50 min	2 h, 45 min
Participants	3	3	17
Debris weight density (kg/m^2)	0.029 kg/m^2	0.014 kg/m^2	0.14 kg/m^2
Debris pieces density (total pieces/m^2)	1.19	0.58	3.26

acknowledge is a rather broad assumption) you could estimate that the Karamana River has 2.16 million pieces of debris along its shorelines. In the case of the Tukad Badung River, we measured 745 pieces of debris along 150 m. At 22 km long, considering both its shores yields a total of 44 km of river shoreline. Extrapolating from these data, we could estimate that the Tukad Badung has 218,285 pieces of debris along its shorelines. While we would not propose that an assessment of 100–150 m is sufficient to determine the amount of waste along a river of 22–67 km, we do find that an increased effort to ground-truth waste along waterways in a consistent, replicable way can lead to better modeling and estimates of the way litter moves through and remains in freshwater systems.

RECOMMENDATIONS FOR COLLECTING ON RIVERSIDES

Collecting riverside can be different from seaside. Often, when working on the beach we must be wary of glass, medical or other unsanitary waste, but not wildlife (snakes, crocodiles, alligators, mammalian predators), thorns, or stinging insects, all of which may be more of a concern riverside. In this way, while boots and insect repellant may not be necessary for beachside collecting, they are recommended for riverside cleanups. As safety comes first, we suggest researchers pick safe shorelines considering slope or height. In addition it is important to find safe access to the riverbank considering brush and other natural or unnatural blockages along the shoreline. Riversides can be extraordinarily inaccessible. While our recommendation is that researchers select an area of 100 m in length for data collection, such a length may be impossible given conditions riverside, as was the case for the Tukad Badung transition zone in Indonesia (shown in **Figure 6**). In an effort to collect data despite lack of accessibility, researchers opted for a 50 m long collection area. While this was not ideal, it allowed for data collection in the transition zone, an important element of that particular study. In comparison see the

FIGURE 5 | Map of Indian site (Map by P. Kamil).

FIGURE 6 | An example of an unsafe riverbank in the Tukad Badung River transition zone area. It is full of detritus, raising the possibility of exposure to reptiles, particularly snakes. Detritus covers the land structure underneath, increasing the risk of accident if the underlying ground is not solid enough for debris collection. There is also no human access to the area (Photo by P. Kamil).

relatively accessible site along the Karamana river in India, shown in **Figure 7**.

If researchers collect data on specific locations (e.g., source or transition zones), we recommend a hydrology analysis first using available GIS tools, then a site visit to the area before bringing volunteers to the sites. A field site that looks accessible from satellite imagery may be inaccessible in actual condition. This way, researchers will save time and effort enabling efficient data collection. Whether river or ocean, this method does not include wading into the water to remove the debris—but instead measuring what accumulates on the banks. It should be noted that it provides limited information about the debris flowing through a river system, and does not provide information about debris accumulating on the river bottom, in underwater vegetation, or in sediments. Other methods of analysis are needed to understand how debris accumulates in rivers in these scenarios.

CONCLUSIONS

Our proposed methodology is a modification and new application of the Opfer et al. (2012) methods focusing on one-time analysis of a river shoreline. Current methods vary widely– with researchers in some cases selecting random transects along riversides or picking contiguous areas in different river zones depending on proximity to pollution. Each comes with costs and benefits. We do not presume that this method can answer every question about river debris, but currently, people are not collecting along riversides in a concerted way to understand conditions on the ground. We propose that they

FIGURE 7 | This area became part of the site for collection along the Karamana River. While brush and debris exists along the water's edge, the ground is solid and the approach is flat (Photo by K. Owens).

do, and by doing so, add to the knowledge on the fate of debris and the missing plastics question. This method allows for the production of data that can help us understand how debris accumulates along global rivers. When rivers flood, a great deal of this debris makes its way from riversides into oceanic systems or may be pulled from riverside dumping areas into freshwater systems. Better data about river shorelines can help us holistically understand the issue of marine debris– which should more broadly be considered the problem of global plastic pollution. The benefits of this method are many. It allows for consistent, replicable data gathering at sites around the world. Because of the size limitations, the work can be managed in a relatively short amount of time with a small group of researchers or volunteers. The goal of this method in application is not to clean the world's riversides. As is the case with beach cleanups, cleaning river shorelines globally is not a long-term solution to the problem of debris. The value of this method in application is allowing researchers to quickly and cost-effectively understand the on-site debris density and provide a snapshot of accumulation data. It allows researchers around the world to begin to ground-truth the myriad estimations of debris traveling through but also accumulating in river systems, important habitats in their own right. With better data and a deeper understanding of these systems, we can more effectively address the litter that chokes the world's riverways and seas.

DATA AVAILABILITY STATEMENT

This work details methodology, using studies that are being published in other formats to describe the methodology in application—we therefore do not share a research result and the work is not explicitly based on a dataset. DOIs of the referenced data sets are available upon request.

AUTHOR CONTRIBUTIONS

KO and PK contributed to the conception and design of this study and co-wrote the first draft of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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The Metacoupling Framework Informs Stream Salmonid Management and Governance

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Stream salmonid fisheries are ecologically and socioeconomically important at local to global scales throughout the world. Although these fisheries are interacting systems of biota, habitats, and humans, systematic social-ecological integration across space and time is scarce. However, theoretical and methodological advancements in the study of coupled human and natural systems (CHANS) offer new insights for stream salmonid research, management, and policymaking. The metacoupling framework is a novel tool for studying and managing social-ecological linkages that occur within stream salmonid fisheries as well as between adjacent and distant fisheries (i.e., metacouplings). For instance, coldwater streams containing brook charr (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) in Michigan, United States, encompass metacoupled movements of water, information, fish, people, and money throughout CHANS that provide drinking water, recreational fisheries, and employment. However, groundwater withdrawal is altering stream hydrology and causing public controversy over how hydrological changes affect salmonid populations and thermal habitats. Using this complex social-ecological scenario as a case study, we describe the utility of the metacoupling framework for fisheries systems analysis and demonstrate how this approach promotes metacoupled governance– management of relationships among metacoupled systems rather than specific physical places alone– to better sustain stream salmonid fisheries locally, regionally, and globally. Overall, stream salmonid science and management can be enhanced by using the metacoupling framework to synthesize social and ecological information, characterize cross-scalar tradeoffs and feedbacks, understand stakeholder diversity, and ultimately develop metacoupling-informed policies that promote socially and ecologically desirable outcomes.

Keywords: brook charr, brown trout, metacoupling framework, coupled human and natural systems, salmonid management

INTRODUCTION

Fisheries are ecologically, socioeconomically, culturally, and nutritionally important resources at local to global scales. For instance, fish are predators of– and prey for– numerous aquatic organisms, transfer energy among trophic levels, recycle nutrients within and between aquatic and terrestrial ecosystems, and serve as indicators of environmental impairment (Fausch et al., 1990; McIntyre et al., 2007; Frisch et al., 2014). In addition, fish support commercial, recreational, and subsistence fisheries and associated economies while playing important roles in religion, art, folklore, mythology, and other aspects of human culture across the world (Moyle and Moyle, 1991; Taylor et al., 2007; Liebich et al., 2018). Moreover, fish are vital for food security in many of the world's low-income food-deficit countries. Fish is the primary protein source for one in five people throughout the world (>1 billion), with 3.2 billion people depending on fish for at least 20% of their animal protein intake (Food and Agriculture Organization [FAO], 2018).

As such, it is clear that fish contribute much to the integrity and sustainability of aquatic ecosystems and human systems alike. Fisheries are generally defined by three major components (i.e., biota, habitats, humans) and their associated structures, functions, and interactions (Hubert and Quist, 2010). Each of these components has individually received ample research attention extending back to the dawn of fisheries science (Baranoff, 1918; Ricker, 1954; Vannote et al., 1980; Dietz et al., 2003; Hilborn et al., 2004). However, research on the linkages and feedbacks among fisheries biota, habitats, and humans– indeed, the very identity of fisheries as coupled human and natural systems (CHANS) – is comparatively scarce, representing a hindrance to socially, ecologically robust fisheries management that achieves objectives set for fish and human stakeholders alike (Carlson et al., 2017b, 2018). To date, fisheries CHANS research has yielded insights for understanding social-ecological couplings at relatively large scales (e.g., national, global; Wilson, 2006; Pinsky and Fogarty, 2012; Österblom and Folke, 2015; Tapia-Lewin et al., 2017). Studies such as these lay a foundation for more comprehensive fisheries CHANS research that explicitly evaluates social-ecological linkages at local to global scales. Such multi-scalar fisheries research has been uncommon to date and resulted in relatively limited understanding of– and few management programs that leverage– the magnitude, causes, and effects of fisheries interactions locally, regionally, and globally. Recently, researchers have classified these local to global interactions as metacouplings (i.e., socioeconomic and environmental interactions within individual CHANS, as well as between adjacent and distant CHANS) and developed a metacoupling framework for evaluating and ultimately managing social-ecological systems locally, regionally, and globally (Liu, 2017, 2018; Liu et al., 2018).

Since publication of the first metacoupling study approximately two years ago by Liu (2017), the metacoupling framework has not been widely applied to fisheries. This is unfortunate as the metacoupling framework provides aquatic resource professionals with a propitious tool for investigating when, where, why, and how fisheries function as CHANS and understanding the causes, effects, and management/policy relevance of fisheries' social-ecological interactions, locally and globally. For instance, invasive species, climate change, watershed fragmentation, and habitat degradation (via land-use change, groundwater withdrawal, etc.) are anthropogenic stressors that increasingly affect fish production, recruitment, and survival locally and throughout the world, often in negative ways (Roni et al., 2008; Myers et al., 2017; Carlson et al., 2019a). As such, the metacoupling framework provides a systematic, adaptive approach for studying these coupled human-natural stressors and associated fisheries effects (i.e., metacouplings) in terms of their flows (e.g., fish, money, information), human and organizational actors, drivers, and consequences. In turn, diverse social-ecological information provided by the metacoupling framework (e.g., cross-scalar tradeoffs, feedbacks, surprises; Liu, 2017) is a leverage point for sustainable fisheries management and governance that improves social and ecological outcomes at local to global scales (Carlson et al., 2017b, 2018).

Salmonid fisheries are ideal systems for metacoupling research due to their global distribution coupled with their regional and local importance (e.g., ecological, socioeconomic, recreational, commercial, cultural, nutritional) throughout the world (Lynch et al., 2002; Quinn, 2005; Prosek, 2013). Stream salmonid fisheries in the Midwestern United States provide billions of dollars in annual economic benefits to local communities and have a long, rich history of supporting human recreation and nutrition (Weithman and Haas, 1982; Gartner et al., 2002; Schroeder, 2013; Anderson, 2016; Carlson et al., 2016; Cooke et al., 2017; Carlson and Zorn, 2018). In the State of Michigan, United States, stream-dwelling brook charr (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) have enormous socioeconomic and recreational significance. For instance, brown trout are the primary target of anglers in many Michigan rivers, making the species a fisheries management priority for the Michigan Department of Natural Resources (DNR) Fisheries Division, which considers brown trout an "important naturalized species" rather than a harmful non-native species (Michigan Department of Natural Resources [MDNR], 2015). Brook charr and brown trout support multimillion-dollar sport fisheries in Michigan and represent a crucial component of statewide fisheries that generate US$2.5 billion in retail sales and $4.2 billion in overall economic effect (U.S. Fish and Wildlife Service [UWFWS], 2013; Zorn, 2018). These species help support 38,000 angling-related jobs in Michigan and enrich the angling experiences of 586,000 riverine anglers spread across 8,159,000 angling-days every year (Southwick Associates, 2012; Zorn, 2018). Moreover, naturally-reproduced brook charr and brown trout in Michigan streams (n = 2.7 million annually, 3.5 times the number stocked) provide an economic benefit of $5.6 million every year (Wills et al., 2006; Zorn et al., 2018).

Given their unquestionable socioeconomic and societal value and important ecological roles as predators and prey, brook charr and brown trout are ideal species for integrative social-ecological research using the metacoupling framework. However, salmonid research to date has generally not accounted for the social-ecological interactions involved in brook charr and brown trout fisheries at both intra- and inter-stream scales. As such, the purpose of this study was to evaluate how Michigan stream salmonid fisheries are socioeconomically and ecologically connected within and between adjacent and distant streams using the metacoupling framework, with the goal of developing an approach for leveraging multi-scalar social-ecological information to advance the sustainable management of salmonid fisheries in Michigan and beyond. Our analysis focused on Chippewa Creek and Twin Creek,

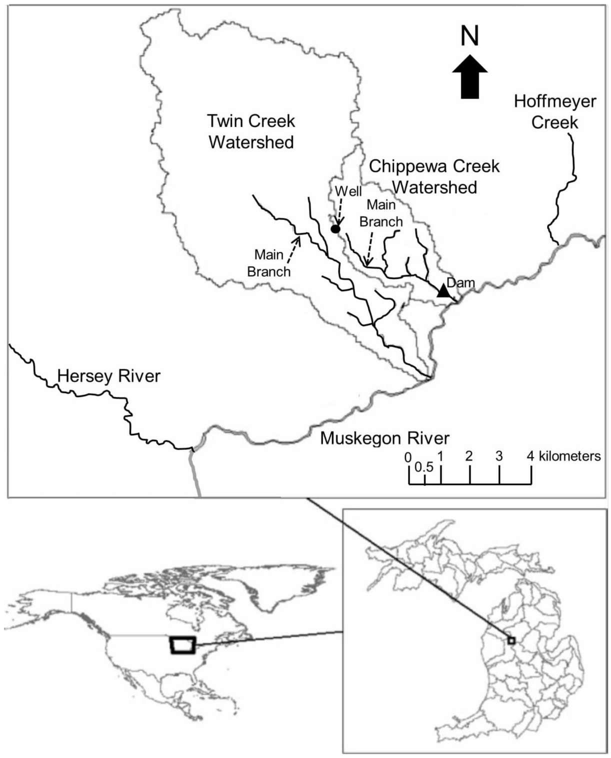

FIGURE 1 | Map of the study area, including the Twin and Chippewa creek watersheds, Hoffmeyer Creek, and the Hersey River in Osceola County, MI, United States. The black circle denotes a large-capacity (0.0040 m^3/s, 100,000 gallons per day) groundwater well owned by Nestlé Water North America. The black triangle shows a dam in the lower portion of Chippewa Creek that prevents upstream fish movement.

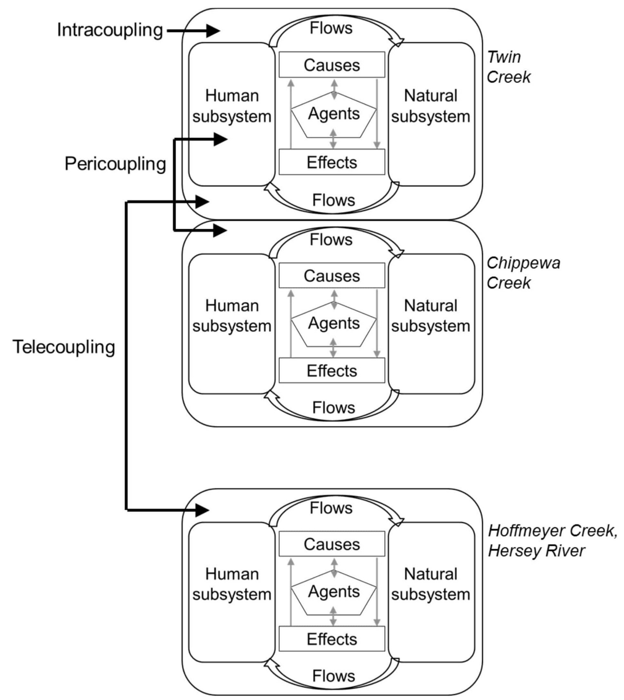

FIGURE 2 | Diagram illustrating metacoupling:social-ecological interactions within a particular or local fishery (intracoupling) as well as between adjacent fisheries (pericoupling) and between distant, non-adjacent fisheries (telecoupling). Different coupling types are illustrated using rivers from the study area (see **Figure 1**). White and black arrows depict flows, defined as movements of water, information, fish, people, and money within and between fisheries. See **Table 1** for details on metacoupling systems, flows, agents, causes, and effects.

two coldwater, groundwater-dominated streams containing brook charr and brown trout whose watersheds share a common boundary in Osceola County, MI, United States (**Figure 1**). These rivers are impacted by land-use change and groundwater withdrawal resulting from human development, timber production, and a large-capacity (0.016 m^3/s, 360,000 gallons per day) groundwater well owned by Nestlé Water North America (hereafter Nestlé) that lies on the streams' shared watershed boundary (**Figure 1**; Waco and Taylor, 2010). Our objectives were to characterize the social-ecological structure (e.g., systems, causes, effects) of stream salmonid metacouplings–particularly those related to groundwater withdrawal, land-use change, and stream temperature–in Twin and Chippewa creeks and demonstrate how the metacoupling framework provides the information depth and breadth necessary for ecologically and socioeconomically informed groundwater governance and salmonid management programs. Given the ubiquity of CHANS in aquatic and terrestrial environments throughout the world, we hope to lay a foundation for future metacoupling research within and beyond stream salmonid fisheries so that other areas of conservation science and practice can adopt, and benefit from, a social-ecological and local-regional-global (i.e., metacoupled) perspective.

MATERIALS AND METHODS

Metacoupling Framework

The metacoupling framework builds on concepts such as globalization (socioeconomic interactions between human systems over distances), teleconnection (environmental interactions between natural systems over distances), and telecoupling (socioeconomic and environmental interactions between CHANS over distances; Dreher et al., 2008; Liu et al., 2013). The metacoupling framework makes conceptual and empirical advancements over the above paradigms because it simultaneously considers socioeconomic and environmental interactions (unlike globalization and teleconnection) at local, regional, and global scales (unlike telecoupling; Liu, 2017). In other words, the metacoupling framework is designed to assess human-nature interactions at three distinct spatial levels: local (within individual CHANS such as Twin Creek), regional (between adjacent CHANS such as Twin and Chippewa creeks), and supraregional (between non-adjacent CHANS such as Twin and Hoffmeyer creeks). Together, these local interactions (intracouplings), regional interactions (pericouplings), and supraregional interactions (telecouplings) constitute metacouplings (**Figure 2**).

TABLE 1 | Summary of systems, flows, agents, causes, and effects associated with metacouplings involving Michigan stream salmonid fisheries. Intracoupling, pericoupling, and telecoupling processes are denoted by I, P, and T, respectively.

Components of the metacoupling framework		Examples
Systems (units in which humans and nature interact)	Sending (origins/sources/donors)	Twin Creek
	Receiving (destinations/recipients)	Chippewa Creek
	Spillover (systems that affect/are affected by sending-receiving system interactions)	Systems that affect/are affected by social-ecological interactions within or between Twin and Chippewa creeks (e.g., Hoffmeyer Creek, Hersey River, anglers, and landowners affected by ineffective groundwater governance) (Hughes, 2006; Waco and Taylor, 2010; Department of Environment Great Lakes and Energy [DEGLE], 2017; Carlson and Zorn, 2018)
Flows (movements of material, information, people, etc., within/between systems)		Movement of water (e.g., surface water, groundwater), information (e.g., fish population indices, groundwater policies), fish (e.g., brook charr, brown trout), people (e.g., groundwater extractors, anglers, tourists, land owners), and money within (I) and between (P, T) systems (Hughes, 2006; Waco and Taylor, 2010; Li et al., 2015; Papadopulos & Associates, Inc, 2016; Department of Environment Great Lakes and Energy [DEGLE], 2017; Public Sector Consultants [PSC], 2017; Carlson and Zorn, 2018; Michigan Department of Natural Resources [MDNR], 2019)
Agents (autonomous decision-making entities that directly or indirectly facilitate or hinder metacouplings)		Groundwater extractors, anglers, landowners, tourists, government agencies, non-governmental organizations, businesses (e.g., bait and tackle shops, restaurants) within systems (I) or between systems (P, T) (Hughes, 2006; Waco and Taylor, 2010; Carlson and Zorn, 2018; Michigan Department of Natural Resources [MDNR], 2019)
Causes (factors that influence emergence or dynamics of metacouplings)	Environmental	Abundance of groundwater available for extraction within streams (I), surface and subsurface movement of water within (I) and between (P, T) streams, aquatic habitats suitable for fish survival and movement within (I) and between (P, T) streams (O'Neal, 1997; Hughes, 2006; Waco and Taylor, 2010; Li et al., 2015; Papadopulos & Associates, Inc, 2016; Michigan Department of Natural Resources [MDNR], 2019)
	Socioeconomic	Water bottling and sales, angling, tourism (I, P, T) (Hughes, 2006; Public Sector Consultants [PSC], 2017; Carlson and Zorn, 2018; Michigan Department of Natural Resources [MDNR], 2019)
	Political	Desire to use groundwater for human needs such as drinking water (T), desire to conserve groundwater to protect aquatic ecosystems (I, P, T), developments in groundwater policy and management (e.g., extraction regulations via best management practices, certification requirements, etc., as assessed by the Groundwater Conservation Advisory Council; I, P, T) (Hughes, 2006; Waco and Taylor, 2010; Department of Environment Great Lakes and Energy [DEGLE], 2017)
	Cultural/nutritional	Angling, tourism, food provisioning (fish), drinking water (I, P, T) (Hughes, 2006; Waco and Taylor, 2010; Cooke et al., 2017; Carlson and Zorn, 2018; Michigan Department of Natural Resources [MDNR], 2019)
Effects (impacts or consequences of metacouplings)	Environmental	Decreased surface and subsurface water levels and flows within and between streams due to groundwater withdrawal but few documented effects on salmonid populations (I, P, T) (Waco and Taylor, 2010; Li et al., 2015; Papadopulos & Associates, Inc, 2016; Michigan Department of Natural Resources [MDNR], 2019)
	Socioeconomic	Economic impacts (e.g., increased jobs and economic activity; I, P, T), social impacts [e.g., disapproval of groundwater withdrawal by many anglers and landowners (I, P, T), preference for intracoupling- and pericoupling-scale governance (I, P)], policy impacts (e.g., groundwater governance approaches that overlook the concerns of local communities; T) (Hughes, 2006; Waco and Taylor, 2010; Department of Environment Great Lakes and Energy [DEGLE], 2017; Public Sector Consultants [PSC], 2017; Carlson and Zorn, 2018)

Metacouplings– and the intracouplings, pericouplings, and telecouplings they encompass– have five common elements: systems, flows, agents, causes, and effects (Liu et al., 2013; Liu, 2017; **Figure 2**). Systems (i.e., CHANS) are defined according to their position relative to flows (movements of organisms, money, information, people, etc.). Sending systems are those in which flows originate, receiving systems are those to which flows move, and spillover systems are those that affect– or are affected by– interactions between sending and receiving systems (Liu et al., 2013; Liu, 2017). For example, when two stream salmonid fisheries (A and B) are connected by flows of fish, money, information, and people, and agricultural expansion leads to deforestation within stream A, effects of land-use change (e.g., reduced fish growth, survival, habitat quality/quantity) may cascade to stream B or "spill over" to affect streams C, D, etc. (spillover systems) that are not directly involved in sending-receiving system interactions. Agents are the individuals, organizations, governments, and other entities (including fishes, climate, etc.) involved in human-nature couplings. All couplings are driven by causes (e.g., ecological, economic, social, political) and produce effects (social-ecological outcomes and consequences; **Figure 2**).

By systematically assessing these five metacoupling elements, researchers can address important questions about the structure and function of social-ecological interactions in fisheries. For instance, how are individual stream salmonid fisheries connected to adjacent and distant fisheries via social-ecological linkages (e.g., fish movement, human movement, information transfer, monetary exchange)? What are the implications of metacouplings for stream salmonid management and governance? Regarding groundwater withdrawal in particular, how can metacoupling analysis holistically link potential changes in stream hydrology and salmonid thermal habitats to human values and attitudes about groundwater extraction and thereby inform water and fisheries management decisions?

Metacoupling research is broadly categorized as empirical (i.e., analysis of author-collected data; Liu et al., 2015; Sun et al., 2017) or synthetic, involving integration of prior research on metacoupling systems, flows, agents, causes, and effects that were studied without formal application of the metacoupling framework (Hulina et al., 2017; Carlson et al., 2018). The present study is both empirical and synthetic, as we collected much of the social and ecological data on which this manuscript is based (Hughes, 2006; Waco and Taylor, 2010; Carlson and Zorn, 2018) and, over time, integrated these data using the metacoupling framework. Such is the nature of metacoupling research, wherein multiple studies build on each other and eventually facilitate social-ecological synthesis (Liu, 2017). We recognize that Michigan stream salmonid fisheries encompass a metacoupled system involving social-ecological phenomena (e.g., watershed fragmentation, invasive species, stocking; Cooper et al., 2016; Zorn, 2018; Smith et al., 2019) beyond those studied herein. However, we focused on groundwater withdrawal, land-use change, and stream temperature due to the unique social-ecological importance of these issues in Twin and Chippewa creeks. Although these topics have been researched extensively in our study area and associated data are abundant (Hughes, 2006; Waco and Taylor, 2010; Department of Environment Great Lakes and Energy [DEGLE], 2017; Public Sector Consultants [PSC], 2017), previous research has been monothematic– it has emphasized either social or ecological phenomena rather than social-ecological interactions. As such, there is a need to investigate social-ecological dynamics of groundwater withdrawal, land-use change, and stream temperature using the metacoupling framework. These reasons for studying certain metacoupled issues before others (i.e., importance for the study area, available data) are common to all metacoupling analyses, which are inherently iterative due to the infeasibility of investigating all metacoupling components simultaneously given limitations in time, money, personnel, etc. (Liu, 2017). Instead, metacoupling framework operationalization– a multi-phase process of goal-setting, system selection, literature review, coupling delineation, and research communication (Liu, 2017) – demands subdividing metacoupling investigations into smaller interconnected projects and eventually synthesizing them, as is done herein for Hughes (2006), Waco and Taylor (2010), Carlson and Zorn (2018), and related studies. The present study is the first investigation of fisheries metacouplings related to groundwater withdrawal, land-use change, and stream temperature in our study area, laying a foundation for future metacoupling analyses of other social-ecological phenomena.

Study Systems and Data

Brook charr are native to Michigan's Upper Peninsula and coastal streams in the northernmost portion of the Lower Peninsula (Zorn et al., 2018). Brook charr were first introduced to streams in southwestern Michigan in 1879, whereas brown trout were first introduced to Michigan in 1884. Both species inhabit Twin and Chippewa creeks, which are relatively small streams flowing 10 and 5 km, respectively, before reaching their confluence with the Muskegon River (**Figure 1**). Despite their size, Twin and Chippewa creeks are classified as Designated Trout Streams by the Michigan DNR in recognition of their cold, groundwater-dominated thermal conditions and forested riparian zones and watersheds that create high-quality physicochemical habitats for salmonids and aquatic macroinvertebrates (Waco and Taylor, 2010; Wesener, 2010; Michigan Department of Natural Resources [MDNR], 2019). Both streams have simple fish communities primarily composed of brook charr, brown trout, mottled sculpin *Cottus bairdii*, creek chub *Semotilus atromaculatus*, and central mudminnow *Umbra limi* (Michigan Department of Natural Resources [MDNR], 2019). These fish communities are novel (i.e., historically created by salmonid stocking) yet stable and self-sustaining, as neither Twin nor Chippewa Creek has been stocked with brown trout or brook charr since the 1930s, 1940s, and 1950s (Michigan Department of Natural Resources [MDNR], 2019). In this study, the ecological impacts of groundwater withdrawal and land-use change are considered relative to these novel fish communities. However, it is recognized that brown trout (and, in some cases, brook charr) introductions can have profound effects on aquatic ecosystems, including population fragmentation and local extinction of native fishes and aquatic invertebrates, interspecific competition for food and resting spaces, and food web restructuring (Fausch and White, 1981; Townsend, 1996; Spens et al., 2007; Budy et al., 2013). Although ecological concerns about salmonid introductions receive comparatively little attention in Michigan, where brown trout are managed as an "important naturalized species" and brook charr are native throughout most of their range in the state (Michigan Department of Natural Resources [MDNR], 2019), future research on stream salmonid metacouplings in other parts of the world should consider undesirable ecological effects of these species.

Overall, we focused on Twin and Chippewa creeks because they are high-quality salmonid streams, groundwater is being withdrawn by an industrial-scale water bottling facility in their watersheds, and these systems are vulnerable to land-use change resulting from human development and timber production (Waco and Taylor, 2010). In addition, groundwater withdrawal has been studied in Twin and Chippewa creeks for two decades (Malcolm Pirnie Inc. [MPI], 2000; Li et al., 2015; Advanced Ecological Management [AEM], 2016; Papadopulos & Associates, Inc, 2016; U. S. Geological Survey. [USGS], 2020a,b), associated data are available and warrant analysis, and this issue has great metacoupling relevance amid ongoing public controversy regarding the social-ecological effects of groundwater extraction on salmonid populations and human communities (Hughes, 2006; Waco and Taylor, 2010; Department of Environment Great Lakes and Energy [DEGLE], 2017). These complex social-ecological conditions are best addressed using a framework such as metacoupling that synthesizes social and ecological information across spatial scales (Liu, 2017).

We projected effects of various potential groundwater withdrawal regimes on baseflow and stream temperatures in Twin and Chippewa creeks using Interactive Groundwater (IGW), a computer-based hydrology tool for quantifying and simulating groundwater flow based on geology, elevation, topography, and surface water features within streams and their watersheds (Li and Liu, 2006). IGW models were first calibrated to assess how various levels of groundwater withdrawal– 0.0044 m^3/s [70 gallons per minute (gpm)], 0.0095 m^3/s (150 gpm), 0.0252 m^3/s (400 gpm), 0.0442 m^3/s (700 gpm), 0.0631 m^3/s (1,000 gpm), and 0.1262 m^3/s (2,000 gpm/) – would affect stream baseflow in Twin and Chippewa creeks (Waco and Taylor, 2010). At present, the continuous rate of groundwater withdrawal in these streams is 0.016 m^3/s (250 gpm); an increase to 0.025 m^3/s (400 gpm) was approved by the Michigan Department of Environment, Great Lakes, and Energy (DEGLE) in April 2018 and is in the process of being implemented. Groundwater extraction models were then combined with an assessment of how four hypothetical land-use changes (i.e., forest to pasture, grassland to urban, agriculture to grassland, forest to shrub land) would affect groundwater recharge rates (Waco and Taylor, 2010). Using outputs from the above models, a U.S. Geological Survey (USGS) stream temperature model (SSTEMP; Bartholow, 2002) was used to predict how summer stream temperature (July, August) and discharge would change as a result of changes in baseflow caused by groundwater withdrawal and land-use change. Full methodological details are available in Waco and Taylor (2010). Results from Waco and Taylor (2010) were integrated with findings from other hydrological research in Twin and Chippewa creeks (Malcolm Pirnie Inc. [MPI], 2000; Li et al., 2015; Advanced Ecological Management [AEM], 2016; Papadopulos & Associates, Inc, 2016) to understand the effects of groundwater withdrawal on stream temperature, discharge, water levels, and salmonid thermal habitats. This included an assessment of ongoing daily (15min interval) measurements of discharge in Twin and Chippewa creeks (U. S. Geological Survey. [USGS], 2020a,b) that were initiated by the USGS in late November/early December 2018 to provide an independent third-party review of groundwater withdrawal's hydrological effects. Expanding hydrological and ecological results from Waco and Taylor (2010) to a full-fledged metacoupling investigation examining social-ecological couplings required information on economic contributions and human perceptions of groundwater withdrawal and land-use change within and beyond Twin and Chippewa creeks. With its rich groundwater and surface water resources, the State of Michigan is home to numerous water- and fisheries-related governmental agencies (e.g., DNR; DEGLE) and non-governmental organizations (NGOs; e.g., Muskegon River Watershed Council, Michigan Citizens for Water Conservation, Michigan Trout Unlimited) that advocate for aquatic resource conservation. Combined with the abundance and social-ecological importance of stream salmonid fisheries in Michigan (Carlson and Zorn, 2018; Zorn, 2018; Zorn et al., 2018), the diversity of groundwater stakeholders operating at local, regional, and supraregional levels– scales corresponding with those of the metacoupling framework (i.e., intracouplings, pericouplings, telecouplings) – renders Michigan an ideal study area for aquatic metacoupling research. Groundwater withdrawal increased in Michigan in the mid-2000s due to expansion of water bottling facilities, prompting the need for salmonid thermal habitat research (e.g., Waco and Taylor, 2010) and creation of a Groundwater Conservation Advisory Council (hereafter Groundwater Council). Composed of representatives from diverse sectors (e.g., agriculture, utilities, business/manufacturing, local government, NGO, general public), the Groundwater Council was tasked with studying the sustainability of Michigan's groundwater use and determining how the state could best regulate groundwater extraction via best management practices, certification requirements, and related approaches.

Recognizing that Michigan's groundwater withdrawal issue involves metacoupling dynamics (e.g., extraction's effects on local/regional/state economies, human opinions and attitudes, stream salmonids and thermal habitats), we conducted semi-structured interviews of 30 Groundwater Council members and their colleagues in 2005 to measure human values, attitudes, and policy preferences regarding groundwater use and sustainability (Hughes, 2006). The interview methodology and questions were scrutinized and approved by the Michigan State University Institutional Review Board (IRB #05-292) to ensure that the research approach was appropriate for a human-subjects investigation. Interviewees were groundwater policymakers and/or researchers that spanned a wide range of ages, political identities, and education levels (**Supplementary Table S1**), providing a robust human dimensions dataset that was essential for management-relevant metacoupling research (Liu, 2017). As described fully in Hughes (2006), interviews typically lasted for 1hand involved fixed and open-ended questions regarding social-ecological effects of groundwater withdrawal and groundwater's economic contributions in Michigan. Interview information of particular relevance for metacoupling analysis included Groundwater Council members' perceptions of how spatial scale influences groundwater-related issues in Michigan (e.g., water quality, extraction policy effectiveness, information dissemination) and their opinions regarding the scales (i.e., stream, watershed, state, Great Lakes region) at which groundwater withdrawal decisions should be made. These data were compared with hydrological information using the metacoupling framework to identify couplings (intracouplings, pericouplings, telecouplings) that need to be created and enhanced for socially and ecologically informed groundwater management.

We also evaluated economic contributions of groundwater withdrawal in terms of jobs and economic activity supported at the intracoupling, pericoupling, and telecoupling scales using data from a report published by Public Sector Consultants (Public Sector Consultants [PSC], 2017). The intracoupling (county) scale included the Osceola and Mecosta counties, the pericoupling (regional) scale included five counties across the Muskegon River watershed (Kent, Mecosta, Montcalm, Newaygo, Osceola), and the telecoupling (statewide) scale encompassed all of Michigan. Input-output analysis and IMPLAN (IMpact analysis for PLANning) software were used to estimate economic contributions of Nestlé's groundwater withdrawal operations, facility expansion, and capital expenditures in 2017. Economic contributions were classified as direct (annual employment and spending), indirect (annual employment and spending generated via purchase of goods and services), and induced (annual economic contributions from household spending of people directly or indirectly employed by Nestlé's economic activity; Public Sector Consultants [PSC], 2017). Full methodological details are available in Public Sector Consultants [PSC] (2017).

In addition, we worked with the Michigan DNR to design and conduct an Inland Trout Angler Survey (ITAS) in 2015 to assess opinions and practices of Michigan's stream salmonid anglers with respect to salmonid regulations and management priorities in inland waterbodies (i.e., streams, inland lakes; Carlson and Zorn, 2018). The survey was developed to provide information on these relatively unstudied characteristics of Michigan salmonid anglers– the last analogous study occurred in 1981 (Fenske, 1983) – for incorporation into the DNR's first statewide management plan for inland populations of brook charr, brown trout, rainbow trout *Oncorhynchus mykiss*, lake trout *Salvelinus namaycush*, and splake *Salvelinus fontinalis* x *S.namaycush*. Like other stream salmonid angler surveys (Responsive Management, 2008; Schroeder, 2013; Petchenik, 2014), the ITAS included questions (n = 57) about stream salmonid anglers' preferences for fishing methods, angling regulations, salmonid species, and waterbodies (including Michigan counties of primary fishing activity). The survey also asked anglers about their opinions regarding the DNR Fisheries Division's salmonid management activities and identified their residences, particularly counties and zip codes (Carlson and Zorn, 2018). SurveyMonkey software was used to deliver the ITAS to Michigan's 83,000 salmonid anglers in March 2015. Full survey details are available in Carlson and Zorn (2018).

We analyzed ITAS data to generate an overall picture of fishing practices and fisheries management opinions of Michigan stream salmonid anglers while also identifying differences between key segments of the state's salmonid angling population to provide a basis for understanding fisheries metacouplings. In particular, the ITAS was used to obtain information about the metacoupling components– flows (e.g., information, people, money), agents (e.g., anglers, fisheries agencies), causes, and effects– that link Twin and Chippewa creeks and other rivers in our study area (**Figure 1**). For instance, intracoupling, pericoupling, and telecoupling flows of anglers were measured by subdividing ITAS respondents (n = 4,161) by Michigan county of primary fishing, county of residence, and zip code of residence. We emphasized the location of Twin and Chippewa creeks in Osceola County and, more specifically, zip code 49631 (where these streams are primary trout fishing destinations). The number of stream salmonid anglers who lived and fished in Osceola County (i.e., intracoupling flow) was compared with the number of anglers who lived outside but fished in the county (i.e., pericoupling/telecoupling flow) to delineate angler-flow metacouplings at the county scale. The same logic was applied to zip code 49631 to approximate intracoupling, pericoupling, and telecoupling angler flows at the stream scale (Twin and Chippewa creeks). In addition,ITAS data were partitioned into "members" and "non-members" of stream salmonid angling groups (i.e., Michigan Trout Unlimited, Anglers of the Au Sable, Federation of Fly Fishers), enabling assessment of attitudinal and behavioral differences (e.g., stream selection factors, preferred fishing regulations and tackle, salmonid management opinions) between these different "agents" of angling. Overall, findings from our groundwater, land-use, and stream temperature modeling (Waco and Taylor, 2010), Groundwater Council interviews (Hughes, 2006), and the ITAS (Carlson and Zorn, 2018) were integrated with other information sources (e.g., Li et al., 2015; Department of Environment Great Lakes and Energy [DEGLE], 2017; Public Sector Consultants [PSC], 2017; U. S. Geological Survey. [USGS], 2020a,b) using the metacoupling framework to identify ecologically and socially balanced strategies for groundwater governance and salmonid management. These balanced, metacoupled strategies were defined as those that holistically integrate environmental and human information across spatial scales and account for potential social-ecological trade-offs in groundwater and fisheries decision-making.

RESULTS AND DISCUSSION

Intracouplings

Intracouplings are social-ecological linkages that occur within, in this case, individual stream salmonid fisheries (**Figure 2**). Examples of intracouplings affecting salmonid fisheries include groundwater extraction (via changes in water volume, temperature, etc.), land-use change (via changes in water quality, physiochemical habitats, etc.), angling and fish stocking (via changes in fish abundance, size, etc.), and watershed fragmentation by dams and roads (via changes in water depth, discharge, habitat connectivity, etc.; Waco and Taylor, 2010). An intracoupled system such as the Twin Creek salmonid fishery consists of human subsystems (e.g., local economy, communities of anglers, and tourists) and natural subsystems (e.g., salmonid populations, habitats, local weather) as well as flows, agents, causes, and effects that link the human and natural subsystems (**Table 1** and **Figure 2**).

Flows of water, fish, people, and money connect human and natural subsystems in Twin and Chippewa creeks. These flows are promoted or inhibited by agents such as groundwater extractors, Groundwater Council members, anglers, governmental agencies, and NGOs (**Table 1**). For instance, a 2006 decision by the Michigan DEGLE (then the Department of Environmental Quality) allowed Nestlé to construct a large-capacity groundwater well near Twin and Chippewa creeks (Waco and Taylor, 2010). In the context of groundwater withdrawal, movement of water from aquifers (sending systems) to the Nestlé water bottling facility (receiving system) is an intracoupling flow. In this case, causes (reasons why intracouplings occur) are water bottling, resultant drinking water sales and revenue for Nestlé, and water's abundance in this groundwater-rich region of Michigan (**Table 1**). Effects of groundwater withdrawal include county-level economic contributions, including 284 jobs and $24.2 million in total economic activity in 2017 alone (**Table 2**; Public Sector Consultants [PSC], 2017), and social effects such as disapproval of groundwater stakeholders (e.g., anglers, landowners) who oppose groundwater extraction because they believe it decreases stream water levels, salmonid abundance, and angling quality (Hughes, 2006; Waco and Taylor, 2010; Department of Environment Great Lakes and Energy [DEGLE], 2017; Public Sector Consultants [PSC], 2017).

TABLE 2 | Economic contributions of groundwater withdrawal (jobs, total economic activity) at the intracoupling, pericoupling, and telecoupling scales.

Type and scale of contribution	Jobs	Total economic activity (millions)
Company Operations (2017)		
Intracoupling	199	$13.2
Pericoupling	370	$35.4
Telecoupling	765	$160.9
Facility Expansion (STANWOOD, MI)		
Intracoupling	12	$0.9
Pericoupling	24	$2.1
Telecoupling	41	$6.5
Capital Expenditures (2017)		
Intracoupling	73	$10.1
Pericoupling	240	$34.4
Telecoupling	467	$67.6
Total Contribution		
Intracoupling	284	$24.2
Pericoupling	634	$71.9
Telecoupling	1,273	$235.0

Input-output analysis and IMPLAN (IMpact analysis for PLANning) software were used to estimate economic contributions of Nestlé's groundwater withdrawal operations, facility expansion, and capital expenditures in 2017 (data obtained from Public Sector Consultants [PSC], 2017). The intracoupling (county) scale included the Osceola and Mecosta counties, the pericoupling (regional) scale included five counties across the Muskegon River watershed (Kent, Mecosta, Montcalm, Newaygo, Osceola), and the telecoupling (statewide) scale encompassed all of Michigan (MI).

However, scientific evidence to date suggests that groundwater withdrawal and land-use change have relatively minor effects on stream salmonid thermal habitats in Twin and Chippewa creeks. For instance, groundwater extraction regimes ranging from 0 to 0.1262 m^3/s (2,000 gpm) were projected to increase summer stream temperatures in Twin and Chippewa creeks by $\leq$ 0.91°C (**Supplementary Tables S2, S3**), and 0.10°C was the largest stream temperature increase predicted from land-use change, particularly a grassland-to-urban transition (**Supplementary Table S4**; Waco and Taylor, 2010). In Twin Creek, an observed decrease in baseflow of 0.0449 m^3/s (712 gpm) caused surface water levels to decrease by 9.8 cm between 2006 and 2015 (Papadopulos & Associates, Inc, 2016). In Chippewa Creek, a baseflow decline of 0.0110 m^3/s (173 gpm) reduced surface water levels by 3.7 cm. Research suggests that these hydrological changes have not altered salmonid thermal habitat quality, which is considered excellent in both streams and characterized by water temperatures and depths that are cold and deep enough to withstand 0.91°C warming and a 9.8 cm water level decline (Waco and Taylor, 2010; Wesener, 2010; Li et al., 2015; Papadopulos & Associates, Inc, 2016).

Moreover, in the 14 months since the USGS began monitoring Twin and Chippewa creeks (U. S. Geological Survey. [USGS], 2020a,b), discharge has remained relatively consistent beyond expected daily and seasonal fluctuations (**Supplementary Figures S1, S2**), suggesting minimal impacts of recent groundwater extraction on stream hydrology and salmonid thermal habitats. Intracoupled flows of fish (e.g., movement within Twin and Chippewa creeks) have been largely unaffected by groundwater withdrawal and land-use change (Waco, 2009; Waco and Taylor, 2010; Li et al., 2015; Papadopulos & Associates, Inc, 2016; Michigan Department of Natural Resources [MDNR], 2019), yet human subsystems in Twin and Chippewa creeks are marked by controversy over groundwater withdrawal. In particular, local anglers and landowners claim to have observed local reductions in stream water levels, salmonid abundance, and angling quality due to groundwater withdrawal since 2006, and they feel victimized by a groundwater governance process that has overlooked their ecological and recreational concerns about groundwater extraction (Hughes, 2006; Department of Environment Great Lakes and Energy [DEGLE], 2017). The personal experiences of these stakeholders (e.g., catching fewer fish, feeling unrepresented in groundwater governance), coupled with claims by governance organizations (as yet unsupported by data) that groundwater withdrawal has not affected salmonid populations, have made anglers and landowners a spillover system (**Table 1**) whose frustration is growing will likely expand if groundwater withdrawal rates increase, as proposed by Nestlé. Such spillover effects have motivated anglers and landowners to travel to public meetings throughout the region, including those held at Ferris State University (Big Rapids, Michigan) in April 2017 and 2018, to voice their concerns over groundwater withdrawal (Department of Environment Great Lakes and Energy [DEGLE], 2017).

The Twin and Chippewa creek salmonid fisheries also feature intracouplings related to fish, people, and money. Not only do salmonids move naturally within the streams, anglers fish in the rivers and spend money at local businesses (e.g., bait and tackle shops, restaurants) in pursuit of recreational experiences and fish for consumption (**Table 1**; Carlson and Zorn, 2018; Zorn et al., 2018; Michigan Department of Natural Resources [MDNR], 2019). Effects of these intracouplings include fish harvest as well as fish consumption and human nutrition (fish is an excellent source of protein, micronutrients, and essential fatty acids; Cooke et al., 2017; Bennett et al., 2018; Carlson and Zorn, 2018). In addition, angling is a source of psychological well-being, community cohesion, and revenue generation in local economies (Knuth, 2002; Zorn, 2018; Carlson et al., 2019b).

Pericouplings

Whereas intracouplings are social-ecological linkages within individual stream salmonid fisheries, pericouplings are social-ecological linkages between adjacent fisheries systems (**Figure 2**). Although Twin and Chippewa creeks each have intracoupled flows of water, information, fish, people, and money, the adjacency of these streams permits between-system, pericoupled flows (**Figure 2**). For instance, water moves between the streams via surface, hyporheic, and groundwater flows; salmonids and other fishes move naturally between the streams; and people (e.g., anglers, landowners, tourists) move between the watersheds, often causing additional flows of money and information (**Table 1**; O'Neal, 1997; Li et al., 2015; Advanced Ecological Management [AEM], 2016; Papadopulos & Associates, Inc, 2016; Carlson and Zorn, 2018; Michigan Department of Natural Resources [MDNR], 2019). In addition, groundwater withdrawal generates pericoupled economic contributions, including 634 jobs and $71.9 million in total economic activity in the five-county region surrounding Twin and Chippewa creeks (**Table 2**; Public Sector Consultants [PSC], 2017). Not only do these pericouplings affect water and fish distribution as well as corporate and consumer spending at a multi-river scale (O'Neal, 1997; Public Sector Consultants [PSC], 2017; Carlson and Zorn, 2018; Zorn, 2018; Zorn et al., 2018), they influence stakeholder perceptions of groundwater governance. For instance, the majority of Groundwater Council members (77%, n = 20; **Supplementary Table S5**) stated that groundwater withdrawal decisions should account for individual streams and their connections across aquifers and watersheds (i.e., intracouplings and pericouplings), linkages whereby groundwater extraction can affect hydrology of non-target streams (Hughes, 2006). Such intracoupling- and pericoupling-scale governance corresponds with scales at which groundwater modeling and aquifer recharge occur in the study area (Waco and Taylor, 2010; Li et al., 2015; Papadopulos & Associates, Inc, 2016), suggesting a metacoupling "win-win" scenario wherein governance preferences and hydrological phenomena are spatially aligned. However, this is not always the case. For example, in selecting groundwater-related problems in Michigan, a plurality of Groundwater Council members (36%, n = 11) chose water quality. This suggests a metacoupling "mismatch," as a socially-identified problem (water quality) cannot be fully addressed using socially-preferred solutions (intracoupling- and pericoupling-scale policies) because water quality impairment is driven by metacoupled ecological stressors such as point-source and non-point-source pollution, climate change, and land-use change that transcend intracouplings and pericouplings (Waco and Taylor, 2010; Carlson et al., 2017a,c). In Twin and Chippewa creeks, additional data are needed to evaluate how water quality is affected by groundwater withdrawal and other metacoupled ecological stressors, allowing for development of water quality management approaches that account for intracouplings, pericouplings, and telecouplings.

In some cases, pericouplings between stream fisheries are disrupted by stressors such as groundwater withdrawal and watershed fragmentation. For instance, groundwater withdrawal reduces surface and subsurface water levels and flows between Twin and Chippewa creeks, but studies indicate minimal effects on salmonid populations (Waco and Taylor, 2010; Li et al., 2015; Advanced Ecological Management [AEM], 2016; Papadopulos & Associates, Inc, 2016). In addition, pericoupled fish movements from Twin Creek to Chippewa Creek are impeded by an impoundment near the latter's confluence with the Muskegon River (**Figure 1**), even though downstream movements from Chippewa to Twin creek are unimpeded (O'Neal, 1997; Waco, 2009; Waco and Taylor, 2010; Michigan Department of Natural Resources [MDNR], 2019). Ultimately, groundwater withdrawal's real and perceived effects have ignited public controversy in the absence of community-engaged governance, which seeks to incorporate the social-ecological concerns of all stakeholders and thereby build trust and shared understanding (Hughes, 2006; Ansell and Gash, 2008). Without such governance, communities of anglers and landowners are spillover systems without adequate representation in the policy arena.

Telecouplings

Telecouplings, unlike intracouplings and pericouplings, are social-ecological linkages between distant, non-adjacent fisheries systems (**Figure 2**). For instance, the arrival of the Nestlé corporation in the Chippewa Creek and Twin Creek watersheds was caused by an information telecoupling involving a policy decision at Nestlé headquarters (in Stamford, Connecticut), with subsequent Michigan DEGLE approval, to bottle water and generate revenue in a groundwater-rich region of Michigan. Likewise, for 67 years, organizations such as the Michigan DNR, Michigan DEGLE, and Advanced Ecological Management have practiced aquatic resource management in Twin (and more recently Chippewa) Creek by collecting hydrological and biological data (e.g., water temperature, discharge, fish, and macroinvertebrate abundance) and distributing these data via information telecouplings throughout the region and the state (Michigan Department of Natural Resources [MDNR], 2019). Telecouplings also affect stakeholder perceptions of groundwater governance, as evidenced by Groundwater Council members' general lack of support for telecoupled groundwater withdrawal policies– those scaled to the state and Great Lakes basin levels, favored by 23% of interviewees (n = 6) – compared to intracoupling- and pericoupling-scale policies (**Supplementary Table S5**).

In addition, understanding telecouplings is important for groundwater governance and policy development because they can eclipse smaller-scale couplings with negative effects. For instance, agents such as the Michigan DEGLE promote groundwater regulation and conservation (i.e., causes) by developing statewide and regional policies for groundwater withdrawal. By and large, these telecoupling- and pericoupling-scale policies do not contain local, intracoupling-level information about how groundwater extraction will affect specific streams or communities of anglers, landowners, and other groundwater stakeholders. Moreover, groundwater policies are disseminated throughout the State of Michigan via information telecouplings (e.g., online/printed reports and news articles; Department of Environment Great Lakes and Energy [DEGLE], 2017; **Table 1**) rather than localized intracouplings that target stakeholders who live or fish near water bottling facilities and wells. The predominance of telecoupling-scale policies and information exchange influences stakeholder perceptions of groundwater governance. For instance, Groundwater Council members stated that groundwater-related problems in Michigan include ineffective state-level groundwater withdrawal policies (30%, n = 9 respondents), lack of publically-available local information on withdrawal (27%, n = 8), and public misconceptions of withdrawal's local effects (7%, n = 2; Hughes, 2006). They believed that these problems could be best addressed by making policies and public outreach efforts more locally relevant (i.e., by enhancing information intracouplings). However, as exemplified in Twin and Chippewa creeks, flows of groundwater-related information within and between decision-making organizations (e.g., DEGLE, Nestlé) have not incorporated the concerns of local communities, making them spillover systems that are largely excluded from groundwater governance processes (Hughes, 2006; Department of Environment Great Lakes and Energy [DEGLE], 2017). Overall, emphasis on policy and information telecouplings at the expense of intracoupling-informed groundwater governance has caused public outcry and exacerbated a controversy over groundwater extraction that would have been less acrimonious if intracoupling-level concerns of local communities had been addressed.

Telecouplings also link coldwater streams and anglers. For instance, Twin Creek is connected with Hoffmeyer Creek, the Hersey River, and other salmonid streams within and outside Osceola County by telecoupled flows of anglers (**Table 1**). In a statewide survey of Michigan stream salmonid anglers (Carlson and Zorn, 2018), 53 of 4,161 respondents (1.3%) stated that Osceola County was their primary fishing county (**Supplementary Table S6**). In comparison, only 19 of these respondents (0.5% overall) lived in Osceola County, suggesting that the county had 1.6 times as many non-local (pericoupled/telecoupled) anglers as local (intracoupled) anglers in 2015. Extrapolating these percentages to the 83,000 stream salmonid anglers in Michigan (Carlson and Zorn, 2018), Osceola County had an estimated 1,079 stream salmonid anglers, 415 of whom were intracoupled and 664 of whom were pericoupled/telecoupled (**Supplementary Table S6**). Hence, more anglers moved into (and out of) Osceola County to fish for stream salmonids than those who fished and lived within it. Similarly, in the code containing Twin and Chippewa creeks, an estimated 100 stream salmonid anglers were intracoupled and 160 anglers were pericoupled/telecoupled, suggesting that angler movement pericouplings and telecouplings, in addition to intracouplings, play an important role in determining who fishes for stream salmonids in these streams (Carlson and Zorn, 2018).

Moreover, groundwater withdrawal causes telecouplings that affect humans in positive and negative ways. For instance, groundwater extraction has increased telecoupled flows of bottled water from Twin and Chippewa creeks to areas throughout Michigan and the United States, but groundwater withdrawal (originally caused by telecoupled information transfer between Connecticut and Michigan) has decreased surface and subsurface water levels and flows in these streams (Malcolm Pirnie Inc. [MPI], 2000; Waco and Taylor, 2010; Papadopulos & Associates, Inc, 2016; Public Sector Consultants [PSC], 2017). Groundwater withdrawal provides telecoupled economic contributions, including 1,273 jobs and $235.0 million in total economic activity throughout Michigan (**Table 2**; Public Sector Consultants [PSC], 2017), but communities of anglers and landowners are spillover systems, and their ecological and recreational concerns about groundwater extraction have not been adequately addressed by groundwater governance organizations (Hughes, 2006). In fact, public citizens aired their grievances about groundwater withdrawal in Twin and Chippewa creeks over a 205day comment period in which the Michigan DEGLE received 340,000 petition signatures (to stop increased groundwater extraction) and 50,000 statements of concern (e.g., environmental damage, resource rights infringement, water quality impairment), a rate of one comment every 6minfor nearly 7months (Department of Environment Great Lakes and Energy [DEGLE], 2017). Arising from stakeholders locally, regionally, and statewide, these comments generated metacoupled information flow that culminated in strong public opposition to groundwater withdrawal in Twin and Chippewa creeks. In addition, there are concerns that groundwater withdrawal will elicit telecouplings that affect other fish species that use, and move among, rivers and streams in the Muskegon River watershed. These fishes include burbot (*Lota lota*), northern pike (*Esox lucius*), smallmouth bass (*Micropterus dolomieu*), yellow perch (*Perca flavescens*), walleye (*Sander vitreus*), and at least 32 other species native to Michigan (O'Neal, 1997) whose habitats, movements, and ecological and socioeconomic services (e.g., predation, nutrient cycling, angling) could be affected by continuing groundwater withdrawal (Waco and Taylor, 2010; Department of Environment Great Lakes and Energy [DEGLE], 2017) – an important subject for future research.

Insights and Applications of the Metacoupling Framework

By providing an approach for systematic social-ecological integration across space and time, the metacoupling framework advances conventional research methods that focus only on socioeconomic or ecological dynamics operating in specific places. For instance, although uniform statewide regulation of groundwater withdrawal in Michigan is efficient in some ways, investigating social-ecological linkages demonstrates a stakeholder preference for intracoupling- and pericoupling-scale governance that actively engages human communities and considers groundwater dynamics in individual streams and watersheds (Hughes, 2006). Without such insights from the metacoupling framework, important groundwater stakeholders and their concerns have been overlooked, leading to negative social outcomes and ultimately governance that is socially and ecologically imbalanced, as demonstrated in Twin and Chippewa creeks. However, use of the metacoupling framework can impart social-ecological balance to groundwater governance across spatial scales and lead to positive outcomes, including improved relationships among the many stakeholders involved in aquatic resource management (Hughes, 2006).

In addition, by enabling holistic analysis of riverine ecosystems, social systems, and their interconnections, the metacoupling framework promotes aquatic resource management and policy approaches that address multiple social-ecological objectives and potential tradeoffs. For example, Waco and Taylor (2010) predicted that a riparian forest-to-shrub transition in Twin and Chippewa creeks would decrease water temperatures by 0.09°C and thereby help maintain cold thermal habitats needed by brook charr and brown trout (Raleigh, 1982; Raleigh et al., 1986; Lyons et al., 2009). However, metacoupling analysis indicated that this land-use change would also reduce angling (and associated revenue generation for local economies) because streams' forested aesthetic beauty is highly valued by salmonid anglers (Carlson and Zorn, 2018). In fact, anglers ranked aesthetic beauty the most important among 16 decision factors for stream fishing, including the chance to catch brook charr, brown trout, rainbow trout, trophy trout, and large numbers of salmonids (Carlson and Zorn, 2018). Hence, it is important that salmonid managers account for the aesthetic value of forested riparian zones and watersheds alongside other important considerations (e.g., thermal habitat quality, anglers' harvest and tackle preferences) to design socially and ecologically balanced, metacoupled strategies for salmonid management within and beyond Twin and Chippewa creeks. After all, what is ecologically beneficial for fisheries (e.g., thermally favorable land-use changes) can be socially and economically detrimental, and vice versa. By using a metacoupling perspective, fisheries and aquatic resource professionals can identify– and potentially reconcile– social-ecological complexities and tradeoffs in ways that promote holistic, sustainable groundwater governance and salmonid management.

Using the metacoupling framework also helps fisheries professionals differentiate between the many types of stakeholders they serve. For example, in our survey of Michigan stream salmonid anglers, members and non-members of stream salmonid angling groups (i.e., Michigan Trout Unlimited, Anglers of the Au Sable, Federation of Fly Fishers) often held disparate attitudes and opinions regarding stream salmonid fishing and fisheries management. In deciding whether or not to fish a particular stream, angling group members prioritized wild salmonids and trophy-sized salmonids to a greater degree than non-members, who believed that stocked salmonids and the number of salmonids caught were most important (Carlson and Zorn, 2018). Members were less harvest-oriented than non-members, and they attended fisheries-related public meetings more frequently, reflecting their comparatively high degree of personal involvement in Michigan stream salmonid management. By using the metacoupling framework to tease apart these important attitudinal and behavioral differences between fisheries stakeholder groups, fisheries professionals can design management strategies (e.g., catch limits, stocking rates, public outreach approaches) that are appropriately scaled to the diverse angler populations they serve, leading to improved social outcomes in fisheries management.

Similarly, the efficacy of stakeholder communication and engagement activities is regulated by metacouplings. For instance, according to our survey, the most popular resources that Michigan stream salmonid anglers use to plan fishing trips are the DNR Fishing guide (59% of anglers) and DNR online maps (42%; Carlson and Zorn, 2018). In addition, 63% of salmonid anglers use smart phones during fishing trips to access fishing-related information from the internet, which may be an intracoupled, pericoupled, or telecoupled process depending on the proximity between where anglers fish and where their information source is located. Hence, fisheries professionals can best communicate with anglers (regarding fish harvest regulations, groundwater withdrawal, etc.) by understanding the metacoupled nature of information exchange and designing communication mechanisms that cater to anglers' preferences for printed and electronic resources (e.g., websites, smart phone apps) as opposed to using other media (e.g., DNR phone line, map books, bait shop contacts). Overall, the metacoupling framework helps fisheries professionals understand and manage the complexities of fisheries ecosystems and human systems, providing a knowledge base for enhancing the social-ecological resilience of fisheries that have traditionally been viewed through socially or ecologically focused (rather than integrated) lenses (Baranoff, 1918; Ricker, 1954; Vannote et al., 1980; Dietz et al., 2003; Hilborn et al., 2004).

CONCLUSION

In conclusion, the metacoupling framework helps advance stream salmonid research and management in numerous ways. For instance, the metacoupling framework operationalizes the study of salmonid fisheries as CHANS, offering an organized method for assessing the causes and effects of social-ecological linkages across local to global scales and thereby advancing conventional research approaches that are location-specific and either social or ecological. In addition, the metacoupling framework provides novel insights about stream salmonid fisheries (e.g., cross-scalar tradeoffs, feedbacks, surprises). In turn, these insights represent leverage points for ecologically, socioeconomically informed fisheries management, including metacoupled governance of relationships among sending, receiving, and spillover systems rather than specific issues and physical places alone. The metacoupling framework also has substantial flexibility because its systematic structure can be widely applied to disparate fisheries to provide social-ecological insights that advance fisheries science and practice.

Future research directions include better quantifying metacoupled flows of water, information, fish, people, and money within and beyond Twin and Chippewa creeks and mathematically modeling metacouplings– particularly interactions among intracouplings, pericouplings, and telecouplings– via time series approaches, agent-based models, network analyses, and related methods (Liu, 2017; Carlson et al., 2018; Dou et al., 2019). In addition, future metacoupling research is needed on topics not directly studied herein, but which are important for salmonid and broader fisheries management within and beyond our study area (e.g., watershed fragmentation, invasive species, stocking, pollution, fish community interactions, biodiversity conservation; Cooper et al., 2016; Zorn et al., 2018; Smith et al., 2019). Overall, the ecological dynamics, socioeconomic benefits, and public fascination associated with stream salmonids are best understood and managed by conceptualizing salmonid fisheries as metacoupled CHANS.

DATA AVAILABILITY STATEMENT

All datasets generated for this study are included in the article/**Supplementary Material**.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Michigan State University (MSU) Institutional Review Board. The participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

AC conceived the research idea, analyzed the angler survey research, and wrote the majority of the manuscript. WT helped conceive the research idea and provided text in addition to thoughtful comments and revisions. SH performed surveys of groundwater stakeholders on which this manuscript is based and provided thoughtful comments and revisions.

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SUPPLEMENTARY MATERIAL

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Unmanned Aerial Vehicle (UAV)-Based Thermal Infra-Red (TIR) and Optical Imagery Reveals Multi-Spatial Scale Controls of Cold-Water Areas Over a Groundwater-Dominated Riverscape

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The forecast of warmer weather, and reduced precipitation and streamflow under climate change makes freshwater biota particularly vulnerable to being exposed to temperature extremes. Given the importance of temperature to regulate vital physiological processes, the availability of discrete cold-water patches (CWPs) in rivers to act as potential thermal refugia is critical to support freshwater ecosystem function. Being able to predict their spatial distribution at riverscape scales is the first step to understanding the capacity to maintain thermal refuges and to inform future river management strategies. Novel Unmanned Aerial Vehicle (UAV)-based Thermal Infra-Red (TIR) imagery technologies provide an opportunity to assess riverscape stream temperature. On the example of a 50 km linear length of the groundwater-dominated Upper Ovens River (Australia), this study presents a methodology addressing critical challenges in UAV-based TIR and optical data acquisition, processing, and interpretation. Our methodological approach generated 49 georeferenced high-resolution TIR and optical orthomosaicked imagery sets. The imagery sets allowed us to identify river-length longitudinal patterns of temperature and to detect, characterize, and classify 260 CWPs. Both stream and CWPs temperatures increased but presented considerable variability with downstream distance. CWPs were non-uniformly distributed along the riverscape, with emergent hyporheic water types dominating, followed by deep pools, shading, side channels, and tributaries. We found associations between CWPs and key physical controls including land use, riparian vegetation, longitudinal and lateral CWP location, and CWP area size, illustrating processes acting at multiple spatial scales. This study provides a basis for future works on the thermal associations with physical controls over a riverscape, and it highlights the major challenges and limitations of the use of UAV-based TIR and optical imagery to be used in future applications. In conjunction with studies of thermally linked ecological processes, the predictions of CWPs can help prioritize river restoration measures as effective climate adaptation tools.

Keywords: river resilience, climate adaptation, cold-water spots, thermal refuges, stream temperature, habitat heterogeneity, riparian vegetation, remote sensing

INTRODUCTION

The forecast of continued durations of warmer weather, altered precipitation, and modified streamflow patterns driven by climate change will be exacerbated by local anthropogenic pressures in rivers, exposing freshwater ecosystems to a severe threat worldwide (Vörösmarty et al., 2010; Reid et al., 2019). Land-use change, water abstractions, and stream regulation pose severe alterations to rivers, with increased drought severity, high stream temperatures and habitat degradation of most concern (Bond et al., 2008; van Vliet et al., 2013; Geist and Hawkins, 2016). Such unprecedented changes in aquatic systems call for action to develop effective management and mitigation approaches to support river resilience (Palmer et al., 2008; Wilby et al., 2010; McCluney et al., 2014).

As river temperatures are expected to increase globally (Kaushal et al., 2010; van Vliet et al., 2013; Orr et al., 2015), cold-water thermal refugia are increasingly considered as a targeted climate adaptation strategy in the northern hemisphere (Kurylyk et al., 2014; Isaak et al., 2015). Adapted from the definition of climatic refuges by James et al. (2013), here we consider thermal refuges as discrete patches of water at either lower or higher temperature than the main stream, in which biota can persist during periods of unfavorable thermal conditions. Here, we will focus on cold-water patches (CWPs), most relevant as potential thermal refuges during summer. Based on the recognition that stream temperature is the "master" variable controlling biochemical processes in rivers (Caissie, 2006; Webb et al., 2008), thermal refuges need to be incorporated as a key aspect of river habitat structure, and to be considered in freshwater climate adaptation management strategies around the world (Palmer et al., 2008; Keppel et al., 2015; Morelli et al., 2016).

Rivers are complex dynamic ecosystems that vary significantly along their spatial course (Wohl, 2016). Their physical structure can be represented as a hierarchical organization of interconnected spatial scales (Frissell et al., 1986; Thorp et al., 2006; Braun et al., 2012). Such array of physical features play an essential role in determining how heat is distributed (Fausch et al., 2002; Carbonneau et al., 2012). Whilst river temperature is driven by climatic, topographic, and hydrological controls at the air-water interface (Caissie, 2006; Webb et al., 2008); dynamic groundwater inputs (Poole et al., 2006; Arrigoni et al., 2008; Dugdale et al., 2013), in-channel physical complexity (Tonolla et al., 2010; Sawyer and Cardenas, 2012), and shading (Torgersen et al., 1999; Garner et al., 2017) may alter its longitudinal variability. Understanding the spatial variations of stream temperature and the processes governing CWPs within the riverscape is of key concern for managers (Kurylyk et al., 2014; Steel et al., 2017). Whilst the spatial distribution of CWPs was earlier considered by Ebersole et al. (2003b) and Torgersen et al. (1999), recent technological advances in Thermal Infra-Red (TIR) imagery acquisition have propelled investigations of their driving processes at larger spatial scales including entire riverscapes (Handcock et al., 2012; Dugdale, 2016; Dugdale et al., 2019). Monk et al. (2013), for example, demonstrated the links between a range of physical environmental variables and cold-tributary areas using TIR imagery coupled with geospatial landscape information over a reach of the Cains River in Canada. Dugdale et al. (2015), on the other hand, studied the spatial variability of groundwater-based cold-water refuges and their associations with watershed hydromorphology combining TIR and optical imagery in the Restigouche River, Canada. Both TIR and optical imagery were also used along a ca. 50 km river length of the Ain River, in France, to (i) find that CWPs were associated to fluvial geomorphic features (Wawrzyniak et al., 2016); and (ii) demonstrate TIR mapping efficiency to detect groundwater-driven cold upwellings (Dole-Olivier et al., 2019). Whilst the clear effect of controls such as riparian shading, land use and in-channel fluvial geomorphology on stream temperature has been demonstrated (e.g., land use, Allan, 2004; riparian shading, Ebersole et al., 2003a; Garner et al., 2017; geomorphic features, Ouellet et al., 2017), studies of their combined influence over large spatial scales are rare. The incorporation of such key mechanisms into integrated predictive models of thermal refuge distribution will be key to understand and manage future climatic conditions (Fullerton et al., 2018).

Recent advances in the development of UAVs – or drones – equipped with TIR cameras provide small, inexpensive, fast, and flexible solutions to obtain high-resolution TIR and optical (RGB) imagery data (Corti Meneses et al., 2018a,b). UAVs are also capable of surveying large areas that, to date, were primarily carried out using manned aerial vehicles (i.e., helicopter). The use of light-weight uncooled thermal cameras in drones, however, comes with some limitations including sensor and environmentally derived errors (Dugdale et al., 2019; Kelly et al., 2019), and the difficulty in orthomosaicking in the photogrammetric process due to the inherent low contrast of surface features in TIR images (Ribeiro-Gomes et al., 2017). To address these and other issues affecting TIR imagery quality, it is crucial to develop a functional methodology during data acquisition and processing that helps obtain high precision quantitative stream temperature information for its correct interpretation.

To date, most literature on the identification, distribution and use of cold-water refuges is found in the northern hemisphere, focusing in particular on their role to aid salmonids' thermoregulation during hot extremes (Ebersole et al., 2001; McCullough et al., 2009). In contrast, in the southern hemisphere, in south-eastern Australia, significant research progress has been made in understanding flow-associated "climatic" or "drought" refuges (Bond, 2007; James et al., 2013; Robson et al., 2013; Ning et al., 2015), driven by the predicted increased recurrence of droughts due to climate change (Boulton, 2003; Murray-Darling Basin Commission, 2007; Bond et al., 2008). However, such research progress has focused on ephemeral or near-ephemeral streams, leaving an open gap on stream thermal refuge research in perennial rivers in Australia.

The perennial Upper Ovens River (Victoria, Australia) is one of the least modified catchments within the Murray-Darling Basin (Miller and Barbee, 2003). It supports high ecological values due to its distinctly connected surface and groundwater sources (Yu et al., 2013). However, future climatic predictions will make it extremely vulnerable during summer low flows, as the heightened anthropogenic groundwater extractions are likely to create cease-to-flow events with high risk to freshwater biota (Goulburn Murray Water, 2011). Since 2008, the Upper Ovens River has been declared a Water Supply Protection Area, with a priority goal to reduce the risk of aquatic habitat loss during critical low flow periods, by restricting water demands when necessary (Goulburn Murray Water, 2011; Hart and Doolan, 2017). Identifying and understanding the capacity of the system to hold thermal refuges is therefore essential to enable the implementation of well-informed and targeted restrictions, and to support long-term climate adaption and mitigation strategies in the system.

To tackle the above-mentioned gaps, this study takes the Upper Ovens River as a riverscape model to (i) present a methodology addressing the key challenges during UAV-based TIR and optical imagery acquisition, processing and interpretation; (ii) investigate patterns of riverscape stream temperature and CWPs, and (iii) model the associations of CWPs with physical controls at multiple spatial scales. We also discuss the implications of the findings in the context of freshwater conservation and management.

MATERIALS AND METHODS

The Upper Ovens River

The Upper Ovens River (Australia) is part of a vast anabranching system across the south-east Murray-Darling Basin (**Figure 1**) that emerges from the northern part of the Victorian Alps and flows north-westwards (Judd et al., 2007). With a steep surface gradient, the Upper Ovens River presents a variety of landscapes ranging from narrow V-shaped mountain valley forming a single channel, covered by native forests and extensive pine forestry plantations, to a broad flat alluvial floodplain with a meandering multi-channel river, surrounded predominately by agricultural land (Sinclair Knight Merz, 2013).

The average annual rainfall in the Upper Ovens is 1000 mm, with a monthly average between 57 mm in February and 181 mm in July. These result in seasonal stream water level fluctuations of up to 2 m with the highest levels coinciding with maximum peak spring rainfall (Sinclair Knight Merz, 2007).

The geology of the Upper Ovens catchment is characterized by ancestral incision into Ordovician bedrock, which was infilled by alluvial deposits comprising the deeper, coarse-grained Calivil Formation; shallower sands, silts, and clays of the Shepparton Formation; and the recent alluvium of the Coonambidgal Formation (Shugg, unpublished). Groundwater flows both regionally in the Ordovician fractured rock aquifer and locally in the alluvial sediments in the valley. The river and floodplain were dredged over the last 150 years to mine gold. The dredging process involved significant disturbance of shallow sediments by successive excavation, mixing, re-constitution, and re-deposition resulting in substantial changes in stream morphology (Sinclair Knight Merz, 2007).

The Upper Ovens River flows to the northwest, dominated by gaining reaches consistent with topography and aquifer lithology. Groundwater constitutes most of the river flow during baseflow conditions in summer, with total groundwater inflow increasing with river flow. Estimates of the contribution of groundwater to the total flow vary greatly depending on the method but are considered higher in the Upper Ovens River compared to other parts of the catchment (Yu et al., 2013). Rapid groundwater recharge through the permeable aquifers rises the water table. In turn, the hydraulic head gradient toward the river increases and hence causes high baseflow to the river during high flow (wet) periods (Yu et al., 2013). Surface water and groundwater extraction, and change in land use (such as clearing, re-afforestation, or increasing irrigation) can influence the volume of groundwater discharging to the river (Owuor et al., 2016). During summer months, when flows are at their minimum but demand for surface and groundwater are at their highest, the Upper Ovens River experiences significant water stress (Goulburn Murray Water, 2011; Yu et al., 2013).

Methodological Approach

A combination of ground data collection and desktop works are usually required for the acquisition, calibration, correction, orthomosaick stitching, and interpretation of airborne imagery. In this study, we applied a step-by-step approach subdivided into three phases comprising data acquisition, processing, and interpretation (**Figure 1**). In summary, we deployed ground control points (GCPs) and thermal loggers for calibration/validation along the survey area, and we measured them before dual UAV-based flights for thermal and optical imagery data acquisition were carried out. Desktop-based processing encompassed thermal calibration via linear models; temperature drift correction using Partially Overlapped Histogram Equalization (POHE); imagery georeferencing; raster photogrammetric orthomosaicking; georectification; longitudinal temperature adjustment; and thermal validation using temperature logger data. As part of data interpretation, orthomosaicked raster TIR images were polygonized to help CWPs identification based on established thermal thresholds; both physical and thermal attributes were extracted from optical,

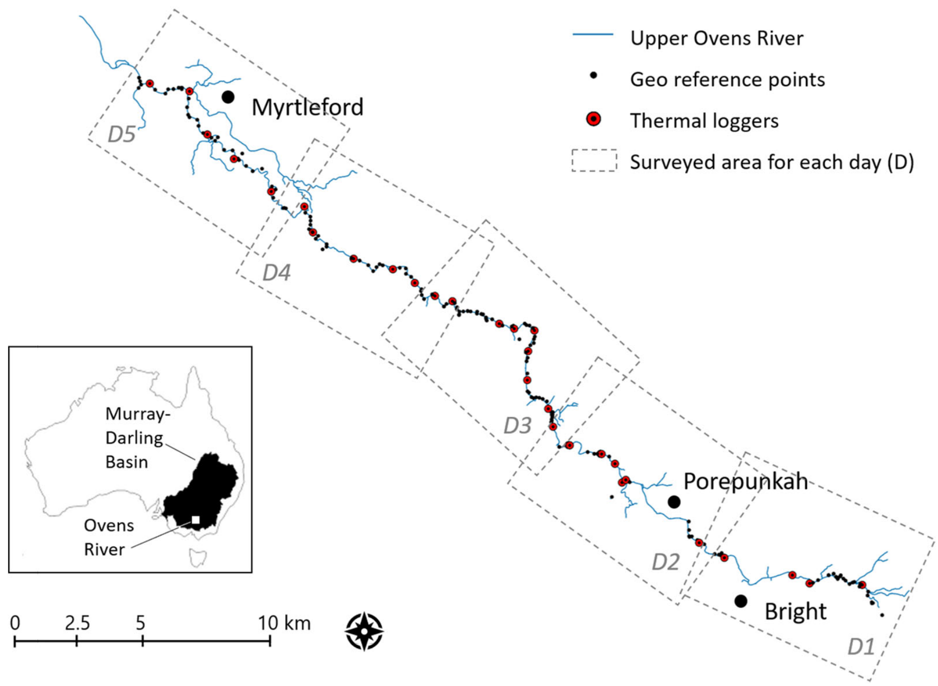

FIGURE 1 | Location of the Upper Ovens River with the position of all Ground Control Points (GCPs) and thermal references, and the delimitation of the areas surveyed each day (D).

and TIR imagery, respectively; and the overlapping of both imagery provided the basis of CWPs classification.

Data Acquisition

Field data acquisition via UAV-based TIR and optical (RGB) imagery took place over five consecutive days with stable warm summer weather conditions (2–7 April 2017), and low flows in the Upper Ovens River (2.4 ± 0.17 $m^3.s^{-1}$, Myrtleford station, Australian Government Bureau of Meteorology, 2018). We covered 7–10 km of linear distance per day including the river length from above Bright to below Myrtleford (50 km in linear length, and ca 95 km in total river length).

Each day, prior to the UAV-surveys, a total of 40–60 GCPs were distributed along the planned surveyed area (**Figure 1**), and their location was recorded using Leica® Viva GS14 RTK differential global positioning system (DGPS), for georectification (**Figure 2**). They consisted of a combination of cold and warm targets to enable their detection by TIR images. The targets were made of 50 × 50 cm metallic sheets (cold) and rubber tiles (warm) marked with a " + " in the middle. We located them in non-vegetated riparian areas or on exposed gravel bars to enable easy visualization from the air, and we retrieved them at the end of each daily survey. A total of 31 Cyclops® temperature loggers were distributed along the surveyed river length for thermal validation over the water target (**Figure 1**). Five to seven loggers were installed across the planned surveyed area prior to the UAV flights, geo-located with DGPS, and retrieved at the end of the day with the time series of water temperature over the flight duration. They were installed approximately 5 cm below the water surface with the aid of a metallic stack located in the river thalweg, and recorded temperatures at 10 min intervals. The logger located further downstream each day was left in the river for the next day survey to enable modeling of temperatures at all logger locations.

We used two drones (Phantom 4 Pro and DJI Inspire 1 Pro of DJI) to collect close-to-nadir optical and TIR imagery simultaneously. Phantom 4 Pro was used to carry a Zenmuse X5 RGB camera to acquire optical photos; and Inspire 1 Pro a Zenmuse XT-Radiometric thermal camera (640 × 512 pixels), with 13 mm wide lenses, for TIR imagery acquisition. We used 23 bases along the surveyed length from which we took off a total of 49 paired flights. Flights were carried out between 12:00 and 14:00 h each day, when the sun reaches its highest position, to allow higher air-water thermal contrast and less shading effect (Dugdale et al., 2015). Some earlier (11:00 h) and later (15:30 h) flights were taken to maximize the daily flight time. They were considered suitable for the detection of thermal differences as continuous logging devices revealed minimum changes in stream temperature within these time thresholds. Besides, *in situ* imagery checks revealed no major differences in stream temperature between these and later or earlier flights. At each base, two professional drone pilots carried out the flights. The use of professional drone pilots was required to comply with the strict Civil Aviation Safety Authority (CASA) regulations in Australia, given that the total drone payload was over 2 kg and the survey areas were public land. The drones flew at a maximum altitude of 120 m above the ground at a speed of 4 m s^{-1} collecting images during both the outward and return flights, allowing

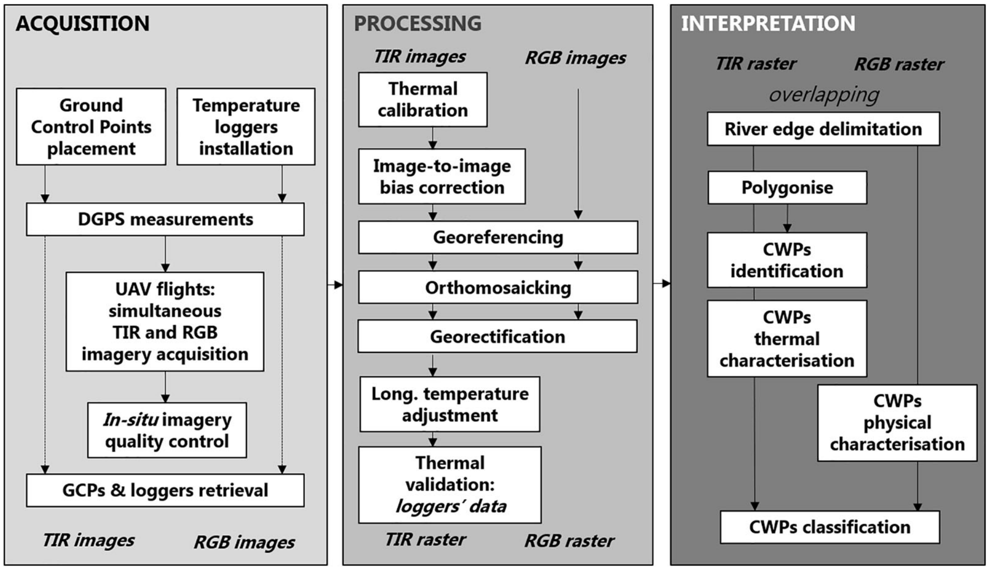

FIGURE 2 | Diagram of the methodological approach for UAV-based TIR and optical (RGB) imagery data acquisition, processing, and interpretation.

80% longitudinal and 60% transversal overlap between adjacent images along and across the river, respectively. The average time of each flight was approximately 5 min covering an average of 990 m river. The UAV flights were carefully planned in advance, and as a safety precaution, the urban areas of Bright and Porepunkah had to be excluded from the survey (**Figure 1**).

To enable thermal calibration, at least three thermal references were deployed and measured at each base. They consisted of two hot references made of black rubber (6 mm thick; R1 and R2 in **Figure 3**) whose temperature was measured using a digital infrared thermometer gun (TN410LCE, ZyTemp, Radiant Innovation Inc., HsinChu, Taiwan), and one cold reference made of a white foam container filled with cooled water (W, **Figure 3**) measured via a YSI® ProDSS handheld multiparameter unit. The radiometric temperature from the TIR thermometer gun was calibrated in the lab using an active blackbody target to yield equivalent physical temperature of targets. When possible, additional river water temperatures (WT1, WT2, WT3, **Figure 3**) were measured to use as additional references for the calibration. All thermal reference measurements were taken both at the beginning and end of each flight to account for any temperature changes during the flight.

After each flight, each set of R-JPEG format TIR and RGB images were quickly mosaicked *in situ* and quality-checked using the Pix4D® (Pix4D, Lausanne, Switzerland) software (**Figure 2**). For low-quality results, the flights were repeated. Final imagery data was safely stored and organized by type (RGB or TIR), downstream order, day and flight number.

Processing

For the initial thermal calibration, we used the ResearchIR Max® software to convert brightness readings (in mV) from the raw images (R-JPEG format) to temperatures. We took the first image from the base of each TIR flight (**Figure 2**) and compared it to the ground-truth data (hot, cold, and river ground calibration targets, **Figure 3**) to fit a linear model to the brightness *vs.* temperature (all resulting R^2-values were between 0.9 and 1, **Figure 3**). Assuming no change in temperatures during the duration of the flight, the linear model was applied to the subsequent images of the flight in Matlab®. In practice, however, thermal correction of the calibrated images was required where image-level temperature drifting was detected. Image-level temperature drifting is frequently observed for uncooled TIR detectors due to the variable conversion parameters from the raw power values to the temperature output (Ribeiro-Gomes et al., 2017; Dugdale et al., 2019). We corrected image-to-image temperature bias using a Partially Overlapped Histogram Equalization or POHE (Drusch et al., 2005; Su and Ryu, 2015) adapted to TIR imagery processing. POHE removed image-to-image bias from a reference image by equalizing histograms over their overlapping part. We corrected individual images against the reference images that contained the ground thermal targets by matching histograms of the pixel-level brightness in the image overlaps. The thermal reference image was usually the first or the last photo taken at each flight, and we used it to correct all successive images within. Despite showing some loss in pixel resolution, the correction successfully removed the image-level thermal drifting without changing the temperature variation (**Figure 3**).

Following image-level correction, we used the Pix4D® software to orthomosaick individual images of each flight into 49 of each optical (RGB) and TIR raster tiles. Initial orthomosaicking was based on the imagery onboard GPS data. We used more accurate DGPS locations of the GCPs for georectification to ensure correct overlapping between RGB and TIR raster imagery (**Figure 2**).

Although the timeseries of stream temperature measured by loggers indicated very low temperature changes within the flight

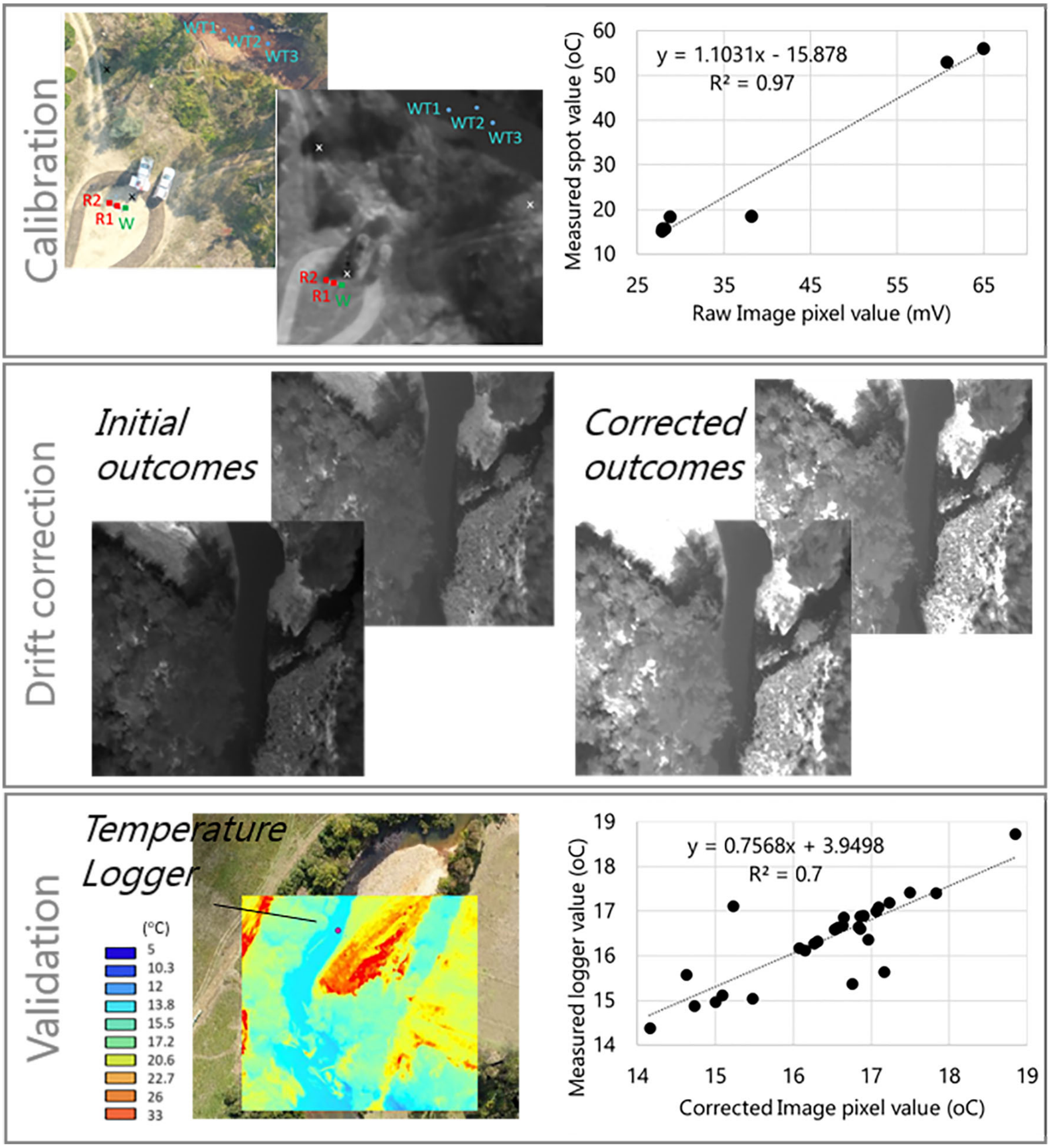

FIGURE 3 | Illustration of the ground thermal calibration targets used in one of the flights as an input to the linear model for TIR imagery thermal calibration (top), outputs of the thermal drift correction (middle), and example of one of the temperature logger location (bottom, left) used as one of the inputs for the final thermal validation (bottom, right).

time windows, the potential temporal temperature variation was adjusted to enable the spatial assessment of stream temperature patterns along the river length. The stream temperature logger data on 5 April 2017 at 12:10 h (middle of the survey) was used as the reference to convert TIR imagery collected over the duration of the survey to a temporal-variation-removed image that is equivalent to a snapshot at the reference time. We assumed that the distribution and size of CWPs between the start and the end of the survey time windows remained invariant. We applied a simple linear adjustment to each entire raster based on the data available from the loggers and the pixel values of their location. Thirty-one logger data points (**Figure 3**) could be used and were visible for approximately 40 TIR raster images (between 1 and 3 loggers per raster, with several loggers visible over two rasters). For those raster imagery with no visible logger data, we used the corrected overlapping imagery from the previous flight to correct the raster. The linear adjustment was done using ArcGIS® 10.4 (Esri) software.

For thermal validation, we used the corrected thermal imagery data prior to adjustment. Temperature values recorded from loggers at the time of imagery acquisition with the corrected pixel values (average 4–6 pixels) of their location within each TIR tiles. The comparison between logger value and corrected pixel data resulted in $R^2 = 0.7$ (**Figure 3**).

Data Interpretation

Visibility of the Upper Ovens river was possible for the totality of the waterbody in most reaches, given the openness of the channel. Only along the lower reaches, where more constrained channels were partially covered by overhanging vegetation, visibility was still possible for more than three-quarters of the water body. The high matching overlap between both TIR and optical imagery sets allowed the delimitation of the river edge (or visible water pixels). We used optical imagery to draw the edge, and we then applied such delimitation to the TIR raster, so that the terrestrial area could be cut out and only riverine water temperature visible (**Figure 2**). Each riverine TIR raster was then polygonized into groups of temperature pixels rounded to the closest whole number to achieve an adequate clustering.

We considered the available range of thresholds to identify CWPs in the literature from 2 to 3°C (Ebersole et al., 2001; U.S. Environmental Protection Agency, 2003; Torgersen and Ebersole, 2012) to 0.5°C (Dugdale et al., 2013; Monk et al., 2013; Wawrzyniak et al., 2016; Fullerton et al., 2018) difference with the main channel temperature. After some preliminary testing on data coherence, we selected the polygons presenting variations in temperature higher than 1°C between the minimum temperatures in the CWPs and the mean stream temperature, and we only included polygons >1 m^2. We visually checked the optical imagery for each of the identified CWPs and removed artifacts or non-true water patches (e.g., shade on the edge of the gravel).

We obtained the minimum temperature for each CWPs by overlapping the identified polygons to their corresponding corrected TIR raster tile and extracting pixel values statistics (CWPs thermal characterization). We calculated mean stream water temperature by extracting pixel point values at 50 m intervals along the river thalweg from the corrected TIR raster tile. We then averaged the extracted temperature values (between 12 and 20 data points) for each tile.

CWPs were classified into five types based on several existing classifications (Ebersole et al., 2003a; Torgersen and Ebersole, 2012; Dugdale et al., 2013; Kurylyk et al., 2014). They included deep pools, tributaries, cold side channels, emergent hyporheic water, and shading (**Figure 4**). Tributary plumes are generated by cold tributaries joining the (warmer) main river channel. Cold side channels are lateral channels that usually emerge from seasonally scoured flood channels. Emergent hyporheic water results from the resurgence of hyporheic flow from the streambed, and it is generally detected at the downstream ends of gravel bars, mid-channel islands, or in sequence with pool-riffle bedforms (Wawrzyniak et al., 2016). Although deep pools are usually formed as a result of stratification, their presence in the Upper Ovens were most likely linked to hyporheic water emerging in pool-riffle sequences, but we did

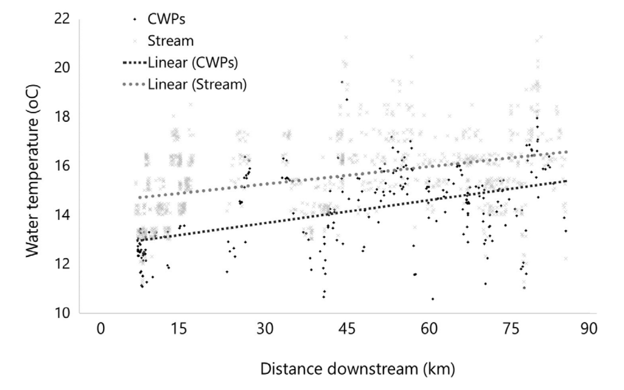

FIGURE 4 | Longitudinal changes in mean stream water temperatures and minimum CWPs temperatures. Note the clusters of no data in the graph reflect the urban areas of Bright and Porepunkah, where no data could be collected, due to flight safety restrictions.

not differentiate between the two. In the case of shading, we considered shading was the sole driver of CWP when the CWP delimitation had the same shape and extent of the visible shading in the RGB image. In addition, we considered shade as a potentially added effect promoting other types of CWPs when shade was observed but differed from the extent and shape of the CWP.

The classification of CWPs helped interpret the potential origin of the cooler water and allowed comparisons to similar studies. We used QGIS (QGIS Development Team, 2019) to enable the visualization of the selected CWP over the optical imagery, so we classified CWPs based on their definition and characterized all key physical attributes associated with each CWP. The exercise was carried out by the same person throughout the whole dataset to minimize its subjectivity.

Associations of CWPs With Physical Controls at Multiple Spatial Scales

A total of 17 physical controls potentially influencing the distribution of CWPs in the Upper Ovens at multiple spatial scales were investigated, including a suite of geomorphological variables and metrics, channel characteristics, riparian vegetation types, land use, and geology (**Table 1**).

At the patch scale (within each CWP), physical controls were characterized using optical (RGB) imagery data. They included the area occupied by each CWP (polygon area in m^2); dominant substrate type within the CWPs (gravel, silt, bedrock) and CWPs depth (shallow, mid-depth, deep), both visible thanks to low flows and clear water conditions. At the reach scale (~50–500 m), surrounding each CWP, the following qualitative and quantitative information was extracted from optical imagery: channel type (cascade, plane-bed, and pool-riffle, Montgomery and Buffington, 1998); number of channels (single, wandering, braided); sinuosity (straight, low, sinuous); mesohabitat type (pool, run, riffle); channel width (in m); and the CWPs placement and occupation in the channel (right bank, left bank, middle of channel, whole channel occupation). In

TABLE 1 | Multi-spatial physical controls of cold-water patches considered.

Variable	Categories/range	Scale
Area	2–3313 m^2	*Patch*
Depth	Shallow, mid-depth, deep	
Substrate	Gravel, silt, bedrock	
Channel type	Cascade, plane-bed, pool-riffle	
Number of channels	Single, wandering, braided	
Sinuosity	Straight, low sinuosity, sinuous	
Mesohabitat	Pool, run, riffle	
Channel width	3–80 m	
Channel placement	Right bank, left bank, middle of channel, whole channel occupation	
Geomorphic feature	Dead wood, eroding bank, gravel bar, none	*Reach*
Shading	None, minimal, low, medium, high, total	*Riparian corridor*
Riparian vegetation type	None, not overhanging, overhanging	
Riparian vegetation strip width	0–174 m	
Downstream distance location	34.9–90079.4 m	*River length*
Geology	Nal, Oap, Qal, Qcl	*Catchment*
Land use	Forestry plantation, farmland, urban, dryland, swamp, remnant native vegetation	

addition, any key geomorphic feature located within or nearby each CWPs (gravel bar, eroding bank, dead wood, none) were recorded. Physical controls at the riparian corridor scale (along the river) were characterized based on the information provided by optical imagery. The riparian vegetation strip width (ranging from 0 to 174 m) was measured; and the riparian vegetation type was classified for each bank into combinations of *none*, *not overhanging* and *overhanging vegetation*, represented by numerical levels from 1 to 6 (e.g., *none in either banks* = 1, *overhanging vegetation in both banks* = 6). In addition, we considered important to characterize the degree of shading present at each CWP at the time of the flight to account for a potential combination of cooling effects. Shading was characterized into six categories including *total* for 81–100% of CWP area occupied by shade, *high* for 61–80% shade occupation, *medium* for 41–60%, *low* for 21–40%, *minimal* for 11–20%, and *none*, for 0–10%. At the river-length scale, the downstream distance location of each CWP was calculated by computing the cumulative linear distance between successive CWPs. At the catchment scale (∼50–100 km), both geology and the surrounding land use were considered catchment controls. Geology information was extracted from the GIS layers provided by the Victorian State Government. It included four main groups: Quaternary non-marine colluvial (Qc1) and alluvial (Qa1) sedimentary rocks, Ordovician marine sedimentary rock (Oap), and Neogene non-marine alluvial sedimentary rock (Na2). Land use was characterized for each of the banks based on optical imagery. To simplify the long list of classes from the original classification, we grouped them into two main groups: anthropogenic (forestry plantation, farmland, urban, industrial) and natural (dryland, swamp, remnant native vegetation). When one of each group was present at each of the banks surrounding the CWPs, a third group (mixed) was assigned (**Table 1**).

To assess the relationship between the above mentioned physical controls and CWPs, we used a general linear model approach (with normal -Gaussian- errors) using the function glm() in R (R Core Team, 2019). To enable relative comparisons, we used the difference between the mean stream temperature and the minimum temperature of each selected CWP as the response variable. Histograms of the temperature difference suggested a weak right skew, so the response variable was square-root transformed.

The 17 predictor factors (**Table 1**) consisted of 5 continuous and 12 categorical variables. Of the categorical variables, we treated those with no ordered relationship as factors in the analysis. Categorical variables with a clearly ordered relationship (e.g., high, medium, low) were coded in the analysis as numeric variables representing their ranked order. Scatterplots of temperature difference against the ordered categories showed that any associations were monotonic (i.e., decreasing, increasing level), so we considered a regression on the ranked order to represent the underlying association. We examined continuous variables for normality and collinearity. Distance downstream was weakly positively skewed and was centralized by a square root transformation. Area was also positively skewed, and a log transformation centralized its distribution. A combination of variance inflation factors (VIF) and bivariate scatterplots was used to assess collinearity between numeric variables. With all VIFs < 5, no evidence of collinearity was found. Linear dependence in the categorical regressors was evaluated by examining the model parameterization via the alias() function in R, which found no evidence of dependence between categorical factors and levels.

We calculated an initial linear model of temperature difference against all the hypothesized predictor variables. Initial diagnostics showed that a standard linear model with normal errors was appropriate. Many predictors did not contribute to the analysis, so we reduced the model using a full-stepwise regression with the MASS:stepAIC() function in R. The stepAIC() function uses Akaike's Information Criterion to compare competing models and penalizes models for numbers of variables retained. Automated stepwise approaches are not guaranteed to find the most appropriate model, so we examined the entry and exits of variables in the model and explored alternative models in a structured approach. Extensive examination of alternatives showed that stepwise selection retained a consistent set of reliable predictors. Analytical assumptions of the final model were assessed graphically by plots of residuals *vs.* expected values, and normality residuals. We found no critical deviations from analytical assumptions. The effects of the variables in the model were assessed for significance with a threshold of 0.05.

RESULTS

Spatial Patterns of CWPs

A total of 264 CWPs were identified along the 50 km stretch (ca. 95 km in total river length) of the Upper River. CWPs showed highly variable minimum temperatures ranging from 10.5 to 19.4°C along the river length, with relatively lower temperatures compared to mean stream temperature (12.5–19.6°C). Despite high local variability, both CWPs and mean stream temperature showed an increasing trend with downstream distance estimated in 0.14 and 0.17°C per linear kilometer (**Figure 4**).

Classification based on optical imagery was possible for 260 of the CWPs. Of those, 130 were classified as emergent hyporheic waters, 74 as deep pools, 41 as shading, 11 as side channels, and 4 as tributaries (**Figure 5**). CWPs promoted thermal differences that ranged between 0.15 and 5°C (based on the pixel data extracted post CWP identification) when compared to the mean stream temperature. Mean thermal differences changed notably depending on the CWPs type, with tributary being the highest and emergent hyporheic water the lowest (**Figure 6**).

CWPs were non-uniformly distributed along the ca 95 km Upper Ovens River length (**Figure 7**). As with CWPs numbers, the total area occupation by CWPs was higher for emergent hyporheic water types (48,377 m^2), followed by deep pools (27,671 m^2), shading (16,961 m^2), side channels (4,325 m^2), and tributaries (632 m^2). Individual CWPs presented a broad range or area size, but shading types showed the highest average (4,134 m^2), closely followed by side channels (3,934 m^2), deep pools (374 m^2) and emergent hyporheic water (3,724 m^2); and tributary types being again the lowest (158 m^2). In terms of relative abundance, the number of emergent hyporheic water CWPs decreased, while deep pools, shading, and tributaries showed an increase with downstream distance (**Figure 7**).

Most side channels, emergent hyporheic water, and tributaries were associated with gravel bars (91, 77, and 67%, respectively). To a lower degree, deep pools were also associated with gravel bars (42%), and with dead wood (27% of occasions). In contrast, shading was not associated with any geomorphic feature in most cases (63%).

Key Physical Controls Influencing Thermal Differences Promoted by CWPs

An initial variable assessment excluded channel type from the model analysis as it did not show any significant association, possibly because pool-riffle type dominated in all except a few samples. The remaining variables were progressively excluded to achieve the best performing model.

The relative thermal difference promoted by CWPs changed with their channel location, riparian vegetation level or type, area, distance from the source, and land use (**Table 2**). The standardized regression coefficients enable comparison of relative strengths of each numeric factor. The area of the CWP had the most considerable effect of the continuous variables, with the relative thermal difference promoted by CWP increasing with their area. The magnitude of this difference was in the order of 2°C from the smallest (bottom five, 2–3 m^2) to the largest (top five, 2,700–3,317 m^2) patches (**Figure 8A**). Temperature differences were greater in higher levels of riparian vegetation (e.g., with overhanging vegetation in both banks). Average temperature differences from the least to the most vegetated were in the order of 1°C. However, the spread of values and extremes of the differences ranged up to 5°C in areas with dominating overhanging vegetation (**Figure 8B**). In contrast, relative temperature differences – after taking other factors into account – were lower than expected with increased

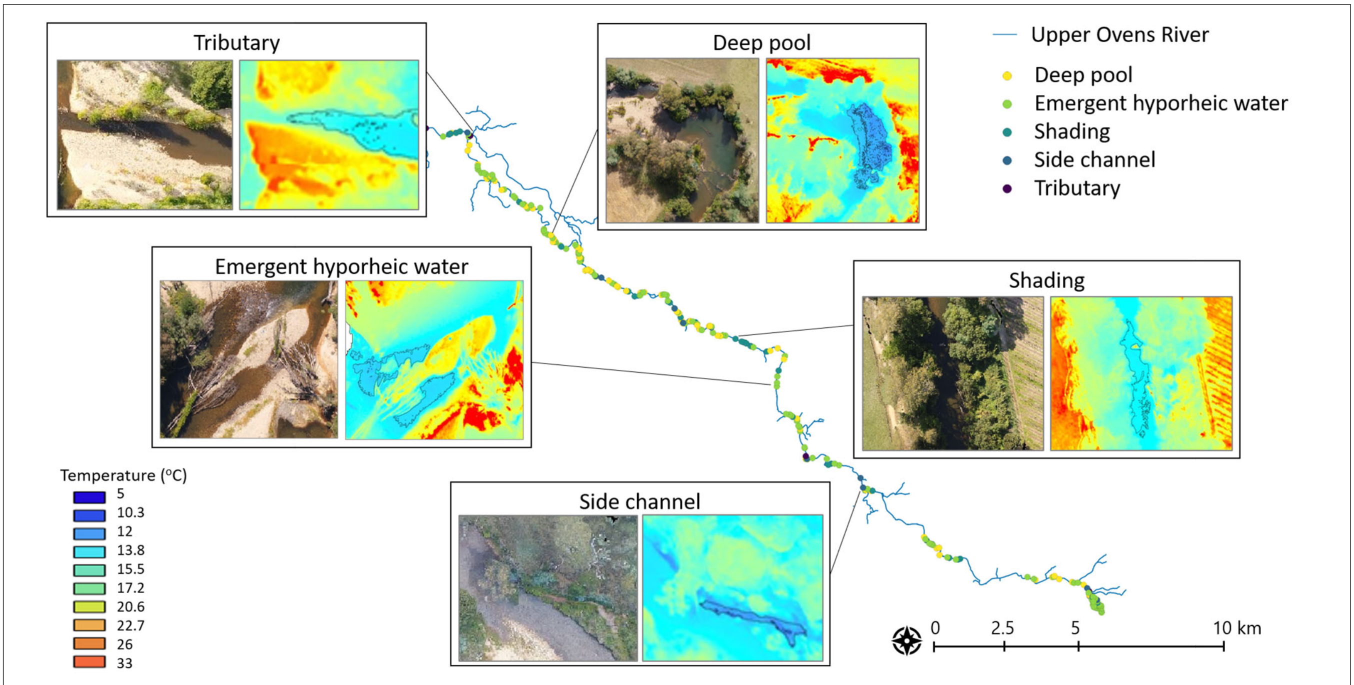

FIGURE 5 | Illustrations of examples for each of the four CWPs types identified, and their locations, along the Upper Ovens River.

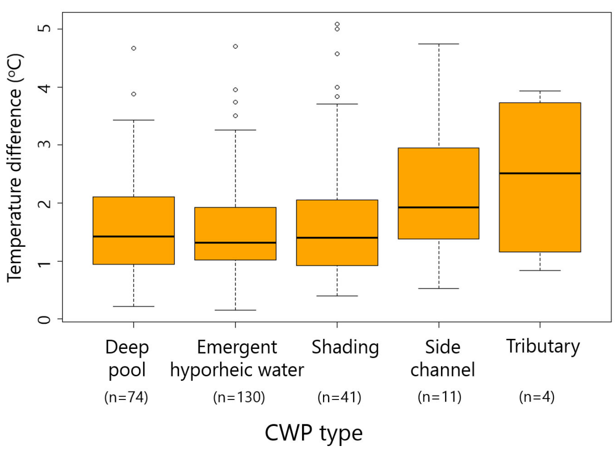

FIGURE 6 | Range of temperature differences promoted by each CWP type in relation to the main channel average temperature. Note that n refers to the number of data points for each CWP type.

distance away from the source (**Figure 8C**). This effect was relatively weak, however.

Channel placement had a weak but significant effect on temperature difference promoted by CWPs (**Table 2**). Differences in temperature promoted by CWPs that occupied the whole channel were similar to those CWPs located in the right bank. Both were higher than those that were in the middle of the channel and left bank, respectively (**Figure 8D**). Model outputs suggest that land use had a marginal effect on the overall analysis, with a p-value just above the minimum 0.05 significance threshold. However, an apparent effect was evident between land use levels (**Figure 8E**). Temperature differences promoted by CWPs increased with the degree of anthropogenic changes to the landscape, with a maximum range of 5°C in the most modified areas. The range of such thermal differences was narrower or more similar within *Natural* land use types. In contrast, the thermal range was broader, or more variable, within *Anthropogenic* land use types (**Figure 8E**).

DISCUSSION

Challenges and Opportunities of the Methodological Approach

We used simultaneous UAV flights to acquire and generate 95 km river length of georeferenced high-resolution TIR and optical orthomosaicked imagery sets, distributed into 49 raster tiles. With these data, it was possible to identify riverscape spatial patterns of temperature and CWPs, and to detect, characterize, classify, and compare discrete CWPs.

The survey in the Ovens river was carried out during the lowest flow period with water still running through, allowing for full hydraulic mixing. In addition, spot temperature measurements in selected accessible deep pools showed almost identical temperatures across the water column (see more details in Casas-Mulet, 2018). Based on these, we assumed no thermal stratification and considered that the caption of surface water temperatures could be used as a representative measurement across the whole water depth. Given the high groundwater dominance in the system, we acknowledge, however, that other methods may be most appropriate for the purposes of direct measurements of groundwater inflow locally (e.g., Gaona et al., 2019). The assessment of river-length scale longitudinal stream temperature patterns can only be realized using absolute values (Loheide and Gorelick, 2006; Wawrzyniak et al., 2013). In this study, this was possible based on the assumption that minimal changes in thermal heterogeneity composition occurred between and within the daily time window of TIR data acquisition. We considered it a reasonable assumption since we carried out all UAV flights during constant low flows on five consecutive days of near-identical climatic conditions, using the same equipment throughout the survey. Minimal changes in stream temperature during the surveying period, confirmed by continuous logging temperature data, also support the assumption. However, to enable comparable interpretations of the outcomes without having to rely on assumptions, the identification of CWPs was based on relative thermal values, taking mean stream temperature as a reference.

Low flows in the Upper Ovens promoted high thermal contrasts between surface and groundwater that enabled the detection of CWPs. The use of adequate cameras and relatively low altitude (sufficient to visualize land features to allow orthomosaicking) drone flights produced high-resolution on-ground pixel size imagery. The ground sample (pixel) distance, or GSD, was approximately 0.1 m for TIR, and 0.05 m for optical (RGB) imagery. Such resolutions greatly aided the detection and identification of CWPs. Low-velocity flights ensured clear color contrast within images and allowed high imagery overlap, both reducing the risks of failure in photogrammetric orthomosaicking reported in Ribeiro-Gomes et al. (2017). High-quality imagery also supported the physical characterization and classification of CWPs. It provided a clear visualization of the river bottom to qualitatively differentiate physical characteristics such as depth and substrate, to identify key geomorphic features such as dead wood and fallen trees, and to assess the degree of shade within all CWPs types.

The delineation of water pixels can be achieved using TIR when water temperature values are within a different range from the surrounding land. Since this was not the case in this study, we took the co-registered TIR and RGB images and used RGB imagery to delineate the river boundaries manually. Given the high matching overlap between both imagery sets, this approach was considered suitable to help identify CWPs polygons. However, the inclusion of co-registered multispectral (VISNIR)-TIR imagery (e.g., Turner et al., 2014) should be considered in future studies to accurately delineate true-water pixels through automatic detection.

The linear models used for TIR calibration were based on *in situ* ground data (hot, cold, and river water thermal references) taken simultaneously during the flights and implemented consistently throughout the dataset. The linear models provided satisfactory outcomes with high R-square values and accurate TIR imagery. High R-square numbers from a small number

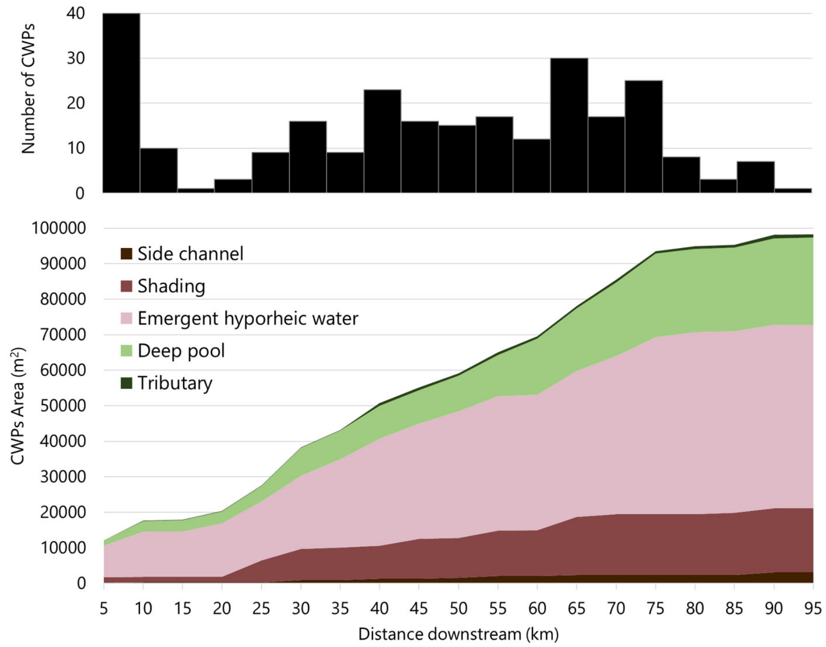

FIGURE 7 | Distribution of CWP numbers (top) and cumulative distribution of CWP types by occupied area (bottom) along the Upper Ovens River.

TABLE 2 | Outputs of the general linear model of the relationship between thermal differences promoted by CWPs (square-root transformed) and hypothesized predictions.

	Regression coefficients			ANOVA			*p*-values
	Estimate	**SE**	***t*-value**	**SS**	**DF**	**F**	
(Intercept)	−0.978	0.332	−2.940				0.004**
CWP area	0.414	0.051	5.740	4.949	1	45.410	<0.001***
CWP channel placement				0.9S5	3	3.012	0.031*
Whole channel occupation	*0.000*						
Middle of the channel	*0.271*	*0.262*	*1.030*				*0.302*
Left bank	*0.260*	*0.276*	*0.940*				*0.347*
Right bank	*0.579*	*0.262*	*2.210*				*0.028**
Downstream distance	−0.259	0.132	−1.960	0.417	1	3.330	0.051
Riparian vegetation type	0.193	0.074	2.500	0.734	1	6.739	0.010**
Land use				0.503	2	2.792	0.053
Natural	*0.000*						
Mixed	*0.445*	*0.255*	*1.750*				*0.082.*
Anthropogenic	*0.715*	*0.320*	*2.230*				*0.027**

*The reduced model was selected by stepwise selection using Akaike's information criterion. The right-hand side of the table presents the ANOVA tests for the factors. The left-hand side presents the parameter estimates. The plain font in the parameter estimates represents the parameter estimate for continuous predictors variables, whereas the italic font represents parameter estimates within levels of a categorical predictor. Regression parameter estimates are standardized coefficients to enable comparison between variables measured on different scales. The plain font of the p-values corresponds with significance of factors in the model, and the italic font corresponds to parameter tests of levels within factors. Estimate, standardized parameter estimate; SE, standard error; t-value, t-test of whether the parameter estimate is 0; SS, ANOVA Sums of Squares; DF, degrees of freedom; F, ANOVA test statistic. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.*

of data points needs to be interpreted with caution, however, this is a common limitation in remote sensing, particularly when data collection needs to be completed within a very short time window. Our calibration approach can be compared to the reportedly improved accuracy calibration based on *in situ* data in Wawrzyniak et al. (2013), only that the use of different media/material for cold (water) *vs.* hot (rubber) targets, whose temperature were measured using various measurement equipment, might have caused errors originating from varying emissivity between the targets and different nature of radiometric and thermo-couple-based sensors. Ideally, multiple calibration targets that have emissivity values close to the primary survey target (e.g., water in this case) should be used, despite the potential logistical inconveniences.

Almost all calibrated TIR imagery presented some thermal drift that required further correction, a common issue for

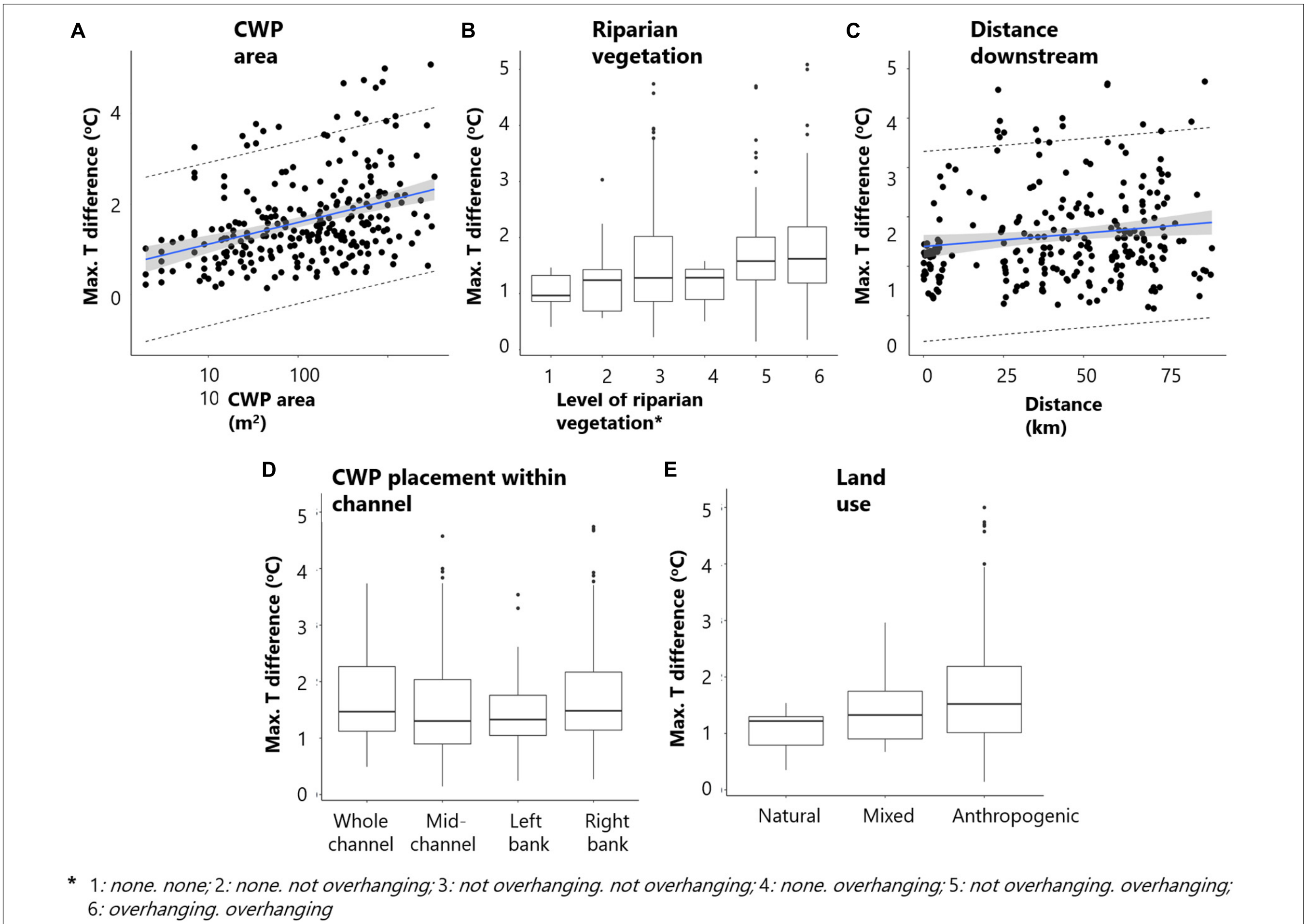

FIGURE 8 | Key variables influencing the maximum thermal difference promoted by CWPs, according to the final selected model. They include CWP area **(A)**, Riparian vegetation **(B)**, distance downstream **(C)**, CWP placement within channel **(D)**, and land use **(E)**.

uncooled bolometer, and reported in Dugdale et al. (2019) and Ribeiro-Gomes et al. (2017). The partially overlapped histogram equalization (POHE) approach used in this study provides a trade-off solution between removing thermal drifting with resulting unchanged actual temperature values and the loss of pixel resolution. The loss of pixel resolution may produce issues in detecting GCPs when orthomosaicking in the photogrammetric process (Ribeiro-Gomes et al., 2017), however, in this study, this was not an issue, as a result of the high-resolution imagery acquired originally. Besides, TIR validation using temperature logger data suggest satisfactory results, albeit the difficulty of processing such an extensive dataset.

Despite the limitations of currently available UAV-based imagery acquisition devices described in Dugdale et al. (2019), this study demonstrated that with the adequate data acquisition, processing, and interpretation approaches, a reliable assessment of river-length patterns of CWPs could be achieved. Overall, the methodological approach described in this study enabled the exploration of CWPs distribution and supported the development of a preliminary model to investigate patterns of potential thermal refuges at multiple spatial scales, contributing to a better understanding of stream thermal heterogeneity drivers (Webb et al., 2008; Monk et al., 2013). This study also provides an opportunity to explore the potential of integrated UAV-TIR systems to assess CWPs patterns across rivescapes.

Spatial Patterns and Controls of CWPs

The non-homogeneous distribution of CWPs aligns with the study of Wawrzyniak et al. (2016) in the Ain River, of comparable dimensions and total CWPs area occupation. The dominance of emergent hyporheic water CWPs seems consistent with the expected groundwater inputs in a gaining system as the Upper Ovens (Yu et al., 2013). Higher thermal differences in tributary CWPs suggest that air-water or altitude-controlled processes may provide cooler waters, either due to the higher shading in such narrower streams (Monk et al., 2013) or their steepness (Webb et al., 2008; Dugdale et al., 2015).

The outputs of the general linear model illustrate a combination of five key physical controls associated with thermal differences in CWPs at multiple spatial scales. They include catchment-scale land use, type of riparian vegetation along the river corridor, downstream distance, reach-scale CWP channel placement, and patch-scale CWP area. While we acknowledge that the model assigns similar larger scale physical controls to different CWPs (e.g., same catchment control > 1 km^2, over several CWPs < 1 m^2), this approach is based on a thorough assessment of the importance of the control variables and their influences at different spatial scales. Surprisingly, the presence of geomorphic features at the reach scale did not appear to be a key driving factor of CWPs in our modeling, despite evidence of individual associations between gravel bars and emergent hyporheic water CWPs types, as per in Wawrzyniak et al. (2016). However, our modeling approach did not target specific CWPs types; it instead aimed at providing an overall view of driving factors; therefore, the data resolution could have played a role in the analysis.

According to the model outcomes, *Anthropogenic* land use types seem to promote cooler CWPs. However, in the Upper Ovens, the effects of land use cannot be interpreted without considering its links to both the riparian corridor (LeBlanc et al., 1997; Allan, 2004) and distance downstream. The upper reaches were dominated by natural open riparian forests surrounding multiple-channel braided and wandering reaches with limited shading. In contrast, the lower reaches were surrounded by anthropogenic land use (e.g., arable land) and presented more constrained channels with narrow, but heavily overhanging shading riparian vegetation. Such a local shading effect in the downstream reaches could potentially have increased thermal differences between the river and any type of CWPs, as opposed to the upstream reaches. At the reach scale, the slightly greater cooling effect on the right *vs.* left bank could reflect the river east-west flow direction, with less sun exposure and increased shading on the right (north-looking). Based on these, it is counterintuitive that the model did not consider shading as an important physical control. We can only assume that the complex physical structure in the Upper Ovens River, combined with the surveying timings and locations played a role, resulting in shading not being strong enough to dent all the other factors, and therefore not represented in the model outcome. At the patch-scale, thermal differences promoted by CWPs increase with the CWPs area. The spatial variation in groundwater influx can likely explain the lack of homogeneous longitudinal patterns in CWPs areas. Patch-scale CWPs area could be interpreted as the local manifestations of larger-scale patterns. Groundwater influxes were variable along the Upper Ovens length, with peaks in the upper and middle reaches (Bright and Porepunkah), as indicated in Casas-Mulet (2018) and Yu et al. (2013). Historical anthropogenic activities could have further influenced such variations (e.g., river dredging, Sinclair Knight Merz, 2007; Yu et al., 2013) by modifying the groundwater inputs mechanisms. For example fine sediment accumulation in the riverbed gravels over time (Casas-Mulet et al., 2017; Auerswald and Geist, 2018; Wilkes et al., 2019) could have clogged the gravels and decrease the amount of emergent hyporheic flow (Poole et al., 2006; Arrigoni et al., 2008). Consequently, the methodological approach described here may also be useful when it comes to assess the effects of river management actions on the distribution and persistence of CWPs, such as streambed restoration actions or groundwater extraction restrictions.

The outcomes of this study illustrate the influence of several multi-spatial scale physical controls on CWPs that had not been assessed in conjunction before. Future works should focus on integrating ecological processes into spatio-temporal riverscape patterns, so the true thermal refugia potential of CWPs is understood.

Applications in Freshwater Conservation and Management

In Australia, an increased recurrence of drought conditions will intensify cease-to-flow events and potentially lower groundwater levels (CSIRO and Bureau of Meteorology (BOM), 2007; IPCC, 2012). Although extreme events are crucial elements of the natural variability shaping the ecology of rivers that enable freshwater organisms recovering from disturbances, intensified pressures could hinder the capacity of communities to persist (Leigh et al., 2015). In addition, anthropogenic threats such as the increasing demands of water retention, diversion and extraction for agricultural irrigation (Pratchett et al., 2011; van Dijk et al., 2013) put increasing pressure on freshwater habitats, lessening the potential resilience of aquatic organisms (Kohen, 2011; Leigh et al., 2015).

Associated effects of increased stream temperature include reduced dissolved oxygen and can result in the physiological tolerance of some species being exceeded (e.g., McNeil and Closs, 2007). Increased stream temperatures may also affect development, growth rates, reproduction, and behavior of organisms. These could favor species with wider thermal windows (Pörtner and Farrell, 2008), or promote the establishment of and spread alien species of fish when coupled with other stressors such as the reduction in discharge (Morrongiello et al., 2011). The availability of CWPs may buffer the effects of extreme events and prevent pushing some ecological processes beyond critical thresholds, protecting species persistence, and maintaining ecosystem functioning (Leigh et al., 2015).

The identification of CWPs is, therefore, the first step toward their conservation and sustainable management (Kurylyk et al., 2014; Geist, 2015). Predictions of CWPs locations and distribution can help prioritize river restoration measures such as targeted riparian vegetation planting to increase shading (Ebersole et al., 2015; Morelli et al., 2016; Fullerton et al., 2018), or in-stream habitat restoration (Gilvear et al., 2013; Pander et al., 2018) with a focus on promoting hyporheic upwelling (Boulton et al., 2010; Pander et al., 2015). Identification and prioritization of the most effective ways of conserving or restoring CWPs also greatly benefit from an evidence-based management approach (Geist and Hawkins, 2016) that requires comparison with baseline data. The identification of water quality thresholds will be required to inform water-allocation decision making (Goulburn Murray Water, 2011) and to manage and protect surface and subsurface induced CWPs. Identifying the factors that give alien species competitive advantages or disadvantages over native species will be key requirements for managing CWPs under climate change. In particular, it will be essential to consider that some aliens will benefit from warmer temperatures, whereas others will be detrimentally affected (e.g., Costelloe et al., 2010).

Further work is needed, building on this and other exploratory studies, to develop tools to predict the distribution of potential thermal refugia at the riverscape, which will be critical to inform long-term measures that maintain resilient thermal landscapes (Bond et al., 2008; Monk et al., 2013; Fullerton et al., 2018). A better understanding of the spatio-temporal extent over which promoting stream thermal refugia can be an effective adaptation tool is required (Morrongiello et al., 2011), and it will enable its integration into legislation and policy frameworks.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

RC-M designed the study, planned and supervised the fieldwork, and carried out the data processing and analysis in consultation with DR. RC-M, JG, and JP conceived the idea of the manuscript and wrote the manuscript in consultation with DR and MS. All authors read and approved the final version of the manuscript.

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Direct and Indirect Climate Change Impacts on Brown Trout in Central Europe: How Thermal Regimes Reinforce Physiological Stress and Support the Emergence of Diseases

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Water temperature is one of the most important abiotic parameters in rivers having direct and indirect effects on fish. Especially cold-water species like the brown trout (*Salmo trutta)* are limited by high temperatures. Beside direct physiological stress, higher water temperatures also reinforce the emergence of diseases. In this study we investigate thermal regimes of rivers based on a large-scale dataset covering Austria (~70,000 km²). The analyses aim to clarify to what extent water temperatures support the emergence of proliferative kidney disease (PKD) and assemble physiological stress for brown trout under current and future climate conditions. Data from 274 gauging stations at 184 rivers were used to calibrate a water temperature model and to investigate critical water temperature thresholds. Therefore, we developed a risk assessment scheme to identify river reaches that already have or will develop critical thermal regimes for brown trout in respect of PKD emergence and thermal physiological stress. The results revealed severe changes in the thermal regimes of the investigated rivers under climate change. Furthermore, the variable characterizing riparian vegetation played a vital role to explain cooling of the water in downstream direction. In respect of PKD, the amount of river reaches having unlikely outbreaks of PKD decreased from 72.6% under current conditions to 37.7% in the far future RCP8.5 scenario. Within small rivers that currently showed optimal thermal regimes over large extents (10,244 km), the habitat suitability will be reduced by combined effects of PKD and physiological stress to 6,554 km. In general, suitable habitats of *S. trutta* will shift upstream, thus to higher altitudes, and to smaller, alpine rivers in Austria. The warming leads to physiological stress that induces a diminished growth due to the non-positive transition of caloric values to growth as well as cardiac dysfunction in brown trout. These factors will further restrict the distribution of brown trout. However, the results also underline the enormous importance of the alpine region as a future refuge for brown trout in Central Europe. Thus, this study will help to inform managers to timely develop robust conservation strategies.

Keywords: river, *Salmo trutta*, water temperature, proliferative kidney disease, Alps, thermal niche

INTRODUCTION

Climate change represents a major driver of biodiversity change (Markovic et al., 2014). Riverine ecosystems are especially vulnerable to the impacts of climate change as warming strongly alters the habitat conditions of fish (Comte et al., 2013). Meanwhile, around 30% of the European freshwater fishes are recognized as susceptible to climate change (Jarić et al., 2019). However, most studies still focus solely on direct effects mediated by temperature increase although climate change and the associated warming will have indirect effects, such as a pronounced emergence of pathogens, too.

In aquatic ecosystems, water temperature is one of the most important abiotic parameters controlling life (Magnuson et al., 1979; Caissie, 2006). As fish are obligate poikilotherm animals, their body temperature and metabolism are regulated by the surrounding water. Fry (1971) described a 5-fold effect of temperature on fish. Besides the controlling and limiting factors of temperature that directly affect the fish, masking factors, are hardly addressed in the context of climate change impact yet. Most fish show preferences to certain temperature ranges that can be tolerated or not (Coutant, 1977). Especially cold-water species like the brown trout, *Salmo trutta* (Linnaeus 1758), are limited by high temperatures. Thus, brown trout are highly sensitive to climate change impacts as the thermal regimes of their habitats are affected by warming. Future scenarios predict a reduction of up to 64% of suitable stream reaches for brown trout in Europe till the 2080s (Filipe et al., 2013).

Besides direct thermal effects like physiological stress, higher water temperatures can also prompt masking and indirect effects on fish such as a more common emergence of specific diseases (Karvonen et al., 2010). Here, a weakened immune response (Bowden, 2008; Bettge et al., 2009a) and faster development of pathogens in warmer environments play a prominent role. The proliferative kidney disease (PKD) is a widespread parasitic disease that especially affects salmonid fish species. PKD can lead to the death of *S. trutta* affecting the wild populations in North America and Europe. Several studies highlighted declines in wild salmonid populations due to PKD (e.g., Sterud et al., 2007; Burkhardt-Holm, 2009). In Austria, PKD is a newly discovered but widespread disease (Gorgoglione et al., 2016; Lewisch et al., 2018; Waldner et al., 2019).

As PKD is strongly temperature-dependent climate change will probably enhance the further emergence of the disease (Okamura et al., 2011). Its emergence is related to the occurrence of prolonged periods of warmer water temperatures that support a faster growth of the Bryozoan host (Okamura et al., 2011). Thus, promoting the development of infections in Bryozoan colonies caused by the parasitic myxozoa *Tetracapsuloides bryosalmonae* (Tops et al., 2009), which is further leading to the clinical outbreak of PKD and mortality in brown trout (Bettge et al., 2009a).

Although much evidence exists on both, the physiological stress induced by water temperature increases and the temperature-dependency of PKD outbreaks in trout, from laboratory studies, less knowledge exists on water temperature related effects on trout populations in the wild. Physiologically, the upper thermal boundary for growth is at about 19.5°C for brown trout (Elliott and Elliott, 2010) due to the non-positive transition of caloric values to growth (Elliott, 1976). With increasing temperature, the energy needed for the metabolism (e.g., swimming and digestion) is exponentially increased as described by the van 't Hoff rule (Ege and Krogh, 1914). With further increasing temperature the physiologic response of the fish intensifies. Subsequently, the cardiac function of *S. trutta* is limited above 20.9°C consequently leading to disturbed cardiac rhythmicity. *In vivo* experiments showed that above 23.5°C, the heart rate gets critical up to heart arrest (Vornanen et al., 2014).

The thermal regimes of rivers are strongly related to atmospheric conditions and to energy input by solar radiation. Environmental factors changing the radiation inputs like shading effects of the terrain topography or the riparian vegetation, therefore affect water temperatures. Moreover, the volume of the water body (i.e., discharge, width, depth, and velocity) influences the daily amplitude of water temperature; for example, wide and shallow rivers heat faster than large rivers or small streams (Caissie, 2006). As the water temperature is highly linked to the same driving forces as air temperature, climate change will lead to further warming (Mohseni et al., 2003). Therefore, most river water temperature regression models rely on air temperature data, as they are linked to the same driving forces (Caissie, 2006).

Based on data from European rivers, Webb (1996) described an increase of +1°C in water temperatures in the last century (1901–1990). In the river Rhine, a 2°C-increase for the summer period was observed from 1978 to 2011 (ICPR, 2013). In the Danube and some of its Austrian tributaries, a temperature increase of about 0.3°C per decade since 1900 was observed (Dokulil, 2018).

Existing field-studies on PKD primarily focus on selected river systems or fish populations (e.g., Waldner et al., 2019). However, analyses on a larger spatial extent are needed to identify the actual and future risks related to PKD and physiological stress on *S. trutta* in general. Most studies address the importance of thermal regimes and climate change for the prevalence, outbreak and mortality of PKD but there is less knowledge about the spatial dimensions of the combined future effects.

We hypothesize that different thermal characteristics are relevant for PKD emergence and thermal stress in brown trout. We assume that both factors will increase with the progress of climate change. Accordingly, we address the following research questions: (1) Which parts of the river network feature a thermal regime supporting the emergence of PKD under current conditions? (2) Which parts of the river network feature a thermal regime supporting thermal stress for brown trout under current conditions? (3) How does the spatial distribution of both implications change under future climate conditions?

MATERIALS AND METHODS

Our analyses included data on water temperature, river characteristics (e.g., slope, catchment size, glaciated area, etc.), and climate covering an area of around 70,000 km² and a river network length of 23,819 km. The environmental information used in the analyses was backed up by evidence-based information from literature on the thermal preferences of *S. trutta* as well as temperature thresholds supporting the emergence and outbreak of PKD in trout.

Water Temperature Data

We used data from 274 river gauging stations in Austria that continuously record water temperature. This was available from the hydrographic services of the federal states (BMLFUW, 2017; **Figure 1**). The dataset for water temperature modeling included 1,831 WTQ95 values (95% quantile of daily mean water temperature in 1 year) from 184 rivers covering the years 2000–2011. This time period was used because of the overlay with a national climate dataset (Chimani et al., 2016).

A larger water temperature dataset covering the years 2000–2015 with 3,000 WTQ95 values from 336 river gauging stations of 221 rivers was used to analyze water temperature thresholds relevant for PKD and thermal stress.

Both datasets did not contain gauging stations from lakes, lake outflows, artificial channels, the Danube, sites above 1,500 m.a.s.l., sites with missing spatial data and sites with manual or not clearly determined water temperature measurement.

River Network and Investigation Segments

The national river network of Austria (BMLFUW, 2016) represented the spatial basis for the analyses on the river segment resolution. It covers all rivers with a catchment size larger than 10 km². We processed the river network in ArcGIS 10.4 (ESRI, 2016) to create regular 5 km ($n = 5{,}985$) reaches that represent the investigation segments. To consider the heterogeneity within the 5 km segments, we further queried all descriptors used in the modeling on basis of 1 km segments and summarized them for each 5 km segment. We excluded river segments with Strahler order <3 and an elevation above 1,500 m.a.s.l. from the dataset as the available water temperature data from the gauging stations did not sufficiently cover these areas.

For each segment, we queried Strahler order ("Strahler"), catchment size ("Catchment"), river slope ("Slope"), hillshade ("HillSha"), tree cover ("TreeDens"), and glaciated area in the catchment ("Glacier"). An overview of all parameters can be found in **Table 1**.

Strahler order for the Austrian river network according to Wimmer and Moog (1994) was available as a line shapefile. We queried Strahler order for each investigation segment. To consider river size effects relevant for the thermal regime, we classified the temperature gauging stations and the investigation segments into four groups covering small to large rivers. Accordingly, for each type, a regression model was calibrated.

The catchment size was calculated on the basis of the Austrian sub-catchments (Fürst and Hörhan, 2005). We located the midpoint of the investigation segments to the according sub-catchment. Then consequently the upstream sub-catchment area was summed up for each midpoint. Categories were classified by a decision tree (Chaid) into 6 groups with WTQ95 as the predicting variable.

River slope was calculated within the 5 km segments as the height difference between starting and endpoint of the segment based on a 10 m digital elevation model available from Geoland.at. (2015a), and then classified into 5 groups after Rosgen (1994).

Two descriptors, hillshade (HillSha) and tree cover density (TreeDens), were used to consider shading effects on the river. Hillshade combines the information on terrain slope and aspect, and thus provides information on topographical shading effects. Tree cover density quantifies the direct shading effects of vegetation along the rivers. Both parameters help to consider the intensity of potential solar radiation onto the water surface.

Calculation of hillshade was based on the elevation and direction angle of the light source, i.e., based on the sun's position on the sky. We selected an angle of 60° as elevation (=summer) and 180° as direction (=South), representing an Austrian summer day (maximum elevation angle in Vienna is 65.2° on June 21st; Geoland.at., 2015b). The continuous hillshade values were classified into 7 categories by a decision tree (Chaid) with WTQ95 as the predicting variable.

Tree cover density was calculated based on the high-resolution layer for tree cover density (EEA, 2018). The density values were queried in a 5 km longitudinal buffer upstream along the river network and 50 m on each side of the river segment line. The derived mean tree cover density was grouped into six categories ranging from very low (≤6%) to very high (>71%).

Glaciated areas within the catchment were derived from the Austrian Glacier inventory 3 (Fischer et al., 2015). Summer cooling effects by glaciers were observed for rivers in several studies (Collins, 2009; Fellman et al., 2014; Williamson et al., 2019). Future scenarios for the development of central European glaciers were derived from Marzeion et al. (2012). The classification of the glacier effects was based on characteristic hydrological regimes of Austrian rivers (Mader et al., 1996; **Table 2** and **Table S1**).

Discharge also plays a role in the thermal regime, but no adequate dataset was available for further modeling. Therefore, we tested correlations at the river gauging stations of summer precipitation amounts, low flow events and water temperature (WTQ95). Within the years 2000–2011 the mean discharge (MQ) and low discharge events (MNQ7) correlated very low with the

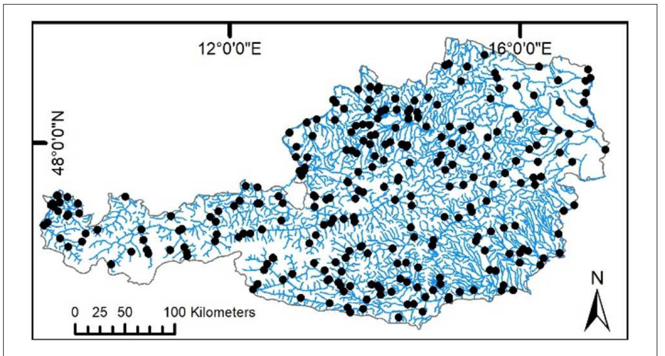

FIGURE 1 | Location of the 274 Austrian river gauging stations (black dots) and the river network (blue lines) included in the water temperature model.

TABLE 1 | Overview and explanation of the descriptors used in the water temperature model, as well as the value ranges in the training data (Value range), the categorized values (Categories used in the model calibration), and the data of the dataset.

Parameter	Description	Value range	Categories used in the model calibration	References
Strahler	Strahler order (after; Wimmer and Moog, 1994)	1–8	1: (3 small) 2: (4 intermediate) 3: (5 large) 4: (≥6 very large)	BMLFUW, 2016
Catchment	Catchment size at the site of the gauging station, respectively at the mid-point of the investigation segment	3.9–25,663 km²	Chaid Groups 1: ≤50 (very small) 2: >50–87 (small) 3: >87–135 (medium) 4: >135-268 (medium/large) 5: >268–3,387 (large) 6: >3,387 (very large)	Fürst and Hörhan, 2005
Slope	Actual river slope (%) of the 5 km reach up- and downstream (2.5 km) based on 10 m DEM	0.01–24.05%	1: ≤0.5 (very low) 2: >0.5–1.0 (Low) 3: >1.0–2.0 (moderate) 4: >2.0–4.0 (steep) 5: >4 (very steep) changed Rosgen, 1994	Rosgen, 1994; Geoland.at., 2015a
HillSha	Hill shade (noon) Angle 60°, 180° represents South based on 10 m DEM	154–253: Q25: 218 Q50: 220 Q75:222	1: ≤208 (high) 2: >208–216 3: >216–218 4: >218–221 5: >221–222 6: >222–226 7: >226 (very low)	Hrachowitz et al., 2010; Geoland.at., 2015a
TreeDens	Tree Cover Density (%) within 5 km upstream an 50 m lateral buffer on each side (full 100 m)	0–96%	1: ≤6 (very low) 2: >6–22 (low) 3: >22–37 (low/medium) 4: >37–53 (medium/high) 5: >53–71 (high) 6: >71 (very high)	EEA, 2018

water temperature with $r = -0.04$ and $r = -0.05$, respectively. Furthermore, the yearly amount of summer precipitation (Precep_Y) divided by the long-term amount of summer precipitation (Precep) correlated with the annual low flow events (MNQ7/MQ) by $r = -0.42$. We included precipitation to characterize the trend of changing hydrological conditions in our analyses as run-off models are majorly driven by precipitation as input, and another run-off model would further increase the uncertainties.

Classification of input variables was conducted to reduce the extrapolation effects of outliers in the prediction dataset not represented in the input dataset.

Thermal- and PKD-Related Risk for Brown Trout

We developed a risk assessment to identify both, (1) thermal regimes that support a higher PKD prevalence in brown trout, and (2) prospective thermal regimes that create thermally stressful conditions for *S. trutta*. Thus, critical temperature thresholds in respect of PKD outbreak and general thermal habitat suitability were identified through a literature review.

Overall, the most indicative parameters in the literature were based on consecutive days (further shortened as "ConsD") and hours (further shortened as "ConsH") exceeding specific mean water temperature values. In detail, a possible PKD outbreak is considered to appear at ≥14 ConsD over 15°C (Burkhardt-Holm, 2009). Low mortalities in field studies occurred at ≥29 ConsD over 15°C and a minimum of additional 10 non-consecutive days (≥15°C) following up to autumn (Schmidt-Posthaus et al., 2015). High mortalities with clinical signs of PKD appear at ≥26 ConsD over 18°C in laboratory conditions (Bettge et al., 2009a). These thresholds were assembled into four classes of temperature-related risk for PKD outbreak (TR-PKD): no outbreak (0), possible outbreak (1), low mortality (2), high mortality (3) (for more details see **Table 3**).

High water temperatures are not only threatening *S. trutta* in terms of emerging diseases, they also induce physiological stress. Critical temperature thresholds were therefore identified for diminished growth (water temperature ≥19.5°C; Elliott and Elliott, 2010) and for the occurrence of cardiac dysfunction in brown trout (water temperature ≥23.5°C; Vornanen et al., 2014). The temperature threshold for diminished growth was set when the 95% quantile was ≥19.5°C, expressing roughly 18 days with thermal conditions for diminished growths. As cardiac dysfunction in *S. trutta* can occur at single (hourly) events, the threshold for our

TABLE 2 | Description of independent variables used in the water temperature model that change under climate change scenarios.

	Description	Training (T)/river network (RN)	Groups/Categories	Baseline 1971–2000/current conditions 2000–2011	Scenarios (RCP4.5/8.5) NF/FF
Precip	Mean precipitation sum (mm) in summer (JJA) period (1971–2000)	T: 170–775 mm (Mean 377) *RN: 167–867 (Mean: 380)*	Continuous	ZAMG, 2016	Leuprecht and Truhetz, 2016a,b,c,d
Glacier	Glacier Area within Catchment (%) in 2006 (2006: 88% left)	T: 0.0–17.1% (Mean: 0.8) *RN: 0.0–27.7% (Mean: 0.4)*	1: ≤ 0.003 (no) 2: > 0.003–2.0 (very low) 3: >2.0–5.0 (low) 4: >5.0–15.0 (medium) 5: >15.0 (high)	Marzeion et al., 2012; Fischer et al., 2015	Marzeion et al., 2012
AirTemp	Mean Air Temperature in summer (JJA) for each year (2000–2011)	T: 12.5–23.4°C (Mean: 18.4) *RN: 10.0–21.9 (Mean: 17.6)*	Continuous	Hiebl and Lexer, 2016b,e	Leuprecht and Truhetz, 2016i,j,k,l
CDD	Cooling degree days in summer (JJA) (°C). Sum of degrees that a day's average temperature is above 18.3°C for each year (2000–2011)	T: 0.2–468.5°C (Mean: 138.3) *RN: 0.4–347.4 (Mean: 106.2)*	Continuous	Hiebl and Lexer, 2016a,d	Leuprecht and Truhetz, 2016e,f,g,h
TRN	Tropical nights: Annual number of days with Tmin >20°C for each year (2000–2011)	T: 0–14 d (Mean: 0.41 day) *RN: 0–15 day (Mean: 0.24 day)*	1: 0 (no) 2: 1 (1 day) 3: >1–7 (1 week) 4: >7–14 (2 weeks) 5: >14–28 (4 weeks) 6: >28 (>1 month)	Hiebl and Lexer, 2016c,f	Leuprecht and Truhetz, 2016m,n,o,p

Range of training values observed for the river gauging stations in normal fond (Values Training) and across the river network in italic (current Conditions 2000–2011), variable type, and data sources.

TABLE 3 | The categories of temperature-related risk of PKD (TR-PKD) with related time periods exceeding daily mean water temperature thresholds (°C).

	Time period	Daily mean temperature (°C)	References	WTQ95 (CRT)	Percent correct (Training/Test) (%)
0	<14 ConsD	≥15	Burkhardt-Holm, 2009	≤15.64	97.5/97.1
1	≥14 ConsD	≥15	Burkhardt-Holm, 2009	>16.64 – ≤17.77	78.2/76.5
2	≥29 ConsD and ≥39 TD	≥15	Schmidt-Posthaus et al., 2015	>17.77 – ≤20.54	66.7/69.1
3	≥26 ConsD	≥18	Bettge et al., 2009a	>20.54	75.7/67.7

ConsD, consecutive days; TD, total days. Results of the classification and regression tree (CRT) classifying WTQ95 into TR-PKD classes and the percentage of correct classification (Percent correct). Colour values relate to the colours in ***Figures 5–7****.*

model was an exceedance of the maximum hourly water temperature ≥23.5°C.

Water Temperature Modeling

Water temperature models were based on linear regression models that have been calibrated for four different river types ranging from small to large rivers (**Table 1**, **Figure 2**). The differentiation of river types was based on Strahler order. As dependent variable, we modeled the 95% quantile of daily mean water temperature (WTQ95). Accordingly, this value is indicating an exceedance of the given value by the 18 hottest days in the year.

The included independent variables were tested for multicollinearity based on the variance inflation factor (VIF <10). Homoscedasticity, linearity and normal distribution of residuals were checked visually based on scatter plots, histograms and distribution curves. The best models were selected by highest adjusted R^2 values (**Table 4**).

As all the identified thresholds for TR-PKD were related to hot events, WTQ95 was tested to be suitable to predict TR-PKD. Therefore, a classification and regression tree (CRT), including a split-sample validation (training 70%, test 30%), was applied using TR-PKD as dependent and WTQ95 as independent parameter. The specifications for the CRT were a maximum tree depth of 5 and a minimum of 50/30 cases in parent/child node.

For the physiological thresholds a second CRT without split validation was applied using daily maximum temperatures ≥23.5°C [TD ≥23.5°C (max)] as dependent and WTQ95 as the independent parameter. The dataset for both CRTs included 3,000 values covering the years 2000–2015.

All statistical analyses were conducted in IBM SPSS 21 (IBM Corp., 2012).

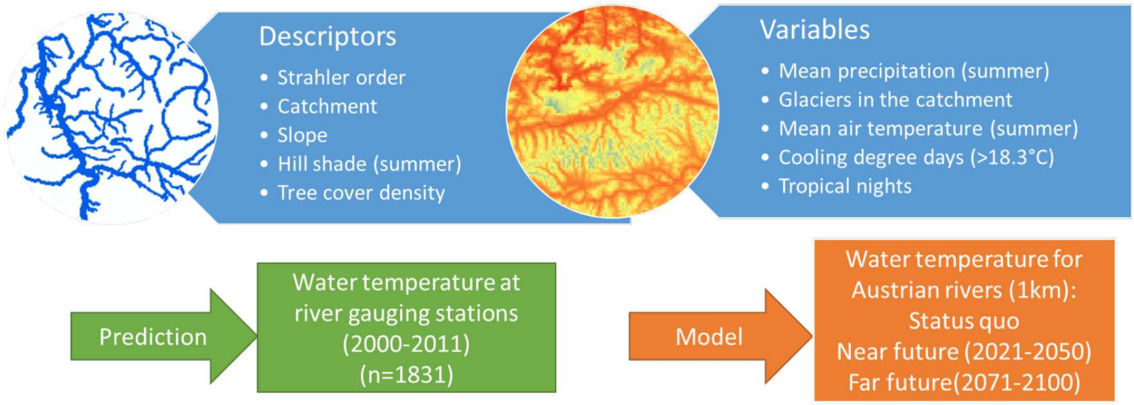

FIGURE 2 | Scheme of the Austrian wide water temperature model.

TABLE 4 | Included variables in the linear regression models of the four rivers types (small to large rivers), including standardized coefficients (Std. Coeff), variance inflation factor (VIF), adjusted R^2 (Adj. R^2), the count (*N*), and the standard error (Std. Error).

River type	Independent variables	Std. coeff	VIF	Adj. R^2	*N*	Std. error
Small	TreeDens	−0.248	1.7	0.63	168	2.4
	HillSha	0.425	1.1			
	Slope	−0.371	1.8			
	CDD	0.158	1.5			
	TRN	0.124	1.2			
Medium	Slope	−0.15	2.5	0.62	433	2.3
	HillSha	10.096	1.2			
	CDD	0.472	2.0			
	Precip	−0.18	1.4			
	Glacier	−0.177	2.7			
Large	Slope	−0.226	1.9	0.64	654	2.1
	Catchment	−0.225	1.7			
	AirTemp	0.576	1.5			
	Glacier	−0.120	1.4			
	Precip	0.163	1.2			
Very large	TreeDens	0.191	1.1	0.78	576	1.7
	Strahler	0.168	1.2			
	Glacier	−0.424	1.2			
	Precip	−0.298	1.3			
	AirTemp	0.231	1.5			
	TRN	0.047	1.2			

Current, Baseline, and Future Climate

We used two data sources to describe the climate conditions in our analyses. The first dataset was used to describe the current conditions (period 2000–2011) that was also covered by the water temperature data from the gauging stations. The second dataset was used for future predictions including a baseline scenario and current conditions (**Tables 1**, **2**). The spatial properties (grain size and coverage) were the same for both, i.e., covering the full investigation area with a 1*1 km resolution.

Future climate conditions originated from a national dataset (Chimani et al., 2016) that has been specifically established as a basis for climate change impact research in Austria. For future predictions, we used two timesteps ("near future" covering the period from 2021 to 2050, and "far future" covering 2071–2100) and two Representative Concentration Pathways (RCPs): RCP4.5 ("effective measures") and RCP8.5 ("business as usual"). The RCPs describe different climate futures depending on the volume of greenhouse gases emitted in the years to come (IPCC, 2014). Among the different scenarios, RCP4.5 is a stabilization scenario and assumes that climate policies are invoked to achieve the goal of limiting emissions and radiative forcing. In turn, RCP8.5 is characterized by increasing greenhouse gas emissions over time, leading to high greenhouse gas concentration levels in absence of climate change policies. Compared to the total set RCPs corresponds to the pathway with the highest greenhouse gas emissions.

RESULTS

The Current State of Temperature-Dependent PKD Risk and Thermal Stress for Brown Trout

The CRT predicted 86.5% of the WTQ95 into the correct TR-PKD class. The validation with 30% of the data showed similar results with 85.2% correct classification. The predicted thresholds are listed in **Table 3**. Both, ConsD ≥15°C and ≥18°C were highly correlated with WTQ95 by $r = 0.85$ and $r = 0.71$, respectively. Similarly, total days (TD) >15°C ($r = 0.92$) and >18°C ($r = 0.8$) showed high correlations with WTQ95. The limit for cardiac dysfunction (≥23.5°C) was exceeded in 455 cases between 2000 and 2015. The CRT showed that at WTQ95 >20.7°C, 99.1% of the river gauging stations ($n = 232$) had at least 1 day with maximum daily water temperature above 23.5°C (**Figure S1**).

Under current conditions (2000–2011) (Bas2011) the thermal habitat conditions for *S. trutta* were adequate in 98.2% of the river network (**Figure 6**). On average, no possible outbreak for PKD (TR-PKD = 0) was found in 72.8% of the river reaches. The TR-PKD increased with increasing Strahler order and ranged from 82.5% (TR-PKD = 0) in small rivers to 52.7% in very large rivers.

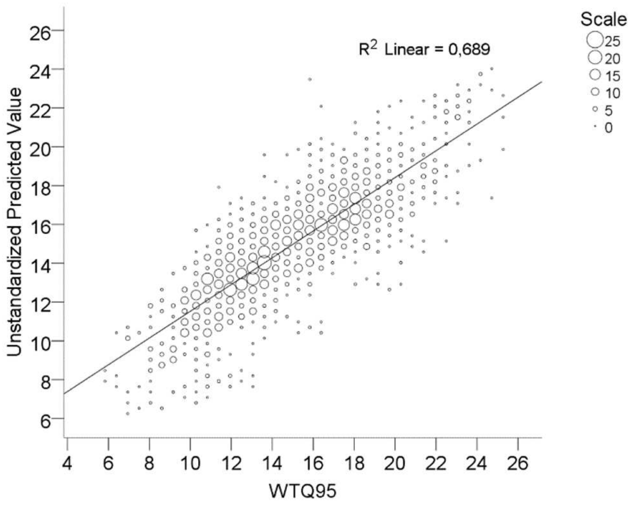

FIGURE 3 | Linear relation of observed and predicted (unstandardized) WTQ95 values (n = 1,831) in (°C).

Water Temperature Modeling and Future Water Temperature

The input variables explained overall 68.9% of the variance in WTQ95 (**Figure 3**). The adjusted R^2 ranged from 0.62 to 0.78 for small to large rivers (**Table 4**). The mean increases of WTQ95 ranged from +0.6 to 0.9°C in the near future and from +1.3 to 3.8°C in the far future compared to the current period 2000–2011 (**Figure 4**). In the baseline (1971–2000), mean WTQ95 was −0.7°C lower than in the current period 2000–2011.

Future Changes of Temperature-Dependent PKD Risk and Thermal Stress for Brown Trout

The results of the modeling revealed severe changes in the thermal regimes of the rivers (**Figure 5**). The river reaches without a possible outbreak of PKD decreased from 72.8% (Bas2011) to 68.9–63.4% (RCP4.5–RCP 8.5) in near future and 60.1–37.8% in far future. In the past (1971–2000) 82.3% of the river length were without risk concerning possible outbreaks of PKD.

In small rivers (Strahler order = 3) the reaches without a risk of a possible PKD outbreak decreased from 82.5% (Bas2011) to 78.4–77.8% in near future, and to 71.3–52.8% in far future. The TR-PKD for low and high mortality ranged between 12.5–29.9% in far future compared to 4.8% under current conditions (2000–2011). The mean altitude of small rivers without a risk for PKD outbreak was 860–957 m.a.s.l (*SD*: 319.7–294.3) in far future compared to 808 m.a.sl (*SD*: 332) under current conditions. For medium-sized rivers the mean altitude was 896–1,035 m.a.s.l (*SD*: 283–238) in far future compared to 835 (*SD*: 301) under current conditions. This represents a shift of up to 200 m in altitude of segments without a risk for possible PKD outbreak.

The river reaches without suitable thermal habitat conditions for brown trout in respect of physiological thresholds (diminished growths) increased from 2.0% (2000–2011) to 2.9–5.3% in near future, and 5.3–31.9% in far future (**Figure 6**). Daily maximum temperature related to cardiac dysfunction increased from 0.1% in 2000–2011 to 0.5–1.2% in near future and to 2.4–22.3% in far future. For Strahler order 3 this effect is less pronounced with an increase from 0% for 2000–2011 to 0.3–0.4% in near future and 1.9–15.2% in far future (**Table 5**).

Combined Effects

The combined effects of disease emergence and thermally stressful conditions for *S. trutta* showed a drastic increase especially under RCP 8.5 in far future (**Figure 7**). Combined effects of diminished growth and low mortality due to PKD (TR-PKD = 2) increased from 1.8% (2000–2011) to 2.1–3.7% in near future and to 3.6–7.5% in far future. The combined effects of cardiac dysfunction and high mortality due to PKD (TR-PKD = 3) increased from 0.1% (2000–2011) to 0.5–1.2% in near future and 2.4-22.3% in far future.

In small rivers (Strahler order = 3) 237–1,850 km river length will be affected by combined impacts of high mortality due to PKD and cardiac dysfunction in far future compared to 0 km in 2000–2011 (**Table 5**). Additionally, 589 km river length of the total 1,659 km with TR-PKD = 2 (low mortality) showed a thermal regime with diminished growth in far future (RCP8.5). This indicates that within small rivers, that to a large extent (10,244 km), currently showed highly suitable thermal regimes the habitat suitability will be reduced by combined effects of PKD and physiological thresholds to 8,852–6,554 km for both RCP scenarios in far future.

DISCUSSION

Our results highlight how thermal regimes are currently distributed in a pre-alpine to alpine river network and how the potential impacts of climate change will affect the emergence of PKD and increase thermal stress for brown trout. Here, we modeled water temperature of the rivers based on general river descriptors and climatic variables sensitive to climate change. Model calibration was based on a high-resolution long-term water temperature dataset covering a large spatial extent. Our regression model was able to explain nearly 70% of the variance in the observed water temperature (represented by WTQ95). This is in line with other regression models for water temperature, e.g., Arscott et al. (2001) modeled average daily summer temperature in a single alpine river catchment based on elevation, azimuth and water depth with R^2 = 0.71. However, our dataset covers a much larger variety of rivers including four river size classes, and thus allows a broader view on how climate change will affect the thermal regimes of rivers in future.

Water Temperature Model

Our water temperature model covered three groups of main factors controlling the thermal regime of rivers: (1) topography, (2) atmospheric conditions, and (3) stream discharge (Caissie, 2006). In the different river size classes that were used for the modeling of the river water temperature these groups were described by different variables. For small rivers, topography

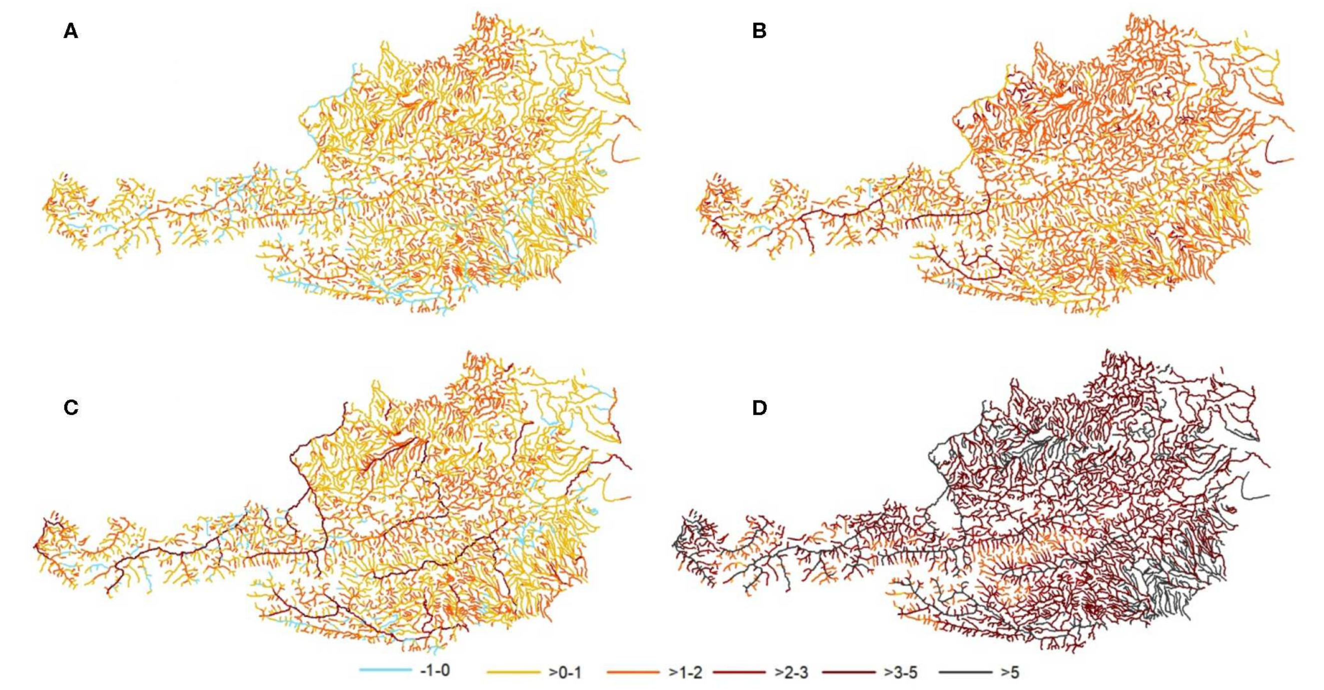

FIGURE 4 | Signal of change of the water temperature model for WTQ95 compared to the current conditions (2000–2011) in degree Celsius (°C) for **(A)** near future RCP4.5, **(B)** far future RCP4.5, **(C)** near future RCP8.5, and **(D)** far future RCP8.5.

was covered by the parameters riparian vegetation (TreeDens) and hillshade (HillSha) representing the shading effects on rivers. Atmospheric conditions were covered by two variables describing air temperature (CDD, TRN). The stream discharge and hydrologic conditions were reflected by precipitation (Precip) and river slope.

The model results showed that especially in small rivers shading effects played a crucial role in the variation of the water temperature compared to medium-sized and large rivers (**Table 4**) as the full river width can be covered by riparian vegetation or by surrounding hills. This is for example underlined by Hrachowitz et al. (2010) who found lowest summer maximum temperatures in small forested streams. Besides canopy, Arscott et al. (2001) found slope as an important variable for the diel temperature variation. We conclude that in small rivers that increasing the amount of riparian vegetation could strongly mitigate climate change effects, by cooling the water in downstream direction, respectively reduce the summation effect along the river network.

For small to large rivers, we found a general water temperature increase with a decrease in river slope. River slope can be used as a surrogate variable to describe the energy budget of the river, and thus characterizing the flow velocities. Basically, river slope is dependent on the terrain relief, and therefore highly correlated to altitude in alpine regions ($r = 0.64$). The effect of river slope and flow velocity on water temperature is related to the contact time of solar radiation with the water surface that is reduced in fast running rivers.

We also considered the effects of glaciers located further upstream in the river network that was found as an important descriptor in the thermal regime of medium-sized to large rivers. Larger glaciated areas within the catchment of a river reach led to lower water temperatures in line with several studies that observed summer cooling effects in rivers by glaciers (Collins, 2009; Fellman et al., 2014; Williamson et al., 2019). However, this cooling effect is related to a certain glaciated coverage within the catchment as Fellman et al. (2014) showed very low effects in river catchments with <2% glaciated area and very high effects with more than 30% of glaciated area.

The atmospheric conditions expressed by the air temperature variables (CDD, TRN, and AirTemp) were positively correlated with water temperature. Generally, the solar radiation is the direct energy input and driver of temperature increase for both, air and water. In our models, we used air temperature variables (CDD, TRN, and AirTemp) focusing on two aspects. Firstly, the average thermal conditions represented by mean temperature. Secondly, we aimed to describe heat waves during the summer period and thus implemented cooling degree days (CDD) and number of tropical nights (TRN). The variable cooling degree days describes hot conditions during daytime and the variable number of tropical nights characterizes nocturnal hot conditions. Especially in respect of heat stress and the emergence of diseases, the duration of heat events and the continuing exceedance of critical temperature thresholds is important for brown trout. Thus, it is important to consider the effects of less cooling during night as the thermal regimes of rivers normally cools during this daytime.

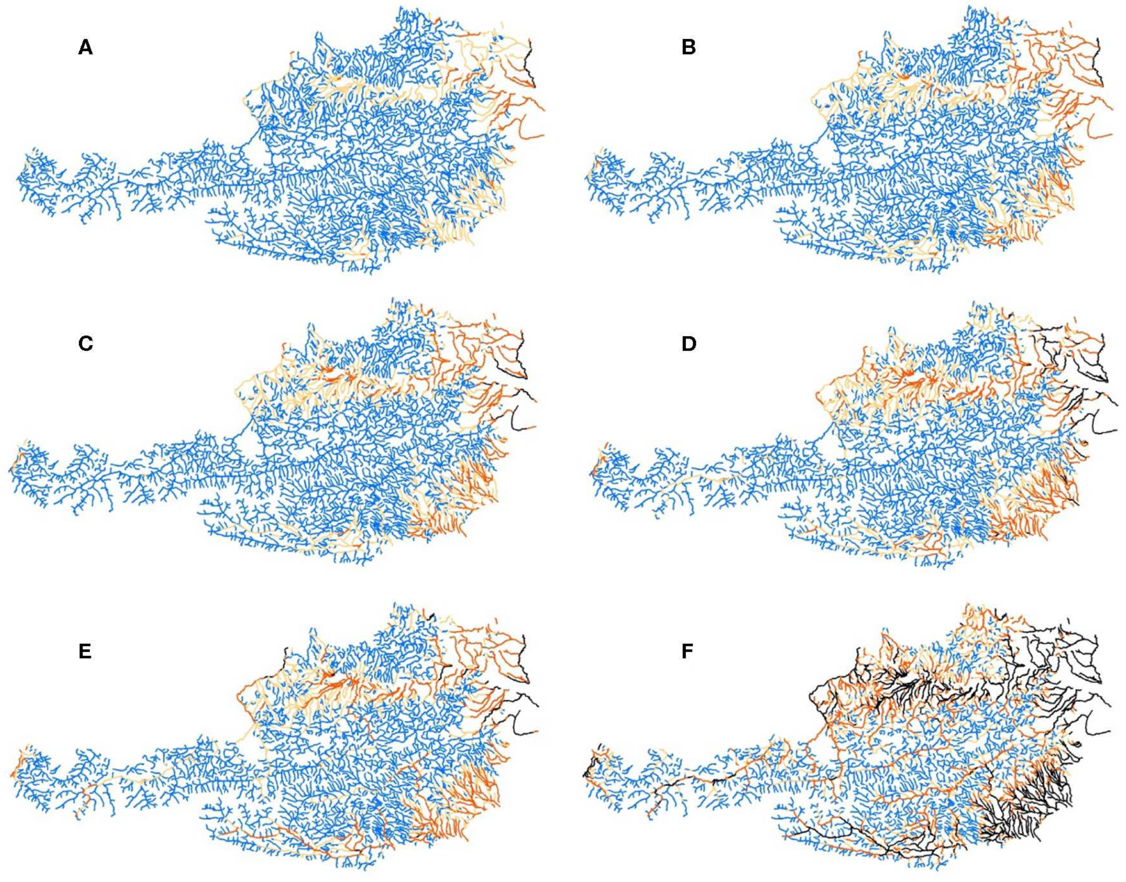

FIGURE 5 | TR-PKD in Austrian rivers for **(A)** in the past (1971–2000), **(B)** under current conditions (2000–2011), as well as for the future scenarios **(C)** near future RCP4.5, **(D)** far future RCP4.5, **(E)** near future RCP8.5, and **(F)** far future RCP8.5. Color codes: No outbreak, blue; possible outbreak, orange; low mortality, red; and high mortality, black.

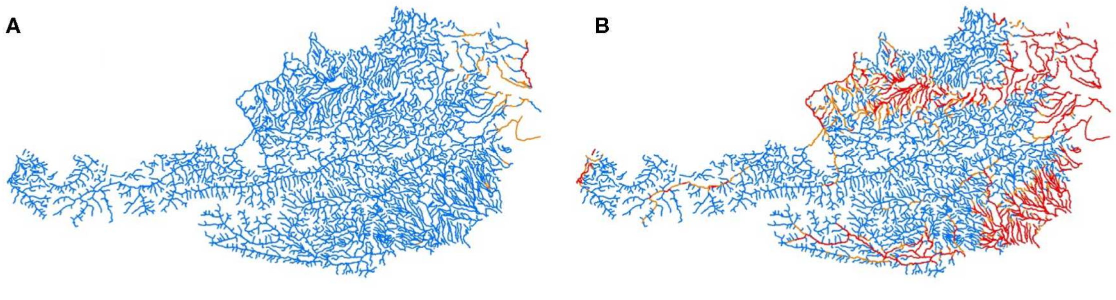

FIGURE 6 | Characterization of thermal stress for brown trout in Austrian rivers **(A)** under current conditions (2000–2011), and **(B)** for the far future RCP8.5 scenario. Color codes: No stress, blue; diminished growth, orange; and cardiac dysfunction, red.

In respect of water quantity, precipitation was negatively correlated with water temperature in medium-sized and large rivers. As the relative yearly summer precipitation (Precep_Y/Precep) correlated negatively with the annual low flow (MNQ7/MQ) events, we conclude that especially summer precipitation influences summer low flow events in the rivers resulting in potential effects on the thermal regime. Furthermore, including elevation into the regression model would further increase the explanatory power of the model. However, this environmental descriptor only represents current conditions and stays stable in future and under climate change impacts.

Temperature-Dependent PKD Risk and Thermal Habitats of Brown Trout

Our approach to use a single water temperature parameter (WTQ95) to describe different heat periods in the thermal regime

TABLE 5 | River network (km) with combined effects of outbreak and mortality due to PKD and thermally stressful conditions for *S. trutta*.

		River length (km) with						
River type (Strahler order)	**Scenario**	**No outbreak**	**Possible outbreak**	**Low mortality**	**+diminished growth**	**High mortality**	**+cardiac disfunction**	**Total length**
Small rivers (3)	1971–2000	11008.7	1176.8	228.1	0		0	12413.6
	2000–2011	10,244	1576.4	588.2	160.7	5	0	
	NF_4.5	9734.3	1673.7	958.4	157.6	47.1	42.1	
	FF_4.5	8851.9	2014.1	1264.9	248.8	282.7	237.1	
	NF_8.5	9662.7	1663.3	1028.6	128.7	59.1	47.1	
	FF_8.5	6554.1	2152.9	1659.4	589.4	2047.3	1849.6	
Medium rivers (4)	1971–2000	4785.9	873.8	163.2	0		0	5822.8
	2000–2011	4036.4	1041.6	744.9	156.6		0	
	NF_4.5	3821.4	1098.9	841.2	180.1	61.3	25	
	FF_4.5	3407.7	1138	1015.8	262.5	261.3	201.3	
	NF_8.5	3824.9	1093.2	873.5	205.1	31.3	5	
	FF_8.5	2,223	971.5	1,166	367.7	1462.4	1343.7	
Large rivers (5)	1971–2000	2427.6	814.1	153.2	0		0	3394.9
	2000–2011	1918.7	904.9	571.3	77.4		0	
	NF_4.5	1782.2	939.5	662.1	79.1	11.1	5	
	FF_4.5	1366.1	989.2	959.7	251.1	79.9	57.4	
	NF_8.5	1468.6	968.5	905.3	214.7	52.4	33.7	
	FF_8.5	226.9	726.9	1427.6	420.9	1013.6	934.3	
Very large rivers (6–8)	1971–2000	1372.9	596	183.5	10.1	35	25	2187.4
	2000–2011	1151.9	776.3	219.2	35	40.1	35.1	
	NF_4.5	1066.3	839.3	206.8	75	75.1	50.1	
	FF_4.5	688.4	914	495	98.4	90.1	70.1	
	NF_8.5	152.1	703.9	1088	337.1	243.5	203.5	
	FF_8.5		64.4	843.6	413.6	1279.4	1182.2	

Scenarios: Past 1971–2000, Current conditions 2000–2011, near future (NF) and far future (FF) for RCP4.5 (4.5) and RCP8.5 (8.5).

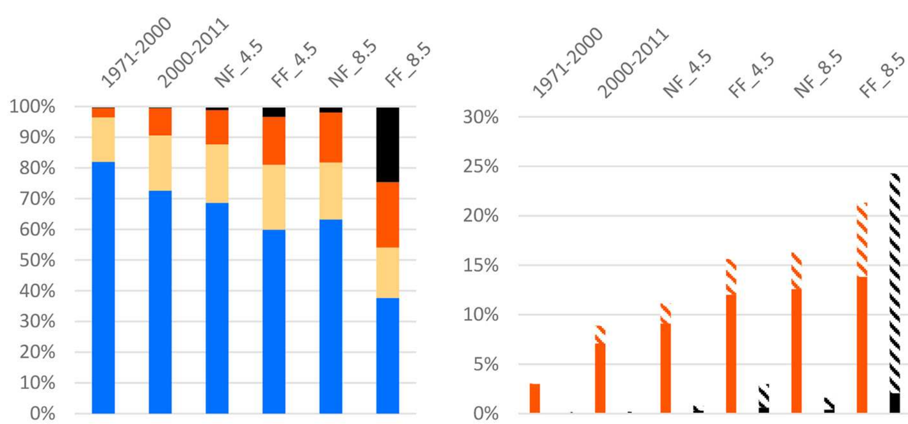

FIGURE 7 | Shares of river reaches with different levels of TR-PKD in Austrian rivers; **Left panel:** No outbreak (blue), possible outbreak (yellow), low mortality (orange), high mortality (black). Combined effects of TR-PKD and physiological thresholds; **Right panel:** Low mortality and diminished growth (orange striped), high mortality and cardiac dysfunction (black striped). With Scenarios: Past = 1971–2000, Current conditions = 2000–2011, and abbreviations for the different scenarios: NF, near future; FF, far future; 4.5 = RCP4.5 and 8.5 = RCP8.5 (8.5).

of rivers, was highly suitable. Exceedance periods of critical water temperatures are important to describe extreme events in the thermal regime. Turschwell et al. (2017) identified consecutive days above temperature thresholds as the best predictor for suitable habitats of a cold-water species. Using such a parameter, we were able to classify the river segments into different risk categories for PKD outbreak and physiological temperature stress. Accordingly, WTQ95 can be seen as a representative water temperature value for hot events and extreme hot events (e.g., $\geq$23.5°C) during summer.

Related to PKD, several authors describe the importance of warm periods in the emergence of the disease. On the one hand, life-cycle fulfillment of PKD is supported by warm temperatures, on the other hand, the progression of the disease itself in brown trout is more serious under warm conditions (Bettge et al., 2009a; Burkhardt-Holm, 2009; Gallana et al., 2013; Schmidt-Posthaus et al., 2015; Bruneaux et al., 2017). Furthermore, warm temperatures enhance the spore production in the bryozoan host, and therefore increase the infection rate (Tops et al., 2009; Okamura et al., 2011). Bryozoans, as the primary host, are organisms with a seasonal life-history; colonies increase in spring and expand prolifically during summer, leading to a peak of infective spore release and resulting in infection of trout (Gallana et al., 2013). Accordingly, Tops et al. (2009) expect that climate change will increase the geographic range of PKD as a result of the combined responses of *T. bryosalmonae* and its bryozoan hosts to warming and higher temperatures.

The combined effects of the disease and additional thermally stressful conditions for *S. trutta* are highly relevant, especially because of the weakened fitness of infected fish, the additional thermal stress on fish physiology, and an enforced immune response of fish in sub-optimal thermal conditions (Bowden, 2008; Bettge et al., 2009b). The proposed temperature-related risk assessment (TR-PKD) covers these major aspects to assess the potential spread and outbreak of PKD in *S. trutta*.

Future Scenarios of Water Temperature, Changes in PKD Risk, and Additional Physiological Stress for Brown Trout

Water temperature is highly linked to the same driving forces as air temperature. Thus, climate change will lead to further warming in rivers (Mohseni et al., 2003). This is in line with our results with a projected increase of WTQ95 ranging from +0.6 to +0.9°C in the near future, and from +1.3 to +3.8°C in the far future compared to the current conditions (**Figure 4**). Similarly, Dokulil (2018) analyzed long-term annual water temperature records of the Danube River and some tributaries (also represented in our dataset) indicating a temperature increase of about 0.3°C per decade since 1900.

Under both future concentration pathway scenarios (RCP4.5 and RCP8.5), our model showed an increase of temperature-related risk for PKD and a decrease of suitable thermal habitat for *S. trutta.* Interestingly, the distribution of PKD-risk for the near future under RCP4.5 is already comparable to the risk found under current conditions (2000–2011). This underlines the progressive and already observable change of the environmental conditions due to climate change. Not surprisingly, downstream sections of rivers are affected first by PKD as these river sections are generally warmer than the upstream parts. In Switzerland PKD-infected fish were mainly found below 800 m.a.s.l. (Wahli et al., 2008). This altitudinal threshold is in line with our findings with a mean altitude of 808 m.a.sl (*SD*: 332.1) for the risk class indicating no PKD outbreak.

In the far future RCP8.5 scenario, the amount of thermally suitable habitats for *S. trutta* will be drastically reduced. For small rivers that currently show highly suitable thermal regimes for a river length of more than 10,000 km, the length of river reaches with suitable habitats will be reduced to ~6,500 km due to the combined effects of PKD and physiological stress. The additional harm due to combined effects of high physiological stress (exceedance of thermal threshold for cardiac dysfunction) and potential high mortality due to PKD increases from 0.1% under current conditions up to 22.3% in the far future RCP8.5 scenario within the whole river network (**Figure 7**). In small rivers, this represents nearly 2,000 river kilometers with a total loss of thermally suitable habitats. This drastic reduction of habitats is in line with Filipe et al. (2013) who modeled a reduction of up to 64% of suitable stream reaches for brown trout in Europe till the 2080s due to climate change. Furthermore, a decline of *S. trutta* is already observed in the alpine region (Zimmerli et al., 2007).

The future distribution of *S. trutta* will be restricted to small and medium-sized alpine and pre-alpine rivers in Austria indicated by a elevational upward shift of around 200 m of rivers without the risk for a possible PKD outbreak in the far future RCP8.5 scenario compared to current conditions. Since the temperature thresholds for PKD-risk are below the physiological thresholds, the habitat reduction of *S. trutta* could be largely determined by the prevalence, outbreak and mortality due to PKD.

However, the results also underline that suitable habitats will remain in the alpine area, even under severe future climate change scenarios such as RCP8.5. This underlines the enormous importance of the alpine region as refuge for brown trout in Europe. Thus, it is highly important to firstly protect and restore existing habitats in these areas, and to secondly consider newly arising pressures on wild brown trout populations due to further human impacts and/or alterations induced by climate change.

The further habitat fragmentation can be a possible effect of climate change. The increasing number of unsuitable habitats also leads to disconnections of river sections that offer suitable habitats. Due to the loss of migration routes the populations can be further fragmented. This problem may be attenuated during the cold season as *S. trutta* could access areas in this time that are unsuitable during summer (Bentley et al., 2015). Furthermore, climate change will also lead to new land use patterns along rivers with potential impacts on wild brown trout populations. In this context the alpine habitats for brown trout must be conserved and managed in a careful and sustainable manner as in wide areas of Europe environmentally suitable habitats can be lost due to climate change (Filipe et al., 2013).

Our risk assessment approach represents a first step to gain more insights how PKD is distributed in rivers over large spatial extents. Thus, the risk assessment provides a basis to set up a screening and monitoring network. More insights into the temporal dynamics of parasite load and PKD symptoms in the wild are needed to further develop robust management and conservation strategies.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

FB, GU, KW, ME-M, and TB contributed to the conception and design of this study. FB und TB developed the water temperature models and the risk assessment, and wrote the first draft of the manuscript. TB ran the analyses. FB, KW, and GU provided feedback on analysis. GU, SA, ME-M, and KW provided revisions and editing. All authors read and approved the submitted version.

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SMART Research: Toward Interdisciplinary River Science in Europe

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Interdisciplinary science is rapidly advancing to address complex human-environment interactions. River science aims to provide the methods and knowledge required to sustainably manage some of the planet's most important and vulnerable ecosystems; and there is a clear need for river managers and scientists to be trained within an interdisciplinary approach. However, despite the science community's recognition of the importance of interdisciplinary training, there are few studies examining interdisciplinary graduate programs, especially in science and engineering. Here we assess and reflect on the contribution of a 9-year European doctoral program in river science: 'Science for MAnagement of Rivers and their Tidal Systems' Erasmus Mundus Joint Doctorate (SMART EMJD). The program trained a new generation of 36 early career scientists under the supervision of 34 international experts from different disciplinary and interdisciplinary research fields focusing on river systems, aiming to transcend the boundaries between disciplines and between science and management. We analyzed the three core facets of the SMART program, namely: (1) interdisciplinarity, (2) internationalism, and (3) management-oriented science. We reviewed the contents of doctoral theses and publications and synthesized the outcomes of two questionnaire surveys conducted with doctoral candidates and supervisors. A high percentage of the scientific outputs (80%) were interdisciplinary. There was evidence of active collaboration between different teams of doctoral candidates and supervisors, in terms of joint publications (5 papers out of the 69 analyzed) but this was understandably quite limited given the other demands of the program. We found evidence to contradict the perception that interdisciplinarity is a barrier to career success as employment rates were high (97%) and achieved very soon after the defense, both in academia (50%) and the private/public sector (50%) with a strong international dimension. Despite management-oriented research being a limited (9%) portion of the ensemble of theses, employment in management was higher (22%). The SMART program also increased the network of international collaborations for doctoral candidates and supervisors. Reflections on doctoral training programs like SMART contribute to debates around research training and the career opportunities of interdisciplinary scientists.

Keywords: river science, doctoral training, interdisciplinary training, international collaboration and mobility, science for management

INTRODUCTION

Interdisciplinary research and training programs are pivotal to address the complex, multi-faceted environmental challenges we are facing. It requires various methods and approaches aligned to individual disciplines (Klein, 1990; Millar, 2013), and sustainable solutions arise through the interaction among disciplines (Kates et al., 2001; Borrego and Newswander, 2010). At the same time, interdisciplinary research requires humility, mutual respect, open-mindedness, and an ability to see things from different perspectives, which again may support creativity and 'thinking outside the box' to generate innovative solutions (Gardner, 2013). New insights and educational value can be gained (Andersen, 2016) when ways of learning and methods of a given discipline are exported to another one and sometimes knowledge and methods from different disciplines can be seamlessly merged, yielding a more holistic, integrated view (Wagner et al., 2011; Andersen, 2016; Power and Handley, 2017).

Today, the need for such a systemic and integrated view on environmental issues is well accepted. Many scientists have therefore welcomed the emergence of unconventional approaches that go beyond their own research areas, leading to rapidly developing interdisciplinary fields starting from hydroecology, ecohydrology, eco-hydromorphology and eco-geomorphology that extend beyond ecology, geomorphology, and hydrology, up to biomedical engineering and bioinformatics (Braun and Schubert, 2003; Porter and Rafols, 2009). River science is emerging as one such interdisciplinary research field because rivers are, fundamentally, complex physical, biological, chemical and socio-economic systems whose watersheds often cross multiple political and administrative boundaries (Thoms, 2005; Dollar et al., 2007). Three elements are critical to support a new paradigm and develop sustainable solutions: interdisciplinary working; international collaboration; management-oriented science.

The relevance of interdisciplinary research in river science has been increasingly recognized over the past two decades (e.g., Thoms and Parsons, 2002; Stallins, 2006; Post et al., 2007; Murray et al., 2008). Lack of interdisciplinarity limits the ability to predict (river) landscape response to human disturbance and climate change (e.g., Reinhardt et al., 2010), and the need for a deeper dialogue between geomorphologists, ecologists and hydraulic engineers is increasingly advocated as priorities to develop effective science for management (Vaughan et al., 2009) and in relation to broad and specific open scientific issues (Rice et al., 2010). Vugteveen et al. (2014) argue that river research needs to be more collaborative and integrated for it to become fully inter-disciplinary in nature. Therefore, we need integration of knowledge and methods across spatial (Thoms and Parsons, 2002) and temporal scales and from diverse disciplines including freshwater biology, limnology, geology, geomorphology, ecology, remote sensing, hydrology, hydraulics, engineering, sociology, economics, and history (Wotton and Wharton, 2006).

Over the last century, river systems have been fundamentally and, in many cases, irreversibly transformed through human interventions (e.g., dam construction, channelization, water abstraction, pollution, sediment mining) with acute and chronic impacts on their flow, sediment, and thermal regimes as well as on their biodiversity, ecosystem functions, and related services (Petts, 1984; Brookes, 1988; Kondolf, 1994; Nilsson et al., 2005; Grill et al., 2019). Partly less obvious, but not less concerning, are the impacts arising from climate change, land use alterations, and societal changes (e.g., artificial light at night, see Hölker et al., 2010) and these are posing enormous challenges to river science and management (Perkin et al., 2011; Gilvear et al., 2016; Reid et al., 2019; Stecca et al., 2019).

A better understanding of the interactions between humans and rivers and "Riverine landscapes as coupled socio-ecological systems" (6th Biennial Symposium of the International Society for River Science, ISRS 2019) is critical to mitigate adverse anthropogenic impacts and to sustainably manage these systems. A common framework and a common set of concepts is fundamental to facilitating effective collaboration and communication of knowledge and approaches between scientists, managers, and policy makers (Dollar et al., 2007). Scientific developments and evolving management trends are fundamentally intertwined (e.g., Graf, 1993) and explicit recognition of this legacy is essential to develop innovative solutions required to face the complex challenges posed by such coupled socio-ecological systems (e.g., Leuven et al., 2007). The individuals who form the scientific and decision-making communities and who work at the boundaries between them (Gieryn, 1995) are key to achieving these goals and real progress will come from co-researching and collaboration between researchers, river professionals, and policy makers (Vugteveen et al., 2014). Millar (2013) has called for greater examination of how interdisciplinarity impacts the research process and the need to begin with the researchers themselves. This paper contributes to the discussions around how we train river scientists of the future (**Figure 1**) so that they are equipped to: address the dynamics of river systems that are interdisciplinary by nature (Palmer et al., 2005), to acknowledge, draw from, and develop an international scientific knowledge system (Pinter et al., 2019), and to play an effective role at the boundary with policy and decision making (Cash et al., 2003), from local to global scales.

FIGURE 1 | Graphical concept of questions in river science being addressed collaboratively by international interdisciplinary teams of scientists.

Thus, the key question addressed with this study is in which way and to which extent an interdisciplinary doctoral program on river science can contribute to both (1) the scientific advancement in the respective research field, and (2) an improved training of the next generation of scientists and managers able to provide them the best tools to tackle the research questions and challenges in river science and management of the future. We specifically focus on the aforementioned key elements of interdisciplinary, management-oriented research, within an international dimension that is key to overcome a parochial approach still characterizing many river management practices worldwide (see Pinter et al., 2019) and that emerged at the same time as a key priority in doctoral education beyond continental boundaries (e.g., Bitusikova, 2009).

In our paper, we share the analysis and reflections from a 9-year doctoral training program, "Science for MAnagement of Rivers and their Tidal Systems" Erasmus Mundus Joint Doctorate, hereafter referred to as SMART EMJD. It was one of the 43 EMJD programs funded by the Education, Audiovisual, Cultural Executive Agency of the European Union (EACEA). Within the broad need to adapt education systems to the demands of the knowledge society, the EMJD action (2009–2013) had the strategic goal of developing structured and integrated cooperation to implement common doctoral programs leading to the award of mutually recognized joint doctorate degrees (European Commission, 2013). The program was born from the sustained collaboration between individual senior scientists (Bertoldi et al., 2009) affiliated to three European universities that set out to train a new generation of river scientists. Through 36 doctoral research projects, organized under three key themes (**Figure 2**), the aim of the program was to address knowledge gaps in river science by adopting a much more integrated, holistic, interdisciplinary approach (Vaughan et al., 2009) with teams comprised of researchers from different educational and disciplinary backgrounds and drawn from a wide range of countries. Such teams help overcome the dangers of a strong disciplinary focus (see Pickett et al., 1994) for example gaps in understanding at the interfaces between disciplines, and a parochial approach (see Pinter et al., 2019). Furthermore, the program aimed to foster co-researching and collaboration between scientists, river professionals, and policy makers throughout the project as a more effective way to ensure more relevant science and improved evidence-based decision-making in river management, something that is unlikely to be achieved through paper-based communication of research results alone (Vugteveen et al., 2014). We share our evaluation of the SMART EMJD program in relation to its three core facets (interdisciplinarity, internationalism, and management-oriented science) to encourage and inform future integrated education and research activities in river science and other interdisciplinary research fields.

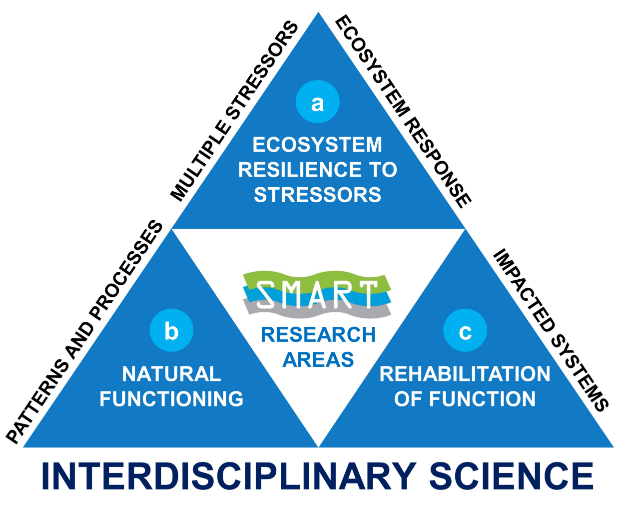


FIGURE 2 | The three research areas (a, b, and c) as defined within the SMART EMJD.

MATERIALS AND METHODS

Case Study: SMART EMJD

The SMART EMJD focused on core disciplines of the natural and engineering sciences relevant to the sustainable management of river systems, from their headwaters to their estuaries, including connected lakes and wetlands, and the interfaces between atmospheric, surface, and groundwater systems (Gurnell et al., 2016). Doctoral candidates were recruited from both EU and non-EU countries to carry out research in diverse teams that cross disciplinary, institutional, and geographic boundaries. International and interdisciplinary perspectives were further promoted through mandatory international mobility periods. The doctoral candidates were required to spend at least 6 months in another country (i.e., at the secondary institution) and 2 months with an associate partner.

Consequently, doctoral candidates were capable to adopt and apply a multidimensional, multi-scale holistic approach to river science. The multidimensional component enforced the consideration of multiple stressors, e.g., altered water/sediment flow and thermal regimes, and degraded ecological status from noise, light, and chemical pollution. It also helped advancing river research, which traditionally focused on a single scale, by covering a range of spatial and temporal scales. A holistic approach allowed for the integration of the complex, potentially synergistic and sometimes overlooked interactions among physical, chemical, and biological components in different river system settings.

A joint doctoral degree was awarded by the primary and secondary institutions to the SMART EMJD doctoral candidates after successful completion of their doctoral thesis with the thesis defense or viva-voce examination taking place at and following the regulations of the primary institution.

Lead Institutions and Associate Partners

Research training was delivered by three lead universities: The University of Trento, in close collaboration with the Edmund Mach Foundation in Italy; the Freie Universität Berlin, in close collaboration with the Leibniz-Institute of Freshwater

Ecology and Inland Fisheries (IGB) in Germany; and Queen Mary University of London in the UK. All three universities exhibited a history of successful research collaboration, and are engaged with practitioners in developing approaches to sustainably manage rivers and their tidal environments. Further institutions from multiple sectors in both EU and non-EU countries contributed to the program as Associate Partners (**Supplementary Table S1**), hosting doctoral candidates for at least 2 months with the aim to facilitate interactions with water policy-makers, river managers, and practitioners (i.e., facilitating transdisciplinary research).

SMART Doctoral Candidates

Doctoral candidates were selected from European and non-European countries following the Erasmus Mundus Program rules and selection was based on their written qualification, CV, personal statement, research proposal, and reference statements; followed by a face-to-face interview (primarily via Skype) with all shortlisted candidates. Funding was provided for five consecutive cohorts (5–10 candidates per cohort), starting in 2011. A total of 42 doctoral candidates, out of 378 eligible applicants, were finally selected (i.e., 11%); 36 candidates successfully completed their thesis (15 from EU and 21 non-EU countries). Of these candidates, 15 joined the University of Trento, 13 the Freie Universität Berlin, and 8 Queen Mary University of London as their primary institutions.

Research Areas

Doctoral research topics in the SMART EMJD were organized within three major research areas, (a) ecosystem resilience to stressors; (b) natural functioning; and (c) rehabilitation of function (**Figure 2**):

1. Ecosystem resilience to human and other stressors. Topics focused on the resilience of river-floodplain ecosystems to both natural and human-induced stressors. These included changes in hydrological connectivity, flow regulation by hydropower facilities, water abstraction, and changes in sediment supply, as well as more recent alterations such as artificial light at night or climate change related drivers.
2. The natural functioning of river-floodplain systems. Topics focused on the reciprocal linkages between physical processes and biota along river corridors, for improved understanding of their natural functioning. These linkages reflect feedbacks between flow, sediments, and vegetation, such as the ecosystem engineering capacity of plants. A special emphasis was given to drivers of bio-morphodynamics influencing the capacity of fluvial systems to self-regulate and attain good ecological status in both "reference" and "impacted" situations.
3. The potential to rehabilitate compromised functions in impacted systems. Topics aimed to evaluate the potential to support or rehabilitate desired functions in impacted river system by implementing eco-morphological measures such as river widening, habitat improvement (e.g., by introducing large wood), and other measures such as the implementation of ecological flows.

Data Collection and Data Analysis

Data were collected by reviewing scientific outputs (up to 31st March 2019) from the SMART EMJD doctoral candidates, and the reports produced by the SMART EMJD administration. Information on research articles was retrieved from Elsevier's Scopus, a database of peer-reviewed scientific literature. Three out of 69 published papers were not covered by Scopus at the time of the analysis. Therefore, they were excluded from further analyses based on the Scopus statistical tools. The numbers of cited references for these papers were retrieved from the Web of Science platform (Clarivate Analytics). The impact from the 69 research articles was assessed by the number of citations and the impact factor of the journal (retrieved from the journal's websites) at the time of the study (March 2019).

The data were explored in relation to the three key elements of the doctoral program: interdisciplinarity, internationalism, and management-oriented science. Two questionnaire surveys were sent to all SMART alumni and supervisors to ask about the overall perception of the program and of its effectiveness. The questionnaires are reported in the SI. The response rate was 69% from the doctoral candidates and 76% from the supervisors. The responses provided insights into the experiences gained through the doctoral program and contextualized the information emerging from the analyses of the scientific outputs.

Interdisciplinarity

There have been a wide range of definitions of interdisciplinary research (e.g., Klein, 1990, 1996; Becher and Trowler, 2001; National Academy of Sciences et al., 2005; Wagner et al., 2011). In this study, we adopted the definition of the National Academy of Sciences et al. (2005) as "*. . .a mode of research by teams or individuals that integrates information, data, techniques, tools, perspectives, concepts, and/or theories from two or more disciplines or bodies of specialized knowledge to advance fundamental understanding or to solve problems whose solutions are beyond the scope of a single discipline or area of research practice*." This definition has been widely adopted (Porter et al., 2006, Rafols and Meyer, 2008; Porter and Rafols, 2009; Wagner et al., 2011). We also adopted the addition proposed by Aboelela et al. (2007) of a requirement of perspectives and skills of the involved disciplines throughout multiple phases of the research process. These key criteria of researchers from different disciplinary backgrounds working in collaboration, with an integrated approach, toward an agreed common goal, and with on-going dialogue is what distinguishes interdisciplinarity from: multi-disciplinarity (*more than one discipline working on the same problem but with no real conversation*); pluri-disciplinarity (*disciplines interacting on the basis of work from other disciplines*); trans-disciplinarity (*the organization of interdisciplinary research by a grand unifying vision*) (see Klein, 1990), and cross-disciplinarity (*a generic, over-arching term for multi-, inter-, pluri- and transdisciplinary*) (Vugteveen et al., 2014).

In our study the criteria used for measuring interdisciplinarity were (1) number of fields/disciplines integrated in the research and (2) expertise of the participants. We considered three major components of river science: landforms, biota and water flow, as identified in earlier literature (e.g., Corenblit et al., 2007, see also D'Alpaos et al. (2016) for a short review of currently used terminology). A research "focus" was then defined by an integrative term that combined research disciplines into a single term (e.g., biogeomorphology), or two adjacent terms (e.g., light ecology). A percentage score was given to quantify the proportion of each doctoral thesis covered by a research focus and was computed as (1/n) × 100% for a thesis that covered n areas. The proportions were related to the core chapters reporting the substantive research results in the doctoral theses, where each chapter was assigned a main research focus according to its content. For example, if a thesis consisted of three research chapters of which two mainly focused on biomorphology and one on ecology, 66% would be given to biomorphology and 33% to ecology for the entire thesis. The main research focus of a chapter was usually described in the thesis, and if not, the author selected the most appropriate focus. The overall contribution of a research focus to the whole of the 36 theses was computed as the sum of each score for that focus weighted by the proportion of theses in which that focus was present.

For all SMART EMJD alumni and supervisors, a background check was conducted to characterize initial disciplinary and specialist fields. This was done by consulting sources such as CVs, personal and university webpages to ascertain postgraduate degree areas and/or reported work experience immediately prior to involvement in the SMART EMJD. The backgrounds of doctoral candidates were defined with reference to the three major research components for river science: "water flow," "biota" and "landforms," which have been labeled as "HYDRO," "ECO," and "GEO," respectively. Twenty-seven doctoral candidates were categorized within one of these fields, one was categorized in geomatics and eight had an interdisciplinary background combining two main areas. Although most supervisors were involved in collaborative research projects spanning different fields, an interdisciplinary background was assigned only to people for whom multiple research areas were equally important. The backgrounds of SMART EMJD alumni were compared with those of the supervisors and the interdisciplinary research areas of the doctoral theses to analyze the knowledge gained from interdisciplinary fields.

Internationalism

The international character of the program was analyzed through the nationalities of SMART EMJD applicants and doctoral candidates and the international collaboration established within the program. Internationalism was also quantified as the proportion of applicants and selected doctoral candidates recruited from 5 out of the 7 continents globally. These values were compared to the nationalities of applicants and selected doctoral candidates of all EMJDs for the year 2015 (including SMART), for which data were available on the funding agency website[1]. We further analyzed international collaboration during the program and relocation of the doctoral candidates after finishing the program, for example returning to their home country or moving to a new country.

[1] https://eacea.ec.europa.eu/erasmus-plus/library/scholarship-statistics_en

Management-Oriented Science

The doctoral theses were categorized according to the research areas defined in **Figure 2**. This analysis was undertaken by detailed screening of the theses to detect the main links to: (a) ecosystem resilience; (b) natural functioning; and (c) river management. Each thesis chapter was assigned to one or more areas and when more than one area was identified the percentage score was equally divided. The science for management domain was further analyzed through the responses to the surveys, and occupations of SMART EMJD alumni at the time of the survey.

RESULTS

Scientific Outputs and Impact

By the end of March 2019, SMART EMJD doctoral candidates had published 69 papers (59 first-authored, 15 co-authored papers), including five papers with two doctoral candidates as authors. Of the 69 papers, 50 were classified in Scopus as primary research articles; seven were classified as review/overviews articles, six as conference papers, and six as short papers. In total, 45% of all papers were accepted for publication before the candidates' defense date, corresponding to an average number of 0.9 papers per candidate, of which 71% were first-authored papers. This was lower than the average number of papers (1.9 papers per candidate before defense, 50% first-authored papers) of a reference group of 32 doctoral candidates enrolled at the same time as the SMART doctoral candidates in doctoral programs at the partner institutions. As expected, the number of papers related to the Ph.D. continued to grow after the defense.

Up to the end of March 2019, SMART EMJD papers were cited in total 831 times, by 709 different publications, including one paper that received 336 citations (Zarfl et al., 2015). There was no correlation between the number of citations of a specific paper and the impact factor of the respective journal (**Figure 3A**). As expected, the number of publications (and citations) increased with time (**Figure 3B**). The impact factor of the journals varied between 1.2 and 11.7 (mean: 4.2) (**Figure 3C**). On average, each SMART EMJD paper received 12 citations (median value: 6), excluding the article by Zarfl et al. (2015).

Interdisciplinarity in the SMART EMJD Research

Doctoral candidates and supervisors considered interdisciplinarity as a major asset of the SMART EMJD research program, indicated through the questionnaire. Among the doctoral candidate participants, 76% found it motivating to do research which included several disciplines and 76% agreed/fully agreed that their doctoral research was enriched by working with supervisors from different disciplinary backgrounds. While more than half of the doctoral candidates (52%) acknowledged that interdisciplinarity presented an extra challenge, 64% indicated that their research project could have been more interdisciplinary than it actually was. Furthermore, 80% stated that the interdisciplinary nature of the SMART EMJD has improved their career options and 92% stated that the program has improved their ability to work in an interdisciplinary context.

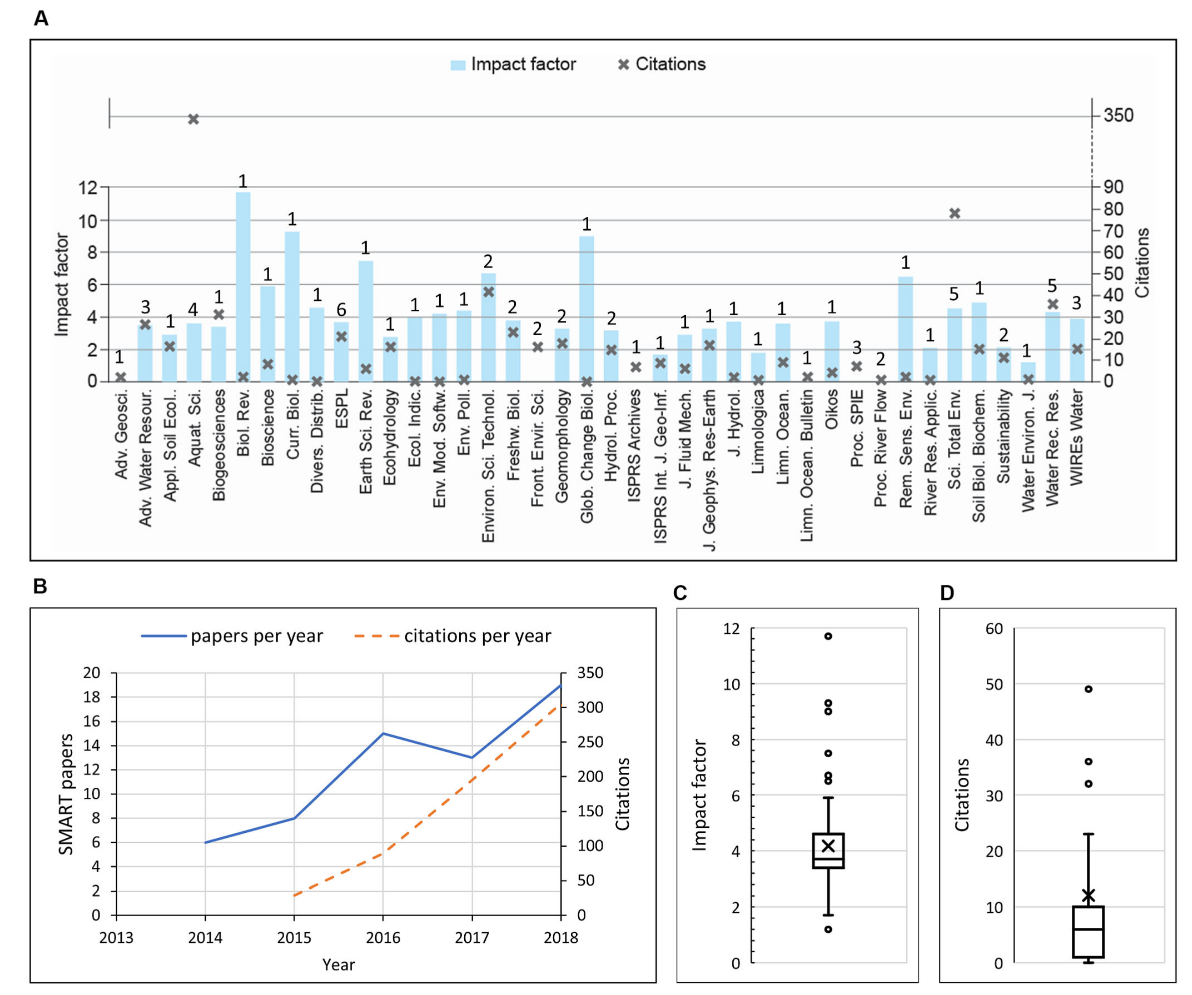


FIGURE 3 | (A) Impact factor and citations per journal or conference proceedings with numbers above bars indicating the total number of published papers within the corresponding journal; **(B)** papers published in the SMART EMJD and related citations per year; boxplots showing distributions of **(C)** journal impact factor and of **(D)** the number of citations for all papers. The horizontal line within the box represents the median, the mean is presented with a cross symbol, outliers as circles, the quartiles are calculated excluding the median (papers and number of citations considered up to March 2019).

Among the supervisors, 69% of the survey participants agreed/fully agreed that their knowledge improved in disciplines beyond their original areas of expertise and 65% of the supervisors indicated that the program has led them to explore other research areas. 50% also stated that the interdisciplinary nature of the Ph.D. topics led to higher quality science compared to topics from traditional disciplinary areas.

Doctoral Theses and Publications

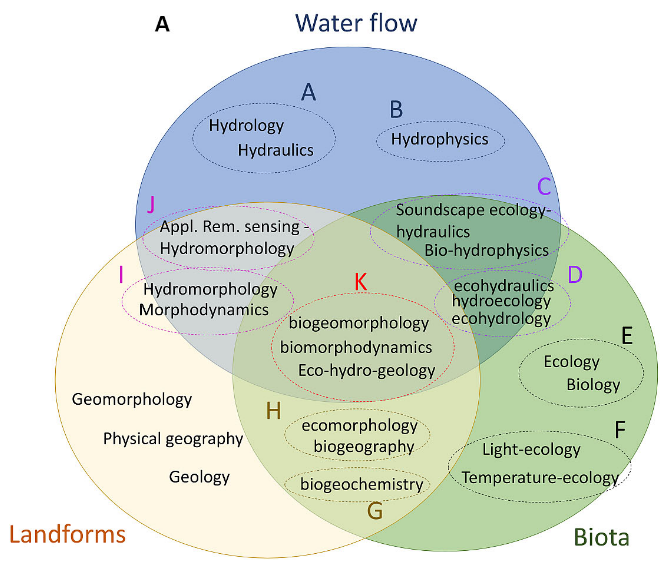
Figure 4A illustrates the identified research foci across all doctoral theses within the three major components: water flow, landforms, and biota. **Figure 4B** lists the percentage contribution of these research foci to the ensemble of the 36 doctoral theses. Interdisciplinary research between the three research components predominates, with 81% of the investigated work concentrated in two or more research foci. Nearly 1/3 of the theses covered the three major components (subgroup K) while only 19% covered one.

Figure 5A presents the total number and relative proportion of papers (from a total of 66 Scopus-indexed SMART EMJD papers) addressing the subject areas associated with the journals within the Scopus databases. **Figure 5B** displays the subject areas for the 709 papers citing the SMART EMJD papers. The results show a similar distribution of the subject areas across published papers and citing papers with environmental science (32 and 36%), agricultural and biological sciences (18 and 23%), earth and planetary sciences (15 and 14%) jointly cover nearly 70% of all identified disciplines.

Disciplinary Backgrounds

Table 1 shows the backgrounds of the doctoral candidates and supervisors for each of the SMART EMJD partner institutions.

From 34 supervisors, 18 had a background within either the ECO, GEO or HYDRO research components, one within geomatics, and 15 already exhibited an interdisciplinary expertise. Each doctoral candidate was appointed to at least two



B

		%
A	Hydrology/Hydraulics	2
B	Hydrothermodynamics Physical hydrology	7
C	Soundscape ecology - hydraulics Bio-hydro-physics	4
D	Ecohydraulics Ecohydrology Aquatic ecology	13
E	Ecology/Biology	2
F	Light-ecology Temperature-ecology	8
G	Biogeochemistry	5
H	Ecomorphology Biogeography	8
I	Hydromorphology Morphodynamics	15
J	Applied remote sensing - hydromorphology	6
K	Biomorphodynamics Eco-hydro-geology	29

FIGURE 4 | (A) Overview of research foci in the SMART EMJD, within the three major river science components: Water flow, Biota and Landforms. **(B)** Percentage contribution of each research focus across all the 36 doctoral theses.

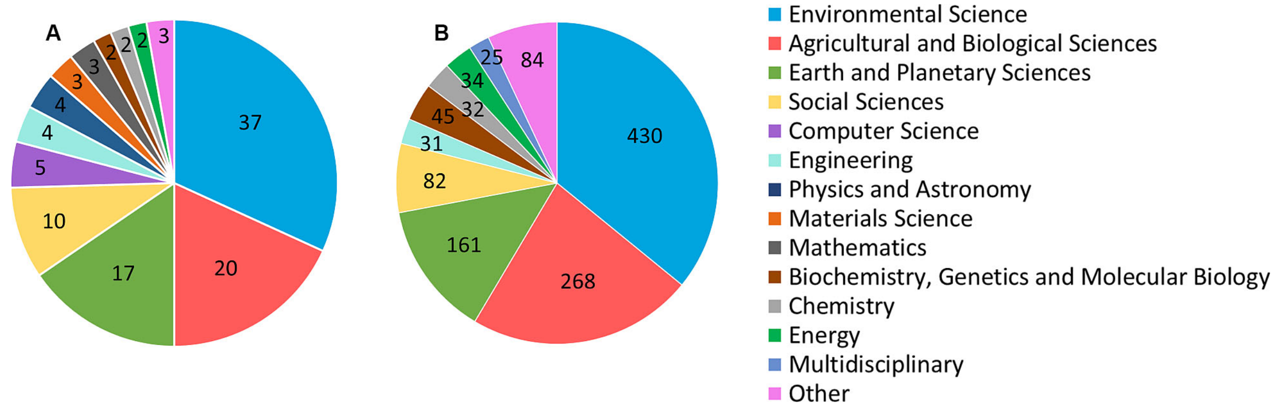


FIGURE 5 | The proportion of different subject areas (size of pie slices) and related number of Scopus documents associated with the journals in which **(A)** the 66 Scopus-indexed SMART EMJD papers have been published and **(B)** all 709 papers citing the SMART EMJD papers have been published.

TABLE 1 | Initial backgrounds of the SMART EMJD doctoral candidates and supervisors per institute.

		ECO	HYDRO	GEO	GEO-MATICS	ECO-HYDRO	GEO-HYDRO	ECO-GEO	ECO-HYDRO-GEO	BIO-GEO-CHEM.	Total
University of Trento	Supervisors		3		1		4				8
	Candidates	2	10		1	2					15
Queen Mary University of London	Supervisors			1			1	1	2	2	7
	Candidates	2	2			3	1				8
Freie Universität Berlin	Supervisors	6	2			3				1	12
	Candidates	10	1					2			13
Associate partners	Supervisors	4	2				1				15

and up to four supervisors. During the SMART EMJD, there were 110 connections established among the 34 supervisors and 36 doctoral candidates. For 35% of those connections, the candidate had a different disciplinary background to the supervisor while for 65% of connections the topical focus was similar. **Figure 6** indicates the growth of the network among supervisors by comparing the existing network before the SMART EMJD (**Figure 6A**) and at the end of the program (**Figure 6B**). A total

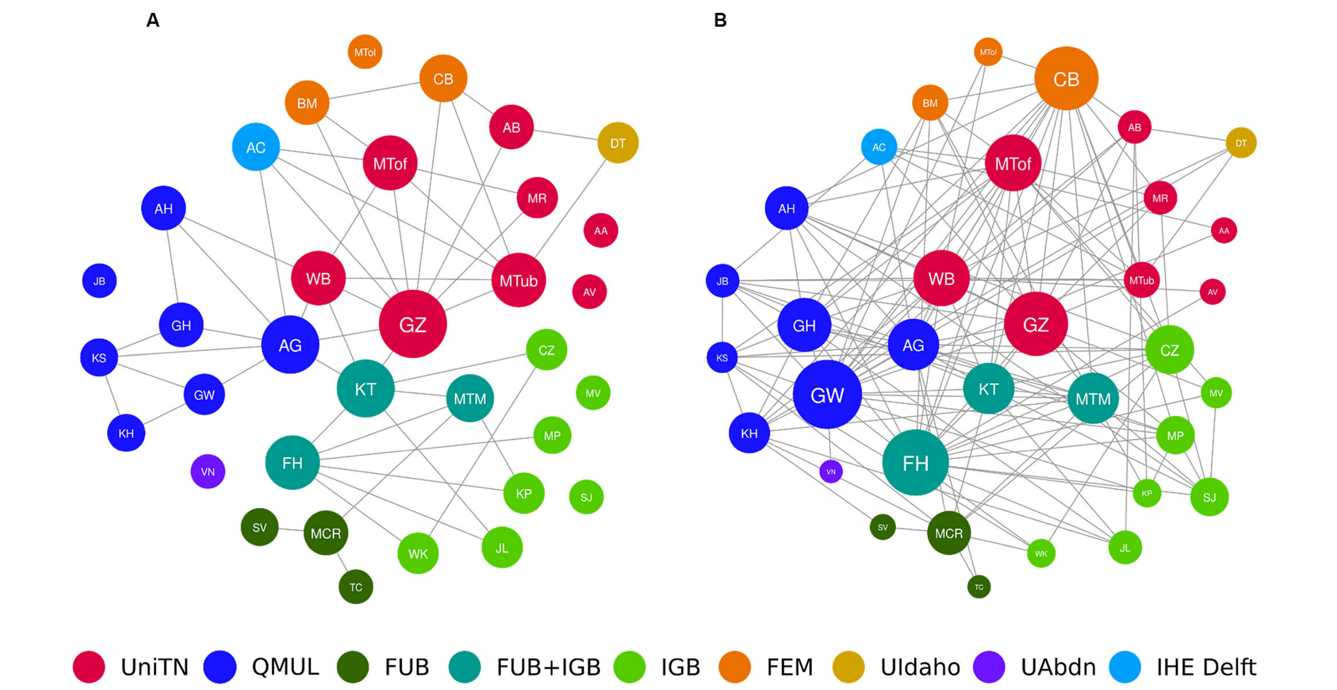


FIGURE 6 | Network maps presenting the scientific connections between supervisors: **(A)** before the start of the SMART EMJD, and **(B)** after the SMART EMJD. Node size is proportional to the relative amount of connections of the supervisor.

of 86 new connections were established corresponding to an increase of 183%.

The interdisciplinary research foci assigned to the doctoral theses (**Figure 4A**) were further compared to the backgrounds of the SMART EMJD doctoral candidates and supervisors. On average, doctoral candidates and supervisors were introduced, respectively, to 1.4 and 1.8 new research foci.

Internationalism

The international dimension of the SMART EMJD was founded upon the recruitment of candidates from EU and non-EU countries working with supervisors from different nationalities, upon the mobility requirements of the program, and upon the locations of the training weeks, meetings and field sites.

The international collaboration within the SMART EMJD primarily occurred within each individual doctoral research project, in which candidates and supervisors were often from different nationalities. Internationalism was further enhanced through periodical meetings and workshops, including an "Annual Week" during which the progress of each doctoral candidate was presented to all participants and assessed by the Academic Board of the program. The Annual Week provided an effective forum for high quality, regular scientific interactions among the doctoral candidates and the supervisors. The doctoral program further allowed doctoral candidates to spend time at different institutes and associate partners providing access to international field sites.

All doctoral candidates who participated in the survey agreed that working in an international context improved their research. Most candidates (96%) agreed that it further improved their capability and preparedness to work in an international environment. In addition, a very strong (global) community was built between the SMART EMJD doctoral candidates and supervisors, which may last for many years, facilitating future opportunities in science and beyond.

SMART Applicants and Doctoral Candidates

In total, 378 eligible candidates applied for the SMART EMJD program (all five cohorts). **Table 2** provides an overview (per cohort) in comparison with all Erasmus Mundus Joint Doctorates for 2015. For the SMART EMJD, the total number of applicants increased after the first year, suggesting a growth in awareness and international recognition of the program. In the 4th and 5th call, applicants were asked where they learnt about the program, with 46 and 53%, respectively, reporting the official SMART EMJD website[2] as the main source. The second source was oral communication (21 and 15%, respectively), while all others indicated other sources of information.

The largest number of applications came from Asia, followed by Europe, Africa and America with no applications from Australia and Oceania. A similar trend was observed in the number of applicants to all EMJDs, although the SMART EMJD had a lower proportion of African and a higher proportion of European applicants.

The proportion of selected doctoral candidates was highest for Europe, followed by Asia, North and South America and Africa. Compared to SMART, all EMJDs supported by

[2] www.riverscience.it

TABLE 2 | Number of applicants (top panel, *n* = 378) and doctoral candidates (bottom panel; *n* = 36) per year and continent for the SMART EMJD and total applicants and doctoral candidates in all EMJDs (including SMART) in 2015.

	SMART EMJD program						All EMJD programs	
	Applicants					% total	Applicants	% total
	2011	2012	2013	2014	2015		2015	
Africa	11	17	12	16	20	**20**	824	**27**
Asia	23	29	36	29	44	**43**	1373	**45**
Australia and Oceania	0	0	0	0	0	**0**	11	**0.4**
Europe	17	25	20	19	24	**28**	621	**21**
North-America	2	5	5	5	1	**5**	99	**3**
South-America	2	3	3	3	7	**5**	100	**3**
Total	**55**	**79**	**76**	**72**	**96**		**3028**	
	Doctoral candidates					**% total**	**Candidates**	**% total**
	2011	**2012**	**2013**	**2014**	**2015**		**2015**	
Africa	0	1	0	0	0	**3**	12	**10**
Asia	4	2	3	3	1	**36**	57	**47**
Australia and Oceania	0	0	0	0	0	**0**	1	**1**
Europe	4	4	3	3	2	**44**	29	**24**
North-America	2	0	0	1	0	**8**	13	**11**
South-America	0	0	1	0	2	**8**	10	**8**
Total	**10**	**7**	**7**	**7**	**5**		**122**	
% selected	18	9	9	10	5		4	

EACEA had slightly more doctoral candidates from Asia and Africa and less from Europe. The number of selected European doctoral candidates, however, is also influenced by the number of designated Erasmus Mundus scholarships for EU citizens. The selection rate is presented in the final row of **Table 2**, indicating the number of selected doctoral candidates over the total applicants. The selection rate varied among SMART EMJD cohorts and was higher than the average figure reported for all EMJDs.

Figure 7 presents an overview of the movement of the doctoral candidates from their home countries to their destination countries at the beginning and end of the SMART EMJD, respectively. Of the 15 EU and 21 non-EU doctoral candidates, 26 now reside in the EU while 10 reside outside the EU. 14 doctoral candidates remained in the country of their primary institution (for 5 their country of origin), 10 returned to their home country, and 10 moved to another country.

International Collaboration and Research

Besides online communication and interactions within each institution, the Consortium-wide meetings included the SMART Annual Week and yearly meetings to select new doctoral candidates and to assess the admission of 3rd-year candidates to the final defense. These meetings fostered international collaboration and development of professional networks both for the doctoral candidates and the supervisors. The research presentations and discussions and social events (field trips, informal lunch gatherings and dinners) were also a key element in breaking down disciplinary boundaries by creating multiple opportunities to communicate with one another and address differences in approaches and terminology. The location of the Annual Weeks started on the braided Tagliamento River in NE Italy, where previous collaboration among the lead scientists of the program started, and then rotated on a 3-year cycle between Trento, Berlin and London including local fieldtrips. The Annual Training Weeks were attended by all enrolled doctoral candidates and by nearly all supervisors. Total duration of these meetings covered 48 days over 8 years and participation can be quantified as a total of 1184 person-days when summing the actual presence of each individual (**Figure 8**). International collaboration was further promoted through the compulsory 6-month mobility to a secondary institution, which is quantified in **Figure 8**.

Candidate mobility between different institutes and associate partners also provided opportunities to access international field sites and the fieldwork itself facilitated further international collaboration. Fieldwork was a component of 24 out of the 36 research projects with the majority of candidates working outside their home country. Fieldwork was undertaken by 10 doctoral candidates in Italy (e.g., Cashman et al., 2017; Zen et al., 2017; Brighenti et al., 2019), 7 in Germany (e.g., Grubisic et al., 2018; Gaona et al., 2019), 6 in the UK (e.g., Faller et al., 2016), 3 in Poland (e.g., Pilotto et al., 2014), 1 in the Netherlands (Belliard et al., 2016), 1 in France (Serlet et al., 2018), and 1 in Romania. Four doctoral candidates did fieldwork in more than one European country. Six SMART EMJD doctoral candidates further analyzed data from one or more rivers using existing national or international databases and GIS analysis in Europe. Three doctoral candidates studied and used existing data of rivers or other freshwater systems in Africa and South America (Monegaglia et al., 2018), New Zealand (Redolfi et al., 2016),

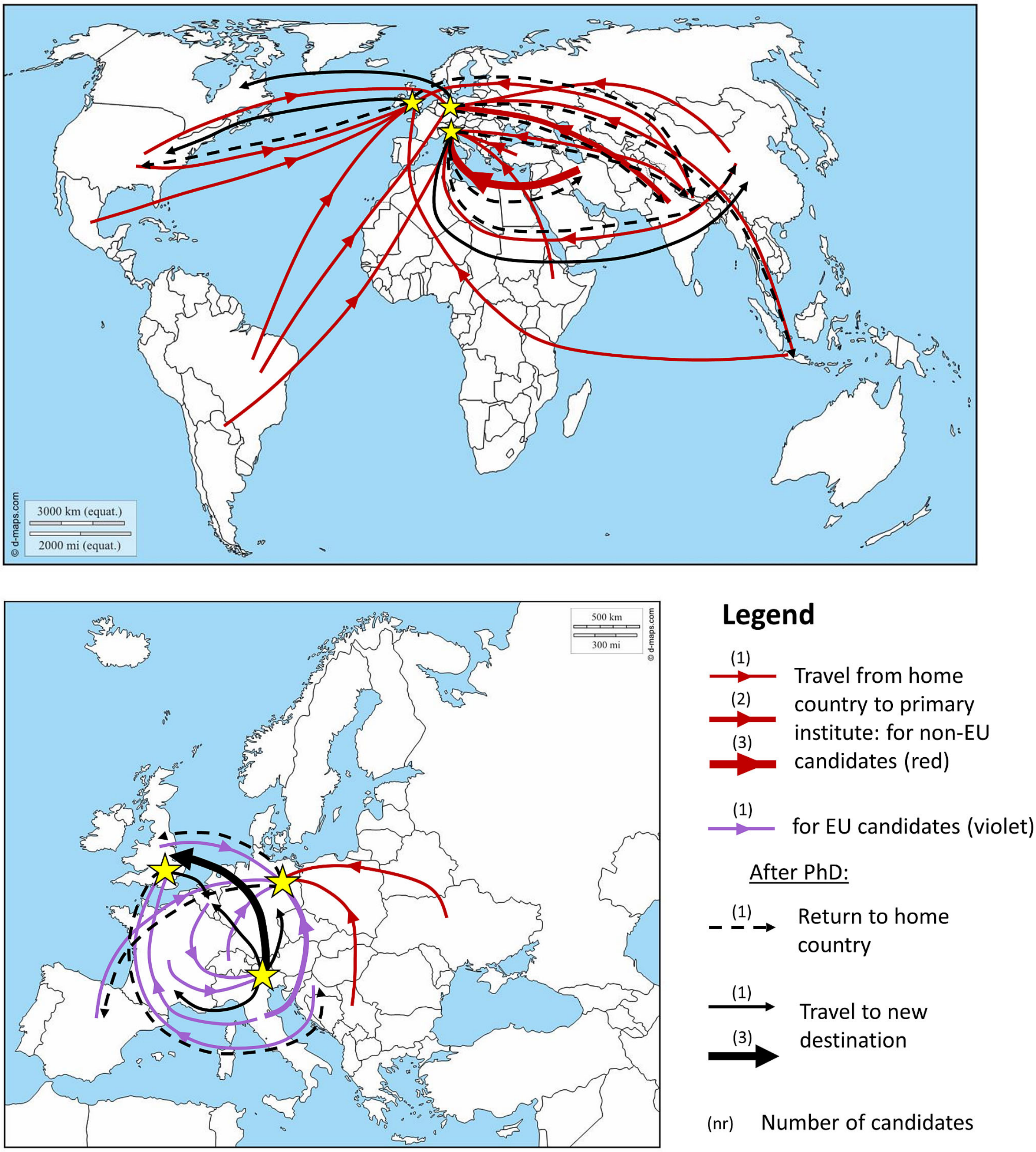


FIGURE 7 | Arrows indicate the movement of doctoral candidates from their home countries to the primary institutions at the start of the program (in red) and for those who did not stay in the same country their return to either their home country (black intermittent arrow) or to a new destination (black arrow). The upper panel shows a global map with travel between Europe and other continents, the lower panel presents a map of Europe with travel within Europe.

and Paraguay (López Moreira M et al., 2018). Finally, 4 doctoral candidates compiled existing data sets for global-scale studies (e.g., He et al., 2019; Shumilova et al., 2019).

Management – Oriented Science

A first assessment of management-oriented science within the SMART EMJD was derived from an analysis of the alignment of each thesis with the three research areas (a, b, and c, see **Figure 2** and description of the case study under Methods). The most prevalent research area was (b) natural functioning (57%), followed by (a) ecosystem resilience to stressors (34%), and finally, (c) rehabilitation of functions (9%), which was the area most directly linked to river management. Research projects in area (c) included: river restoration using large wood and/or vegetation, hydropower management related to sediment flushing, hydro-peaking, and vegetation encroachment,

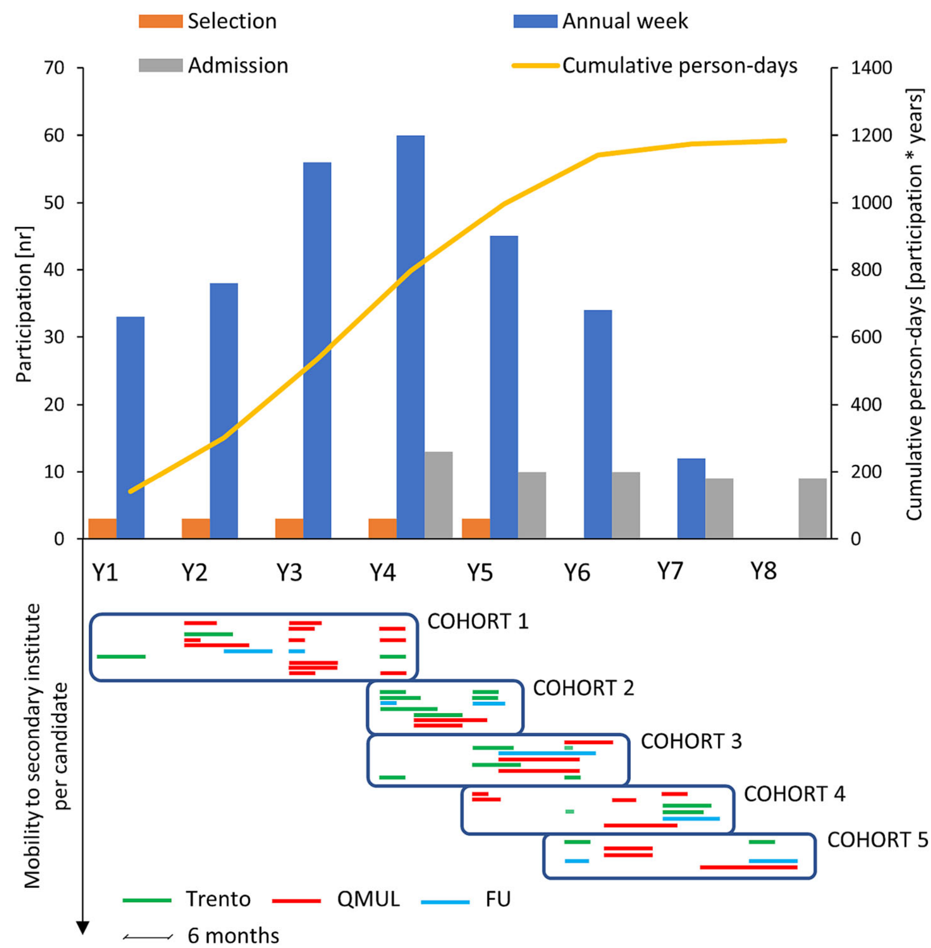


FIGURE 8 | On top: Participation for each meeting event (selection, annual week, and admission) and cumulative days of these meetings. Below: Overview of secondary mobility over time of all doctoral candidates with color indicating the institute.

conservation management and rehabilitation of contaminated (from e.g., heavy metals, nutrients) rivers and lakes. Other indirect links with management included habitat assessment and mapping, reconstructing trajectories in understanding the natural reference conditions, studies on impacts such as artificial light, invasive species, and hydropower.

Collaboration with river managers was more limited than anticipated (see Discussion). Only 12% of the doctoral candidates who participated in the survey confirmed collaborations with organizations directly involved in river management and only three doctoral candidates had an Associate Partner (Environment Agency, United Kingdom) who was directly involved in river management although some doctoral candidates working on impacted rivers and lakes had productive local collaborations for sharing data and knowledge.

In terms of career profiles, at the time of this study, 18 alumni started/continued working in academia, 6 in governmental institutions, 4 in the private sector, 4 in research institutions or an NGO and 1 was unemployed. From the survey, 60% of the doctoral candidate participants and 54% of supervisors believed that the SMART EMJD improved their employability in the river management sector. Overall, 22% of the jobs secured were directly related to management (13% associated with human impacts and 9% linked to policymaking, planning and regulatory services). The remaining 78% of SMART EMJD alumni were involved in other dimensions of river or environmental science not directly related to management.

DISCUSSION

Interdisciplinary approaches and collaboration are necessary to address the most pressing socio-ecological challenges humankind is facing[3], including securing one of our most valuable resources: freshwater ecosystems (Bunn, 2016). Doctoral training programs that move beyond "disciplinary silos" and cut across traditional boundaries provide "fertile environments for collaborative research" (Borrego and Newswander, 2010) and are fundamental to building interdisciplinary research capacity globally. More

[3] http://www.millennium-project.org/projects/challenges

knowledge is needed on the practical and intellectual processes involved in interdisciplinary research training and what Gardner (2013) has called the "socialization to interdisciplinarity." Our reflections on the 9-year SMART EMJD doctoral training program and the lessons learned from an analysis of the three core facets of the program – (1) interdisciplinarity; (2) internationalism; and (3) management-oriented science – help allay some concerns about interdisciplinary training and provide insights for future river science training.

Scientific Outputs and Impacts

The most obvious scientific outputs and impacts of the program are the publications and more are anticipated from manuscripts currently in preparation or under revision. Millar (2013) found that graduates of interdisciplinary research programs tend to achieve a higher publications record. However, the average number of first authored publications before the defense was lower for SMART candidates compared to those in established institutional Ph.D. programs at the three universities. It has to be acknowledged that most SMART candidates had to adapt to a different cultural setting, were required to finish in about 3 years, and had to spend extensive time at two institutions in different countries. At the same time, a higher proportion of first-authored papers for SMART candidates indicates a higher degree of independence and a stronger focus on the specific research goals. Overall, the comparison suggests satisfactory rates of scientific publishing were achieved for the SMART program.

The research outputs covered a very broad spectrum of research foci reflecting how doctoral candidates were exposed to a broad array of research areas. Indeed, it is an ambition of the program to establish longer-term international and interdisciplinary networks and wider career options, to address novel questions and distinct recommendations for river science and management, as well as to meet a broad audience (e.g., Mardhiah et al., 2014; Zarfl et al., 2015; Bodmer et al., 2016; de Souza et al., 2016; Faller et al., 2016; Redolfi et al., 2016; Manfrin et al., 2017; Serlet et al., 2018). Furthermore, as the publications are very recent, citations are expected to increase.

The added value of working in an international and interdisciplinary context resulted in knowledge and appreciation of different perspectives to be gained from other disciplines. The doctoral training program supported the formation of new collaborative research teams, which both doctoral candidates and supervisors found rewarding in terms of gaining skills and insights into disciplines, methods, and organizational structures beyond what a "classical" doctoral project may offer. Established researchers expanded their international and interdisciplinary collaborations through the doctoral supervision and there is a strong motivation from former supervisors and alumni from the program to maintain and grow the networks.

Employability from the program was high and provides reassurances to counter the frequently voiced concern that interdisciplinary researchers face enhanced barriers to career success as has often been the concern (e.g., Loeb, 2020). Programs like SMART EMJD which aim to provide science for management by balancing international experience with established locally-centered practices (Pinter et al., 2019) are perhaps helping to encourage graduates to pursue careers in environmental management as well as science opening up new career opportunities.

Challenges

Despite the many achievements of the SMART program, there remained challenging aspects. Collaboration among different groups and the integration across research projects was limited and the opportunities offered by the program were not fully exploited and, therefore, may have confined additional insights and publications. However, this was difficult to achieve within the constraints of 3 years of doctoral training, including mobility requirements. These constraints may have also limited the average number of publications before the defense and may in some cases represent a disadvantage for candidates when searching for future employment in academia.

The SMART program aimed to attract the strongest applicants globally. However, attracting students from North America and especially Australia and Oceania was a challenge and the reasons are unclear. This trend was mirrored across all EMJDs, so additional efforts will be needed to integrate these continents in future EU-funded programs.

The international aspects of the program, including the mandatory mobility, presented practical challenges compared to other doctoral programs. Key difficulties included finding short-term housing in the different research locations, getting acquainted with new administrative regulations, building up new professional and social relationships, assembling field equipment at new institutions and using new laboratory facilities. Asking for and receiving proper support was easy for some but very challenging for others especially when exacerbated by language barriers that could be mentally straining.

While having an international supervisory team was for most candidates an enriching experience, a few doctoral candidates reported conflicting needs including different goals in research, different styles of writing, as well as diverging expectations. Ensuring regular contact among the team members (for example through frequent Skype meetings) is critical to keep everyone "on board," and designated local support contacts can help to advise on differing institutional requirements such as research progress reporting and thesis structure.

The SMART EMJD was established with a clear goal to integrate river science and management. However, only 9% of all research outputs from the doctoral theses are directly related to the rehabilitation of impacted river systems. Practical barriers to securing placements with environmental management organizations and companies sometimes meant that direct collaboration with river managers and close integration of science and management was more difficult to achieve than anticipated. But a more widespread problem identified in the survey was the ambitious combination of interdisciplinary, international, and management-oriented approaches within in a 3-year doctoral program. The completion of the scientific components including the doctoral thesis, research papers, and presentations at international science conferences were necessarily prioritized. And doctoral candidates undertaking extended periods of intense fieldwork and/or laboratory work struggled to allow sufficient time to develop recommendations for managers.

Finally, awarding a joint doctoral degree between universities belonging to different countries, even within the context of the EU, raised many administrative challenges and required a spirit of compromise. New institutional agreements were put in place that followed the doctoral regulations in place at the primary institution of each candidate and set minimum requirements that could also be accepted by the secondary institution.

CONCLUSION

We have assessed the contribution of a 9-year European doctoral program in river science ("SMART" Erasmus Mundus Joint Doctorate), led by three universities with complementary expertise (engineering; ecology; geomorphology). The program trained 36 doctoral candidates under the supervision of 34 senior researchers with an interdisciplinary and international focus on river systems, aiming to move across the boundaries between science and management. The program was analyzed by reviewing contents of doctoral theses and peer-reviewed, international indexed publications, as well as by synthesizing the outcomes of two assessment questionnaires directed to doctoral candidates and supervisors.

Results focused on the three core facets of the SMART EMJD: (1) interdisciplinarity; (2) internationalism; and (3) management-oriented science. We found that the doctoral program resulted in a highly interdisciplinary (80% of publications) and consistent scientific output, consisting of 69 published papers (of which 66 were Scopus-indexed) papers at the time of performing the analysis for this paper. Through an approximate comparison with the number of indexed papers resulting from "standard," institutional doctorates focused on rivers in the same institutions, it emerges that SMART candidates produced fewer papers on average before their defense, however, a larger proportion was first-authored. Despite the challenges posed by such an ambitious program completion rates and employment were good. In total, 86% of all SMART EMJD candidates successfully completed the doctoral program and nearly all (97%) doctoral candidates were employed very soon after being awarded a joint doctoral degree in river science by two of the partner institutions of the SMART program. Employment occurred both in river-related research (50%) and private/public sector (50%) and was strongly international, likely reflecting the international dimension of the program.

As such, the success of this program is reflected mainly in the large number of peer-reviewed articles with a high degree of interdisciplinarity, a high mobility of the doctoral scientists among the international partners, and a successful career progression, mainly in river science, after award of the doctoral thesis. The three main features that facilitated this success are: (1) the combination of supervisors from different disciplines and their inherent motivation to work across and beyond their own expertise and provide science for river management; (2) the sound (inter)disciplinary background, motivation, and openness of the selected doctoral candidates in taking up the challenge; and (3) the mobility schemes that were integrated in the schedule of each doctoral candidate's study program.

Such an interdisciplinary and international program required a huge commitment by the partner institutions including doctoral candidates, supervisors, and administrative staff with nearly 1200 person-days of joint assessment and scientific meetings in addition to the compulsory mobility arrangements for individual doctoral candidates. But we witnessed the importance of these scientific and social gatherings in enabling interaction and providing the environment in which creativity, novel ideas and solutions, and new opportunities could emerge. We are optimistic that the strong interdisciplinary and international networks fostered within SMART will provide a platform for future research collaborations.

Going forward we hope that future doctoral training programs in river science can learn from programs like SMART and other successful programs closely connected to river management such as the IGERT Ph.D. program in the United States[4], recognizing and working to overcome some of the key challenges (Lindvig and Hillersdal, 2019). Funds to allow graduate mobility and research across multiple river systems are critical and we might also work to realize Geoff Petts' aspiration for a "global river science graduate school" with research students connected by regular e-seminars (Petts, 2013). Integrating new methods and disciplines, including those related to social and human sciences, will also be an important step forward to advancing understanding and management of "rivers as socio-ecological systems" (Kingsford et al., 2011).

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

AS was responsible for manuscript coordination and contributed to the preparation of surveys, data processing, analysis, and preparation of results and writing. GL contributed to the preparation of surveys, data processing, analysis, and preparation of results and writing. GZ and GW contributed to conception and design of the study and extensive revisions and writing. FH, AG, KT, WB, MB, SJ, JL, MM, MCR, MT, SV, and CZ contributed with revisions, comments, and minor writing. MR contributed to the preparation of the first surveys, data collection and processing, and preparation of administrative reports. All authors read and approved the final version of the manuscript.

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[4] http://igert.siu.edu/

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2020.00063/full#supplementary-material

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Modeling the Effect of Enhanced Lateral Connectivity on Nutrient Retention Capacity in Large River Floodplains: How Much Connected Floodplain Do We Need?

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Floodplains have been degraded in Central Europe for centuries, resulting in less dynamic and less diverse ecosystems than in the past. They provide essential ecosystem services like nutrient retention to improve overall water quality and thus fulfill naturally what EU legislation demands, but this service is impaired by reduced connectivity patterns. Along the second-longest river in Europe, the Danube, restoration measures have been carried out and are planned for the near future in the Austrian Danube Floodplain National Park in accordance with navigation purposes. We investigated nutrient retention capacity in seven currently differently connected side arms and the effects of proposed restoration measures using two complementary modeling approaches. We modeled nutrient retention capacity in two scenarios considering different hydrological conditions, as well as the consequences of planned restoration measures for side arm connectivity. With existing monitoring data on hydrology, nitrate, and total phosphorus concentrations for three side arms, we applied a statistical model and compared these results to a semi-empirical retention model. The latter was originally developed for larger scales, based on transferable causalities of retention processes and set up for this floodplain with publicly available data. Both model outcomes are in a comparable range for NO_3-N (77–198 kg ha^{-1} yr^{-1}) and TP (1.4–5.7 kg ha^{-1} yr^{-1}) retention and agree in calculating higher retention in floodplains, where reconnection allows more frequent inundation events. However, the differences in the model results are significant for specific aspects especially during high flows, where the semi-empirical model complements the statistical model. On the other hand, the statistical model complements the semi-empirical model when taking into account nutrient retention at times of no connection between the remaining water bodies left in the floodplain. Overall, both models show clearly that nutrient retention in the Danube floodplains can be enhanced by restoring lateral hydrological reconnection and, for all planned measures, a positive effect on the overall water quality of the Danube River is expected. Still, a frequently hydrologically connected stretch of national park is insufficient to improve the water quality of the whole Upper Danube, and more functional floodplains are required.

Keywords: floodplain, lateral hydrological connectivity, Danube, restoration, reconnection, inundation, nutrient retention, modeling

INTRODUCTION

Rivers and their adjacent floodplain ecosystems are essential for human life and biodiversity, but are among the most threatened ecosystems globally (Tockner et al., 2008). One very important characteristic increasingly recognized by society and politics is also the floodplains' tendency to retain floodwater and nutrients when inundated, which nowadays happens only very rarely during high floods in regulated river systems (Schober et al., 2015). Pressures on floodplains are high, especially around large rivers and in the vicinity of large cities or areas with intensive agriculture. Reduction of river length, cutting-off of side arms, bank stabilization, and the establishment of groins and reservoirs has led to a functional decoupling of river and floodplain, further intensified by resulting riverbed incision. Restoring lateral hydrological connectivity between rivers and their floodplains could bring back ecological functionality and the provision of several ecosystem services, including nutrient retention (Opperman et al., 2010; Thorp et al., 2010; Funk et al., 2019).

Floodplains are seen as important nutrient sinks (Spieles and Mitsch, 1999; McClain et al., 2003; Hoffmann et al., 2011; Hopkins et al., 2018), with a higher retention potential than in the main channel (Saunders and Kalff, 2001; Venterink et al., 2003). For nutrients to be retained more efficiently, the supply to floodplains needs to be assured (Amoros and Bornette, 2002; Hein et al., 2004; Noe and Hupp, 2005). Only dissolved nutrients are transported, dependent on oxic conditions and particles' adsorption affinity, via groundwater seepage. Whereas in times of higher water levels suspended particles and inorganic nutrients are transported into side arms or inundated areas, during periods of no or low supply, internal nutrient cycling prevails (with low concentrations of inorganic forms) (Hein et al., 2004). Once arrived, the retention of these nutrients in floodplains depends on a variety of abiotic and biotic processes. In the case of phosphorus (P), suspended particles can deposit, as well as dissolved forms precipitated with metal oxides or adsorbed to clay particles (Behrendt and Opitz, 2000; House, 2003; Hoffmann et al., 2009). Inorganic nitrogen (N), on the other hand, is most commonly removed through biotic processes, mainly denitrification (accounting for up to 63% TN retention according to Saunders and Kalff, 2001) as a permanent removal (Boyer et al., 2006) and together with phosphate through autotrophic and heterotrophic uptake (Fisher and Acreman, 2004; Venterink et al., 2006; Jordan et al., 2011).

The quantification of the filtering function of floodplains in terms of nutrients is a challenge that scientists have addressed through different approaches, on various temporal and spatial scales. Mass balances operate on a reach scale and use black box approaches for total nutrient retention or release (Venterink et al., 2003; Hoffmann et al., 2011, 2012). Other approaches quantify single nutrient compartments and consider implicit processes, like sedimentation, denitrification, or uptake by biota (e.g., Kronvang et al., 2002, 2007; Forshay and Stanley, 2005; Noe and Hupp, 2005; Venterink et al., 2006; Hoagland et al., 2019). Yet other approaches attempt to assess this function through empirical causalities with predictors on a larger scale (e.g., Behrendt and Opitz, 2000; Venohr et al., 2011; Natho et al., 2013). Only a few studies have investigated the role of large river floodplains for nutrient balances (Venterink et al., 2003, 2006; Natho et al., 2013; Theriot et al., 2013) and the impact of their hydro-morphological restoration (Newcomer Johnson et al., 2016) on different temporal and spatial scales. To optimize the restoration success and plan ecologically oriented floodplain reconnection, it is essential to gain an understanding of the relationship between hydrological connectivity, spatial and temporal nutrient retention, and biogeochemical processes of the floodplain ecosystem (Pywell et al., 2003; Reckendorfer and Steel, 2004). Models are essential to improve this understanding at different spatial and temporal scales, and can be used as a tool to better predict the transfer of nutrients from the river to the floodplain for planned side arm restoration projects.

Nutrient retention in restored floodplains is reported to behave differently for N and P. For N, higher denitrification rates (Gumiero et al., 2011; Hoffmann et al., 2011) and increased deposition of particulate N (Brunet et al., 1994; Keizer et al., 2018) are reported. Regarding P, uptake of phosphate by primary producers can be enhanced (Hein et al., 2004) and trapping of suspended P in restored reaches is reported to increase (Noe et al., 2019), while remobilization of soluble P is frequently found (Venterink et al., 2002; Hoffmann et al., 2011; Noe et al., 2019) especially shortly after restoration in former agricultural areas (Aldous et al., 2007). Restoration of lateral hydrological connectivity is known to reestablish ecological functions in floodplains (Gumiero et al., 2013; Reckendorfer et al., 2013) and a combination of measures may increase restoration success (Newcomer Johnson et al., 2016). This underlines the potential of side arm reconnection as a feasible measure for reducing nutrients in river water and at the same time improving ecological conditions in floodplains.

In this paper, we explore the efficiency of nutrient retention due to side arm reconnections in a case study of the Danube River by applying two modeling techniques. We therefore formulate the following research questions:

1. How do different scaled modeling approaches (semi-empirical, statistical) depict nutrient retention in the Danube Floodplain National Park (DFNP) under different hydrological conditions?
2. How do different connectivity levels in a former braided river floodplain affect N and P retention and what is the effect of reconnection measures?
3. Are these measures sufficient to identify a reduction in river nutrient load, or what extent of restoration measures is needed to observe a significant reduction of the overall riverine loads (>1%)?

Thus, we analyzed how the reconnection of seven floodplain side arms in an ∼30-km stretch of the DFNP east of Vienna affect nutrient retention primarily in the range of restored connectivity levels, excluding very high floods (<1% exceedance in 30 years), and applied a statistical model to quantify nutrient retention during phases of surface water connection and disconnection. To generate a more comprehensive picture across different scales, we compared the outcomes with a mesoscale semi-empirical retention model (Venohr et al., 2011), based on transferable denitrification and sedimentation causalities as the main processes for nitrogen and phosphorus retention, respectively (Behrendt and Opitz, 2000; Zessner and Gils, 2002; Venterink et al., 2006; Mölder and Schneider, 2011). Based on proposed management plans, we calculated scenarios considering current conditions (CUR) and complete floodplain reconnection (ALL), and the effect of increased lateral hydrological connectivity on the reduction of the total nutrient load in the Danube. Accounting for a wet and a dry hydrological year, we wanted to show for the first time the range of nutrient loads that could be retained in floodplains of the DFNP. Finally, we analyzed the similarities and differences between the two modeling approaches to depict relevant drivers and limitations of nutrient retention and the relative contributions of high floods and average discharge conditions.

METHODS

Study Site

The DFNP east of Austria's capital Vienna (**Figure 1**) is, with 96 km², the largest natural floodplain landscape of its kind in central Europe, where the Danube River still has the dynamic character of a mountain river. To ensure navigation and reduce flood hazards, extensive channelization, regulation through rip-raps and groins, as well as active disconnection of the floodplain through levees, have been conducted since the nineteenth century. Additionally, heavy damming since the 1950s has further impacted natural dynamics, with the DFNP being the longest remaining free flowing stretch of the Austrian Danube (36 km) (Habersack et al., 2016).

Starting in 1996, the first side arm in Haslau-Regelsbrunn (3) was partially reconnected, followed by two floodplain systems in Orth (2) and Schönau (1) 5 years later, connected at lower water levels but still in a technical manner (**Figure 1**, **Supplementary Figure 1**, **Supplementary Table 3**). To increase natural dynamics while ensuring navigation, a pilot project by the Austrian waterway administration (viadonau, http://www.viadonau.org) (2012–2014) successfully tested a combination of

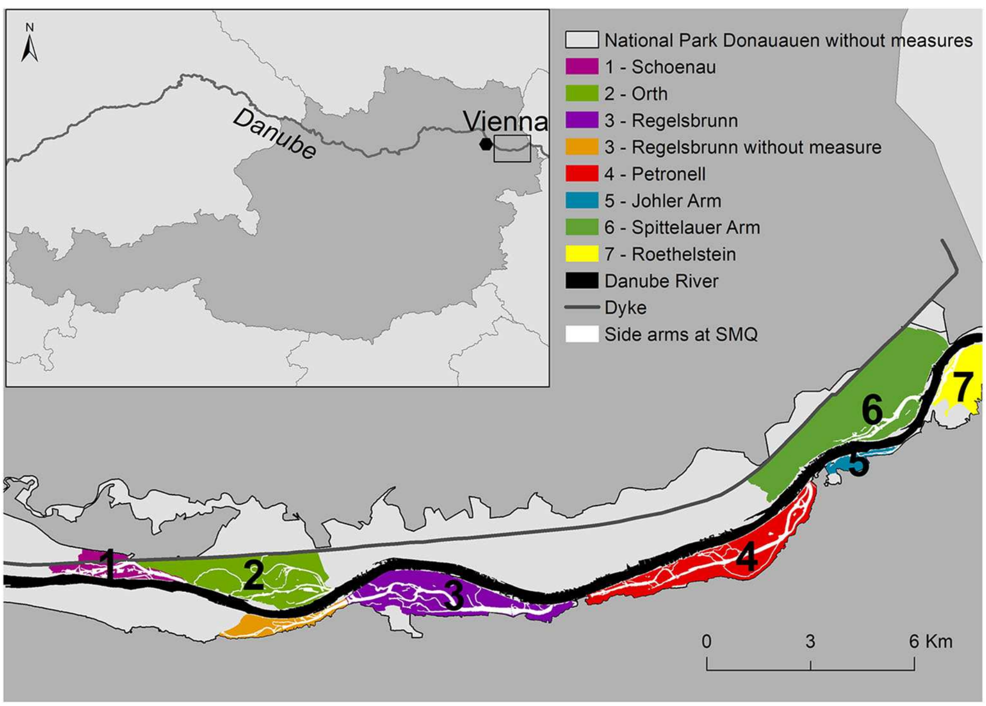

FIGURE 1 | Location of study site with the seven side-arm systems along the Danube River in Austria.

river engineering measures including the complete reconnection of a side arm (Johler Arm—5), optimization of groins, removal of rip-raps, and river bed improvement to counteract riverbed incision. The remaining side arms (Petronell—4, Spittelauer Arm—6, Roethelstein—7) are solely groundwater fed until the Danube discharge reaches >2,600 $m^3\ s^{-1}$, well above mean discharge (MQ).

We consider these seven side arm systems in the DFNP with different degrees of connectivity to the Danube flow regime (**Table 1**) and different sizes (here as length of branch and maximum flooded area) to model retention of nitrate and total phosphorus for wet, dry, and average hydraulic years. The considered river stretch belongs to the Upper Danube Catchment with a nival flow regime influenced by snow melt from the Alps. Hainburg is the representative gauge for the study site. Here, the catchment has a size of 104,727 km^2 and the MQ is 1,930 $m^3\ s^{-1}$. At the study site, the Danube River transports between about 119,015 t (dry year 2003) and 199,000 t (wet year 2002) of dissolved inorganic nitrogen (DIN), with NO_3-N being the main component. The annual load of TP ranges between 2,699 t (dry year 2003) and 6,700 t (wet year 2002) (ICPDR, 2002, 2003).

Management Scenarios

To detect the effect of river restoration, nutrient retention was modeled in the current state (CUR) and in a scenario of complete implementation of all proposed restoration measures (ALL), according to the management and restoration plan of the Austrian waterway authority. This scenario includes the complete reconnection of seven side arms and the maintenance of stable riverine water levels due to sediment addition to the river channel. CUR and ALL were calculated for a hydrograph of an extremely wet (2002) and an extremely dry year (2003) as defined by Weigelhofer et al. (2015).

Data

Hydrological variables of the Danube were obtained by the hydrological portal of Austria (https://ehyd.gv.at/, last download 15th of July 2019) and water quality data on nutrients from the federal ministry of sustainability and tourism database (https://wasser.umweltbundesamt.at/h2odb/, last download 15th of July 2019). Water quality data in the side arms was gathered from monitoring and research projects of past reconnection measures in the systems of Regelsbrunn (2) (Heiler et al., 1995; Hein et al., 1999, 2002), Orth (2) (Hein et al., 2003), and Johler Arm (5) (Viadonau, 2015). Water quality was measured at discharges of the Danube River up to 5,130 $m^3\ s^{-1}$ in the vicinity of the respective inlets and outlets. To ensure comparability, we included only data sets where sampling and nutrient analysis were conducted with standardized methods. The degree and duration of surface water connection of the side arms was approximated in all scenarios by linearly interpolating the flow between the topographical point of inflow and a discharge of 5,130 $m^3\ s^{-1}$. The latter value was obtained from the simulation output of a one-dimensional hydraulic model (HEC-RAS).

Information on DFNP borders was obtained from EEA (2018, https://www.eea.europa.eu/data-and-maps/data/natura-10/natura-2000-spatial-data). Wetted area and water depth at three discharges were obtained by intersecting surface and groundwater tables with the DEM (Hohensinner et al., 2008). For higher discharges, a flood hazard map of a frequent HQ30 flood (9,290 $m^3\ s^{-1}$) for the DFNP (https://maps.wisa.bmnt.gv.at/hochwasser, last download 15th of July 2019) was georeferenced

TABLE 1 | Summary of connectivity-related hydro-morphological characteristics of the side arms in the current state for wet/dry years.

Side arm system (ID number)	Max length [m]	Start of connection [$m^3\ s^{-1}$ of Danube discharge]	Days of connection [$d\ a^{-1}$]	Connectivity class*	Average water depth [m]	Average Q [$m^3 s^{-1}$]	Q at HSQ** [$m^3 s^{-1}$]	Average area [ha]	Max flooded area at HQ_{30}^{***} [ha]	Average HL [$m\ yr^{-1}$]
Schönau (1)	3,637	1,994	235 /72	Medium	1.7 /0.8	199 /66	692	50 /41	172	11,569 /5,096
Orth (2)	5,454	1,758	289 /125	Medium	1.5 /0.8	63 /24	222	81 /46	551	2,392 /1,565
Regelsbrunn (3)	6,430	2,100	208 /52	Low	1.7 /1.0	114 /46	377	166 /130	631	1,706 /935
Petronell (4)	7,709	2,689	98 /16	Low	2.0 /1.3	116 /108	377	174 /144	524	2,037 /2,456
Johler Arm (5)	1,283	917	365 /311	High	2.3 /1.5	52 /22	138	5 /2	59	37,544 /31,356
Spittelauer Arm (6)	2,717	3,618	33 /7	Low	1.7 /1.0	239 /57	323	419 /165	957	952 /486
Röthelstein (7)	2,798	3,518	41 /8	Low	1.2 /0.4	251 /45	375	116 /51	305	4,643 /1,768

Q, discharge; HL, hydraulic load.
Width at inflow/average width of side arm and days of surface water connection during an average hydrological year; for details, see **Supplementary Information.*
***5,130 $m^3 s^{-1}$ at the Hainburg gauge (highest navigable discharge).*
****Within the borders of flood hazard map; HQ_{30} and hydrological basins derived from 1 m—digital elevation map.*

and intersected with DFNP borders, showing that the entire floodplain is inundated at this discharge. To estimate the extent of each side arm system, we delineated watersheds on the basis of a digital elevation 1 m grid (provided by viadonau, tiles 78, 89, and 81) using the ESRI ArcGIS "Hydrology" tool (**Figure 1**). Shortwave radiation data on a monthly mean basis was downloaded from EUMETSAT (http://www.cmsaf.eu/pum) to consider additional nitrate uptake by macrophytes following the method described in Venohr et al. (2011).

Statistical Model

Mass balances for the statistical model were deduced from concentration measurements and the hydraulic model in investigated side arms. During surface water connection, longitudinal concentration differences (dc, in g m^{-3} m^{-1}) were calculated (Equation 2), and during isolation, changes in concentration over time (Δc, in g m^{-3} d^{-1}) (Equation 3). Therefore, the available dataset was divided accordingly, resulting in pairwise observations in upstream and downstream parts of the side arm in the connected state ($n = 54$) or uninterrupted periods between measurements in the disconnected state ($n = 125$).

Statistical models were developed for TP and NO_3-N, each following independent routines on the basis of concentration measurements in all three side arms. For TP, identified significant relationships (**Figure 2**) were used to calculate nutrient retention by applying a multiple adaptive spline regression model (Millborow, 2015). However, because dc and Δc differed considerably between the three side arm systems (**Figure 2**, **Supplementary Table 1**), three different connectivity classes were assigned (**Supplementary Table 2**). The connectivity classes, indicating three different TP retention potentials, were used to extrapolate nutrient retention to side arms without concentration measurements based on the average surface water connection (d a^{-1}) and the ratio of the inlet opening to the side arm width (**Table 1**). Assuming that the maximum retention equals the load entering the side arm, we modeled the longitudinal TP concentration decline as a logistic growth function (Equation 1). TP input from the Danube River was computed according to an adapted exponential discharge-dependent TP concentration model from Zessner and Kroiss (1999). During periods of isolation, concentration differences were not significantly different from zero and therefore not considered in further calculations for TP (one-sample Wilcox-test, $p > 0.1$).

For nitrates, no correlation with any measure-specific parameters could be detected, but retention values significantly exceeded zero (one-sample Wilcox-test, $p < 0.01$, $n = 179$). Therefore, mean retention values in connected (9×10^{-7} g m^{-3} m^{-1}, $n = 54$) and isolated (718×10^{-5} g m^{-3} d^{-1}, $n = 125$) conditions were used to calculate retention. By multiplying the resulting TP and NO_3-N retention rates (g m^{-2} d^{-1}) by the factor 10 and the days under consideration, commonly used rates in kg ha^{-1} $month^{-1}$ or kg ha^{-1} yr^{-1} were calculated.

$$total\ TP\ retention\ (dc) = \frac{\frac{dc}{m} \cdot cin}{\frac{dc}{m} + \left(cin - \frac{dc}{m}\right) \cdot e^{-a \cdot (L^{-1})}} \tag{1}$$

dc = concentration difference of TP between inlet and outlet [g m^{-3}]
dc/m = system-specific retention rate per m [g m^{-3} m^{-1}]
cin = inlet concentration [g m^{-3}]
a = concentration-dependent retention rate (connectivity class) [–]
L = length of the side arm [m]

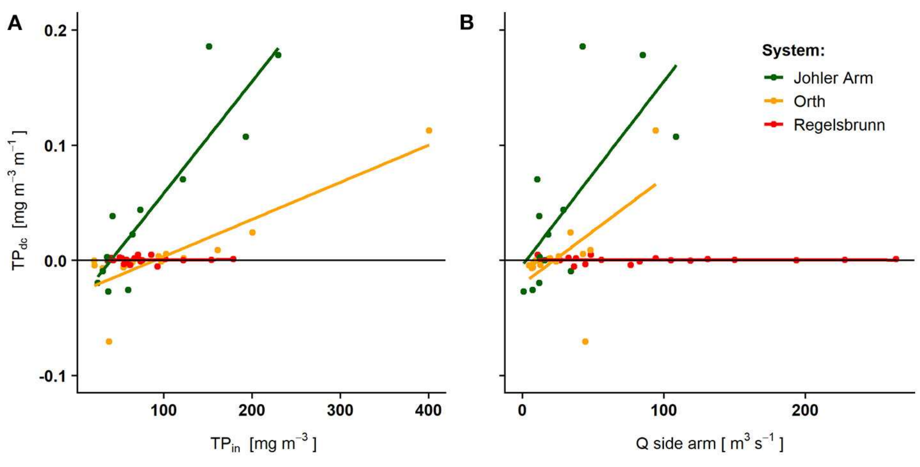

FIGURE 2 | Significantly increasing measured concentration differences ($n = 54$) of total phosphorus with increasing incoming total phosphorus concentration **(A)** and discharge **(B)** along the three differently connected side arm systems: Johler Arm (high connectivity, $n = 17$), Orth (medium connectivity, $n = 16$), and Regelsbrunn (low connectivity, $n = 21$). Positive values indicate net retention and negative value release of TP between two sampling points. For details on the deduction of the statistical approach, please refer to the **Supplementary Information**.

During connection:

$$Ret = \frac{Q \cdot dc}{A} \quad (2)$$

During isolation:

$$Ret = \frac{A \cdot d \cdot c}{A} = d \cdot c \quad (3)$$

Ret = retention [$g\ m^{-2}\ d^{-1}$]
Q = discharge in side arm [$m^3\ d^{-1}$]
dc = concentration difference between inlet and outlet [$g\ m^{-3}$]
Δc = concentration change over time [$g\ m^{-3} d^{-1}$]
A = area [m^2]
d = water depth [m].

Semi-Empirical Mesoscale Model

This semi-empirical mesoscale model is based on two submodels. The first submodel calculates incoming load and inundated floodplain area considering the statistical relationships between the given discharge ratios and the incoming discharge and inundated area on a daily basis for each side arm system (Natho et al., 2013; Natho and Venohr, 2014). With this data given, the nutrient retention was calculated for nitrates and total phosphorus on a monthly basis for each side arm system following the approach of Venohr et al. (2011).

The incoming nitrate and total phosphorus load was calculated on a monthly resolution according to ICPDR (2017). On the basis of the discharge-flooded area relationship, three parameter sigmoidal functions were derived (SIGMAPLOT version 13.0 Notebook, Systat Software Inc.) to describe the proceeding inundation of floodplains of each side arm system with increasing discharge (**Supplementary Figure 2**). This key parameter represents the degree of lateral hydrological connectivity of each side arm system and was developed successfully for rivers in Germany (Natho and Venohr, 2012, 2014; Natho et al., 2013).

As flood waves normally occur over a short period, the incoming nutrient load was calculated on a daily basis with daily average discharge. In line with seasonal dependencies of NO_3-N concentrations found by Zweimüller et al. (2008), Venohr (2006), and Venohr et al. (2011) and complex patterns of TP fluxes during high discharges (Zessner et al., 2005; Bowes et al., 2008; Chen et al., 2013), concentration proxies for NO_3-N and TP were applied (**Supplementary Tables 4**, **5**). The incoming daily load was calculated with an average nitrate concentration for each month and with an average TP concentration considering winter and summer seasons and discharge levels below or above MQ. Based on the daily loads and the known inundated area, the retention model (Equations 4, 5) developed on the mesoscale was applied at a monthly resolution (Venohr et al., 2011):

$$Nret\% = \frac{1}{\left(1 + (a \cdot a_1 \cdot R) \cdot e^{b \cdot T} \cdot HL^{-1}\right)} \cdot 100 \quad (4)$$

Nret% = retention in % of incoming nutrient load [%]
R = short wave radiation [$W\ m^{-2}$]
T = temperature [°C]
HL = hydraulic load [$m\ yr^{-1}$]
a = 5.7 [–], a_1 = 0.025 [–], and b = 0.067 [–]

$$Pret\% = \frac{1}{\left(1 + c \cdot HL^{-1}\right)} \cdot 100 \quad (5)$$

Pret% = retention in % of incoming nutrient load [%]
HL = hydraulic load [$m\ yr^{-1}$]
c = 15.91 [–]

Both Equations (4) and (5) consider hydraulic load (HL) as an equivalent for retention time (see Venohr, 2006 for details), meaning lower areal retention in case of high HL. For nitrogen, temperature and shortwave radiation have also influenced the metabolic rate of denitrification and plant uptake (Venohr et al., 2011).

RESULTS

Model Comparison Under Current Conditions (CUR)

Current Annual Nutrient Retention Rate in the Study Area

As for the mean area-specific retention rates on an annual basis, both models were in a comparable range and predicted higher retention rates in the wet year (**Supplementary Figures 3**, **4**). For NO_3-N, the statistical model amounted to 170 kg $ha^{-1}\ yr^{-1}$, the semi-empirical model 161 kg $ha^{-1}\ yr^{-1}$ and for TP, 5.7 and 4 kg $ha^{-1}\ yr^{-1}$, respectively. In the case of both nutrients, the statistical model showed a higher variation. In the dry year, retention rates were lower than in the wet year, with 77 or 88 kg NO_3-N $ha^{-1}\ yr^{-1}$ and 1.4 or 2 kg TP$ha^{-1}\ yr^{-1}$ for the statistical and semi-empirical models, respectively. When considering the very high discharges in the wet year, the retention rate calculated by the semi-empirical model increased to 198 kg NO_3-N $ha^{-1}\ yr^{-1}$ and 4.8 kg TP $ha^{-1}\ yr^{-1}$ (**Table 2**).

Current Monthly Retention Rates in Two Differently Connected Side Arm Systems

Both models agreed in calculating higher monthly nitrate and total phosphorus retention with increasing discharges in the side arms and days of surface water connection (**Figure 3**). According to the statistical model, nutrient removal in the connected state was considerably higher than in the disconnected state. The contribution to nitrate reduction in the disconnected state quickly became insignificant when the side arm was connected longer than ∼2 days a month (**Figure 3**).

Johler Arm (5, **Figure 1**, **Supplementary Figure 3**) was permanently connected to the main river channel, but inundation of the floodplain occurred only during high flows. In Regelsbrunn (3, **Figure 1**, **Supplementary Figure 3**), inundation occurred less frequently, but only if the inundated area was relatively large. As a consequence, HL was low for Regelsbrunn and extremely high for Johler Arm especially in August (high floods). On a monthly basis, both models represented the occurrence of floods (<5,130 $m^3\ s^{-1}$) differently. Due to the dependence of the semi-empirical model on HL, it showed areal retention peaks (in kg $ha^{-1}\ yr^{-1}$) after floods when the entering nutrient load was still high, but the inundated area was lower than during the flood peak. In contrast,

TABLE 2 | Resulting nutrient retention calculated by the semi-empirical and statistical models for three hydraulic conditions in the study sites.

	NO_3-N retention in kg ha^{-1} yr^{-1}		TP retention in kg ha^{-1} yr^{-1}	
	Wet	**Dry**	**Wet**	**Dry**
Statistical model	170 ± 172	77 ± 115	5.7 ± 11.1	1.4 ± 3
Semi-empirical model	161 ± 138 (198 ±145)*	88 ± 130	4 ± 3.2 (4.8 ± 3.4)*	2 ± 2.5
Difference in % of statistical model	5	−14	30	−42

For the semi-empirical model, the wet year is also calculated considering the very high discharges indicated in brackets with asterisks.

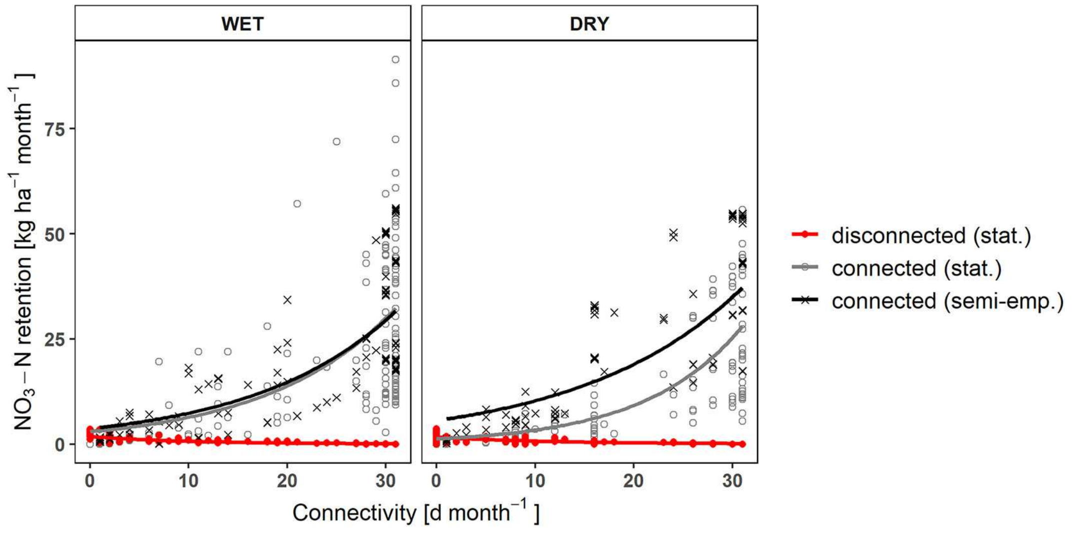

FIGURE 3 | Changes in NO_3-N retention with increasing connectivity ($Q < 5,130$ m^3 s^{-1}) in the current state. Exponential increase as calculated by the two models and linear decrease of the fraction retained during disconnection in the stored floodplain water ($R^2_{wet} = 0.64$, $R^2_{dry} = 0.55$, $p_{\ wet,dry} < 0.001$). By fitting an exponential function [y = b*exp(a*x)], the mean errors of the linear models ($R^2 = 0.39$–0.62, $p < 0.001$) could be further reduced.

the statistical model calculated the highest retention rates during floods reflecting the hydrograph (**Figure 4**), since discharge and dependent nutrient transport were the only variables in the statistical retention model. The biggest difference between the models was visible for TP in Johler Arm for a wet hydrograph (**Figure 4**). Here, the semi-empirical model predicted low TP retention rates due to high HL, but the statistical approach modeled high rates, due to high measured TP retention in Johler Arm and its increase with rising discharge (**Figure 2**).

Effect of Reconnection Measures on Nutrient Retention

Due to the dependence on connectivity in both models (**Figure 3**), reconnection of all side arms (ALL scenario) was predicted to considerably improve nutrient retention capacity in the DFNP. According to both models, the calculated absolute NO_3-N retention in the DFNP doubled in the wet year and even rose by a factor of 3.75–5 in the dry year (**Figure 5**). For TP retention, the trend was similar to NO_3-N according to the semi-empirical model. For the statistical model, TP retention after restoration was higher than the NO_3-N retention in absolute terms. Generally, the reconnection effect was most visible for large side arms with low connectivity under current conditions [Regelsbrunn (3), Petronell (4), and Spittelauer Arm (6); **Figure 6**]. In the current state, NO_3-N and TP load reduction in the floodplains accounted for between a marginal 0.01 and 0.03% for both models and hydrographs. Considering the complete implementation of all restoration measures, load reduction may increase to 0.05–0.07% according to the semi-empirical model. The statistical model resulted in 0.04–0.06% reduction of NO_3-N load and an unlikely high 1.8–3% reduction of TP load in the dry and wet hydrographs, respectively.

Nutrient Retention in the Range of Restoration Compared to Flooding Events

In the wet year 2002, the hydrograph exceeded the highest navigable discharge (HSQ) at 14 days (March, August and November), of which 12 days exceeded an annual flood. The semi-empirical model was found to adequately illustrate these events (**Table 3**). By including these events, the annual retention (t a^{-1}) increased by a factor of 1.6 for TP (0.04% river load reduction) and even 1.9 for NO_3-N (0.06% reduction) compared to discharges <5,130 m^3 s^{-1}. However, if all side arms were completely reconnected (ALL scenario), the annual retention <5,130 m^3 s^{-1} would still exceed the current state including flooding events by a factor of 1.14 for both TP and NO_3-N. If the 14 flooding events were then included in the ALL scenario, the factor would even rise to 1.9 (0.07% river load reduction) and 2.1 (0.1% river load reduction) for TP and NO_3-N, respectively, compared to the current state. This finding supports once more the importance of frequent inundations for the efficient removal of nutrients from floodplains.

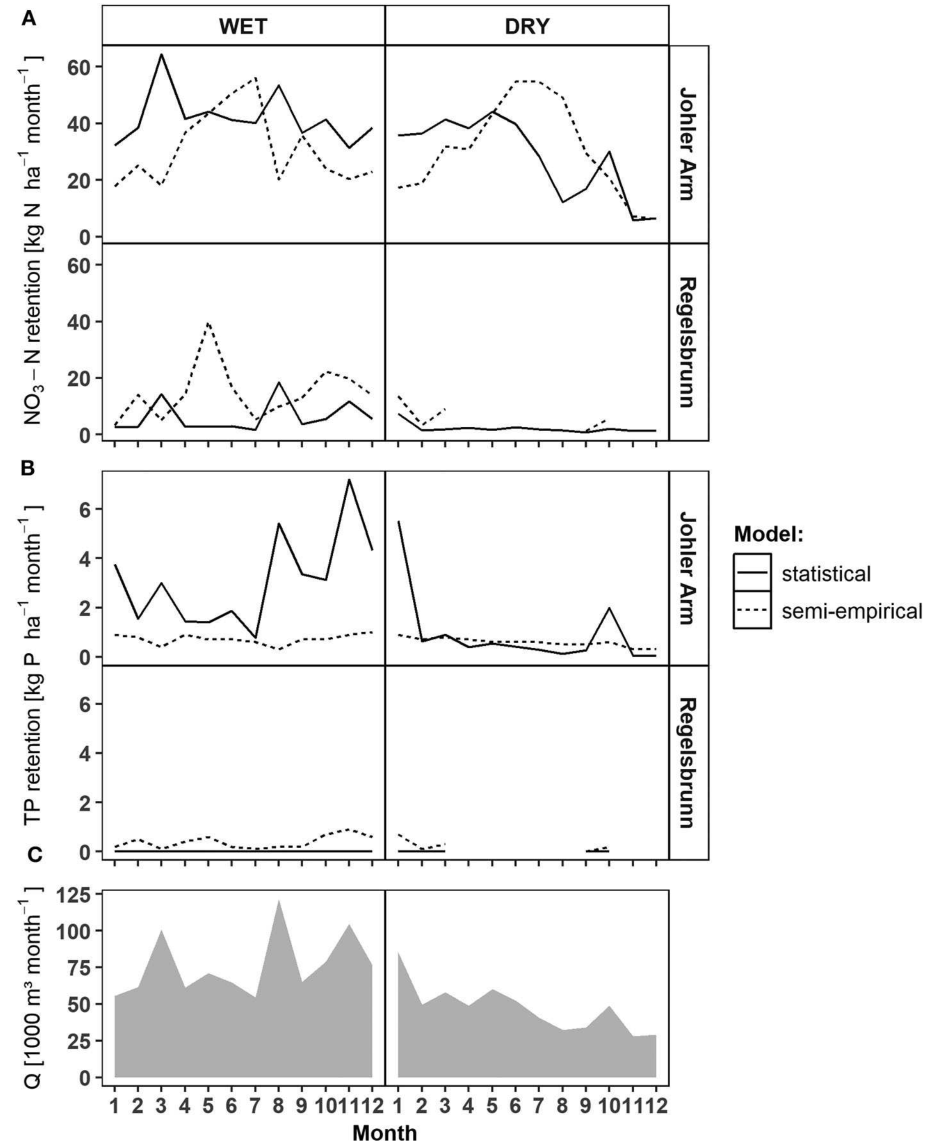

FIGURE 4 | Model comparison of monthly areal NO_3-N **(A)** and TP **(B)** retention values below 5,130 m^3 s^{-1} for the selected side arms Johler Arm (high connectivity) and Regelsbrunn (low connectivity), in which water quality data was available, as well as monthly discharge sums of the Danube River **(C)**. More detailed figures for all side arm systems, scenarios, and model years can be found in **Supplementary Figures 2**, **3**.

DISCUSSION

Model Validation: Comparison of Calculated Retention Values With the Literature

A detailed model validation in terms of observable nutrient retention was not possible because there was no data available suitable for this purpose. Instead, we compared our model results in selected systems and with the literature values presented in **Supplementary Tables 6**, **7**. Whereas, for TP our model results (CUR: 1.4–5.1 kg P ha^{-1} yr^{-1}) lie rather in the lower to mean range of values, our calculated NO_3-N retention (CUR: 65.5–114.5 kg NO_3-N ha^{-1} yr^{-1}) is in the mid- to upper range of values found. The variation in published areal retention rates is great, even though only floodplain systems in temperate areas were selected. Reasons for this may be attributed to differences in floodplain size, hydrological conditions, nutrient loading, vegetation type, sampling design, or retention mechanisms (Fisher and Acreman, 2004). In the case of TP, retention is partly a temporary process of sedimentation (Fisher and Acreman, 2004; Venterink et al., 2006) and a highly variable transport with increasing discharge. Noe et al. (2019) found positive net retention when sedimentation inputs of P were high and leaching rates were low, e.g., processes described by Hoffmann et al. (2012) and (Schönbrunner et al., 2012).

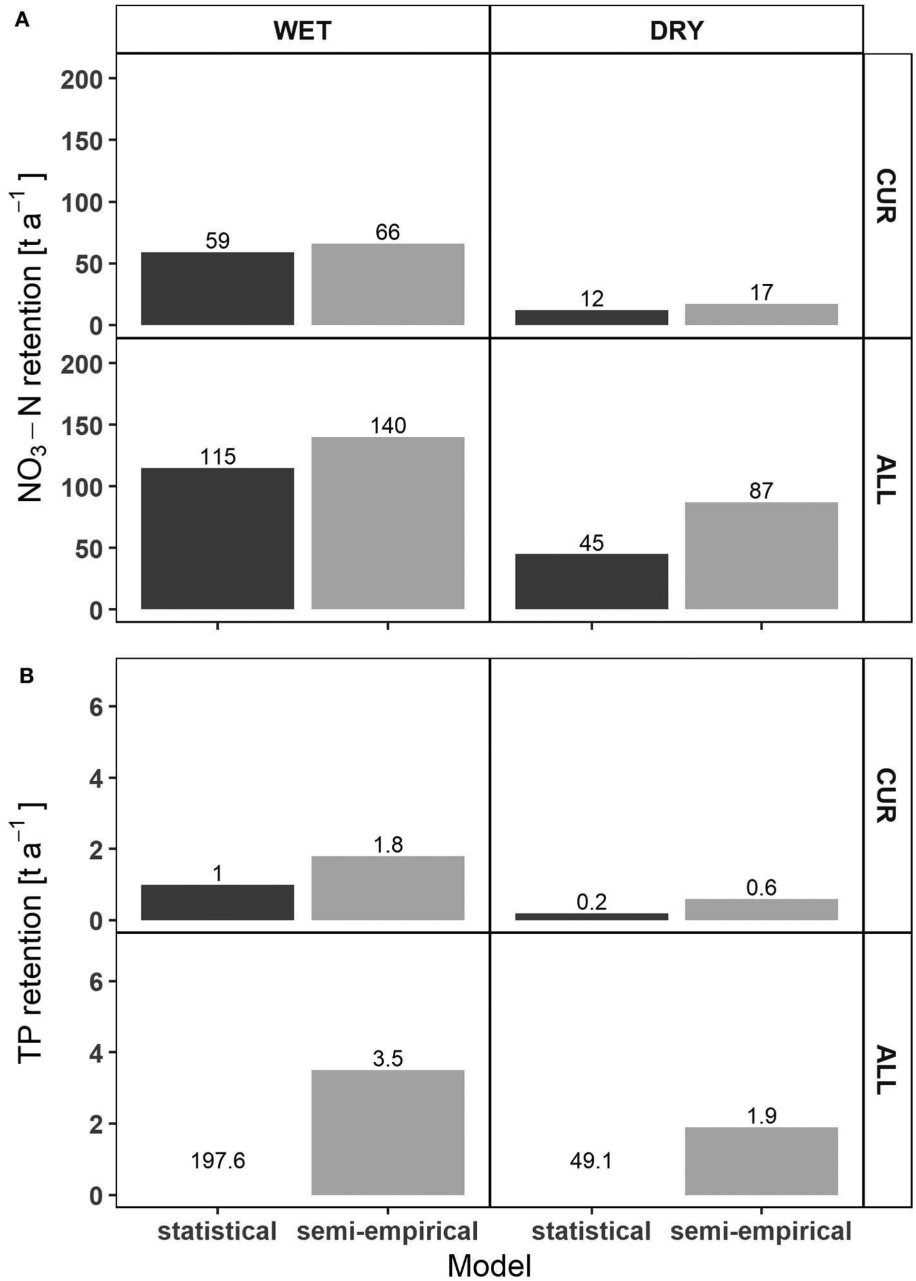

FIGURE 5 | Comparison of absolute NO_3-N **(A)** and TP **(B)** retention in the national park between statistical and semi-empirical models before and after restoration. For reasons of clarity, no bars for TP retention in the ALL scenario of the statistical model are displayed.

Modeled Drivers for NO_3-N and TP Retention and Resulting Model Limitations

Discharge, Nutrient Load, HL, and Nutrient Concentration

Both models consider discharge to be an important driver affecting nutrient loads and hydrological connectivity, but in different ways. The discharge determines how much nutrient load enters the floodplain area, as well as the duration and areal extent of the connected floodplain area, which is considered in the semi-empirical model (**Supplementary Figure 2**). In the statistical model, discharge explains reductions in nutrient concentrations (**Figure 2**). Nutrient loads (Saunders and Kalff, 2001) and hydrological connectivity, both are reported to be among the most important factors for nutrient retention in riparian wetlands found in the literature (Fisher and Acreman, 2004). P and N concentrations in the Danube (0.02–2.1 mg TP L^{-1}, mean 0.06 mg TP L^{-1} and 0.8–4.2 mg NO_3-N L^{-1}, mean 2.0 mg NO_3-N L^{-1}) were low in comparison to other large rivers in central Europe. This might explain the relatively low TP retention rates modeled in this study. Discharge also acts as a surrogate for water residence time (Behrendt and Opitz, 2000), explaining how long the hydraulic load lasts on the system (Natho et al., 2013). On a monthly basis, both models depict brief periods (hot moments according to McClain et al., 2003) that frequently account for a high percentage of the denitrification activity or total phosphorus retention (**Table 3**).

TP and its main component, particulate P, are transported at the highest concentration during high flows only for a short period during the year. Regarding the retention, a decrease is calculated according to the semi-empirical model due to very high HL, which does not allow sedimentation to occur even though the TP load is very high. Due to the dependence of the semi-empirical model on HL, it shows areal retention peaks (in kg ha^{-1} yr^{-1}) after floods when the entering nutrient load is still high, but the HL is lower than during the flood peak. No correlation between HL (m d^{-1}) and TP and NO_3-N retention (mg m^3 m^{-1}) was detected (R^2 < 0.02, p > 0.05) in the statistical model and is therefore not used as a predictor. TP retention is very likely to be overestimated by the statistical model for the ALL scenario, because higher retention with increasing connectivity and discharges is assumed. This severe overestimation stems from the use of the maximal retention rate measured and calculated in the smallest and highly connected Johler Arm (5) for all side arms after complete reconnection. Even though the impact of connectivity on retention efficiency was clearly visible, transfer to other side arms was only possible by assigning connectivity classes and upscaling systems of different scales.

The semi-empirical model uses area and nutrient loads as input data, which is also done by Kronvang et al. (1999) and Hoffmann et al. (2011). Both TP and NO_3-N retention in the Regelsbrunn and Petronell side arms (3 and 4, **Figure 1**) is probably overestimated by the semi-empirical approach. Only four measurements of discharge-area pairs for each side arm system were available to calculate the sigmoidal relationship between discharge and connected area (specifically between Q/MQ = 2 and 5.2, **Supplementary Figure 2**). The inundation area, as a sigmoidal relationship reflecting the lateral hydrological connectivity, is crucial for calculating HL in the semi-empirical model. The larger the area, the smaller the HL and the more time needed for denitrification, as well as for total phosphorus to settle (Saunders and Kalff, 2001; Venterink et al., 2003). The statistical approach was developed independently of the area but based on a measured reduction in nutrient concentration with increasing distance from the inlet, as also reported by others (Kronvang et al., 1999; Saunders and Kalff, 2001; Venterink et al., 2003; Reckendorfer et al., 2013 in an isolated floodplain in the DFNP). Although the model

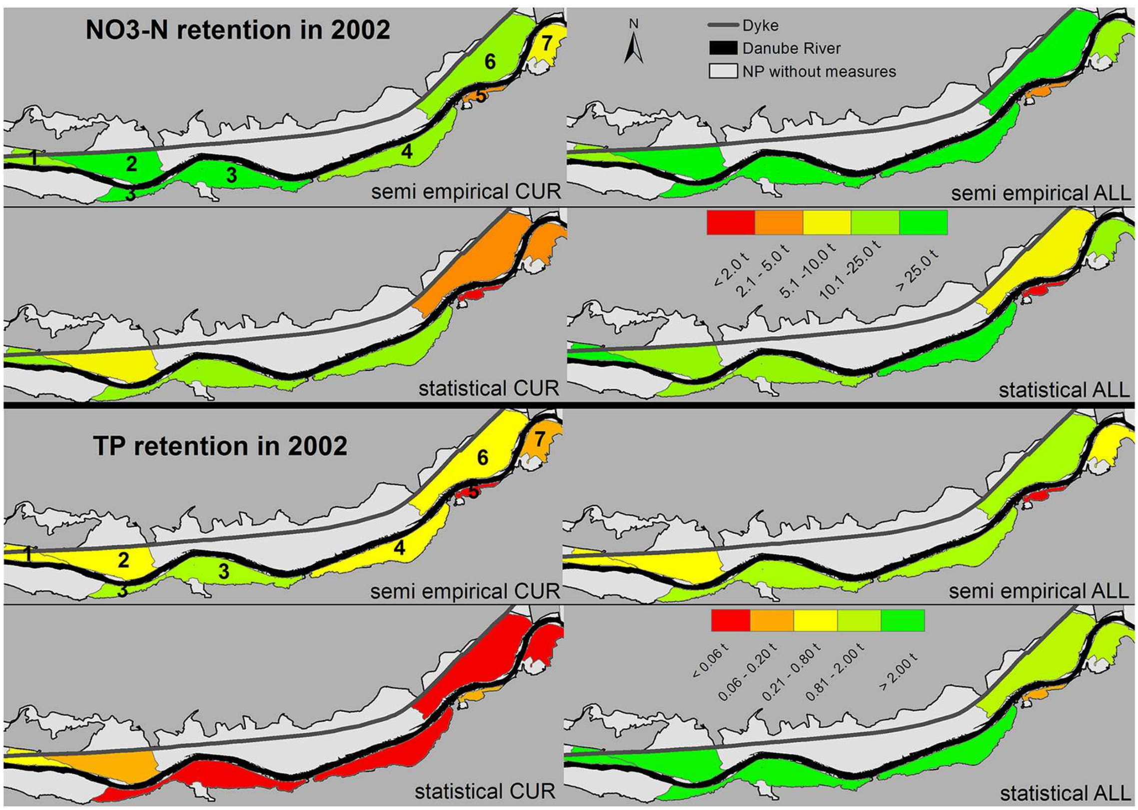

FIGURE 6 | Contribution of each side arm system to NO_3-N and TP retention in the wet year 2002 for the scenarios CUR and ALL. Numbers are given instead of side arm system names and explained in the text.

TABLE 3 | Floodplain characteristics of two differently restored floodplains for July and August 2002 (wet year).

Wet year (2002) CUR	Regelsbrunn (3)			Johler Arm (5)		
	July	August	August*	July	August	August*
Days of inundation	3	17	**24**	31	24	**31**
Average inundated area [ha]	148	197	**298**	2	6	**15**
Average inundated area [%]	23	32	**48**	4	10	**26**
Average discharge [$m^3 s^{-1}$]	52	131	**398**	28	60	**98**
Hydraulic load [$m yr^{-1}$]	1,118	**4,884**	3,225	42,130	**55,406**	20,584
Incoming NO_3-N load [t $month^{-1}$]	19	260	**879**	97	170	**366**
Incoming TP load [t $month^{-1}$]	1	10	**33**	4	6	**14**
Statistical: NO_3-N retention [kg ha^{-1} $month^{-1}$]	1	**20**		28	**42**	
Semi-empirical: NO_3-N retention [kg ha^{-1} $month^{-1}$]	5	10	**33**	**56**	20	44
Statistical: TP retention [kg ha^{-1} $month^{-1}$]	0.0	0.0		0.5	**4.6**	
Semi-empirical: TP retention [kg ha^{-1} $month^{-1}$]	0.1	0.2	**0.5**	0.6	0.3	**0.7**

August[*] considers all discharges (including flood events) and is calculated by the semi-empirical model only, whereas July and August consider exclusively average daily discharges <5,130m^3 s^{-1}. Highest values of each line and side arm are bold.

does not consider favorable redox conditions in sediments or vegetation processes (Fennessy and Cronk, 1997; Fisher and Acreman, 2004; Venterink et al., 2006), it gives reliable estimations for TP retention in the range of the measurements. This is because TP is mainly transported in the particulate form; discharge and concentration are the main factors driving TP removal. However, concentrations or loads considered as the basis for retention can show inverse patterns (Natho and Venohr, 2014) because of the different behavior of nutrient concentrations with increasing discharge. This is also visible for the Johler Arm (5, **Figure 1**), where the decline of nutrient concentration was highest, although the semi-empirical model calculated the highest HL of all investigated side arms (**Table 1**, **Supplementary Figure 2**).

Due to insufficient data on nutrient concentrations at high water levels, the statistical mass balance approach lacks applicability to large flooding events ($Q > 5{,}130\ m^3s^{-1}$), an essential period for nutrient transport, load and retention (Kronvang et al., 2007). TP concentrations in floodplains at very high Danube discharges are hardly measured, and thus information about retention in floodplains is very uncertain (Zessner et al., 2005). Venterink et al. (2003) showed that with an increasing share of discharge entering the floodplain of two Rhine tributaries, P retention tended to increase in absolute numbers, as also found by our statistical approach. However, retention efficiency is reported by the same authors to decrease when more than 15% of the main channel discharge enters the floodplain. Generally, pairwise measurements in times of surface water connection are rare, resulting in only 16 [Orth (2)] to 21 [Regelsbrunn (3)] data points on which the statistical model is built (**Figure 2**). The semi-empirical model, based on causalities at larger scales, shows more reasonable values for the ALL scenario and flood events than the statistical model. It is therefore more robust to model nutrient retention in other large river floodplain systems independent of water quality data in differently connected side arms. However, without comprehensive water quality data for the project area, the semi-empirical model cannot be sufficiently validated.

Contribution of Connectivity vs. Isolation to Nutrient Retention

In the initial phase of disconnection, inorganic nutrients decline rapidly, but with increasing duration of disconnection internal nutrient cycling processes dominate as organic forms prevail, leading to very low nutrient removal rates in the side arms (Hein et al., 2004; Forshay and Stanley, 2005). Whereas, NO_3-N is removed in both disconnected and connected states to different extents, no storage of TP is detected during periods of isolation, as transport depends on hydraulic connection (Noe and Hupp, 2005). Low levels of connectivity and low discharges lead to a net release of TP, whereas higher discharges result in increasing absolute TP storage (**Figure 2**). This lower connectivity can lead to alternations between periods of desiccation and inundation, which enhances phosphorus release upon re-wetting, and in turn could enable eutrophication processes (Schönbrunner et al., 2012). However, in the long run a decrease in phosphorus release after restoration may occur (Noe et al., 2019). This stresses once more the importance of nutrient inputs for system functioning, either through high flows or more frequent inundation following reconnection. Reflecting the results from the statistical model, we conclude for the semi-empirical model that on the yearly basis NO_3-N retention might be negligible on the decoupled floodplain, whereas at finer temporal resolutions a proxy is needed that considers ongoing nutrient retention and release during the (initial) phase of reconnection.

Seasonality

Apart from the HL and nutrient concentrations mentioned above, denitrification is influenced mainly by temperature and oxygen concentrations, whereby the former is also included in the semi-empirical model. In opposition to TP, the higher modeled NO_3-N retention can be attributed to seasonality. This was considered by taking the water temperature into account, which serves as a proxy for increased biological activity of denitrifying bacteria at higher water temperatures and higher nutrient loads in summer. Consequently, lower NO_3-N concentrations in summer were observed in the Danube as reported for other rivers at higher water temperatures (Behrendt and Opitz, 2000; Saunders and Kalff, 2001; Venohr, 2006; Zweimüller et al., 2008). The semi-empirical model considered denitrification as the dominant removal process for nitrates in the DFNP, which is supported by mesocosm experiments by Welti et al. (2012).

An increase in water temperature is concurrent with a decrease in water column oxygen concentration, which in turn promotes denitrification rates (Groffman et al., 2009). In 2002, higher water temperatures of the summer floods outbalanced the high HL because metabolic rates of denitrifiers allow rapid turnover in the case of NO_3-N availability at the sediment water interface (Forshay and Stanley, 2005; Craig et al., 2008). Therefore, it can be concluded that the semi-empirical model is more reliable when predicting hot moments for nitrogen removal. In contrast, the statistical model calculates the highest retention rates during floods reflecting the hydrograph (**Figure 4**), since discharge and dependent nutrient transport are the only variables in the statistical retention model. Nutrient concentrations in side arms were investigated in different projects scattered along a timespan of two decades, and measurements were not taken in the months of January and February, meaning that the annual temperature range was not represented in the data set and summer was overrepresented. In order to eliminate error sources of this kind, continuous concentration measurements in the remaining side arms in the DFNP and at high discharges are required.

Answering our first research question, we can summarize that the two models calculate similar trends in nutrient retention regarding yearly values for the whole area. Considering biogeochemically hot moments, the models depict different patterns due to their different consideration of driving factors. Consequently, both models complement each other. We suggest the semi-empirical model when considering the national park as a whole. When evaluating the effect of small-scale restoration measures, like single side arm reconnections, the statistical model can complement the estimation with more detailed outcomes during phases of isolation and reconnection.

Effect of Side Arm Reconnection and Flooding on Nutrient Retention

The results of both models clearly show that the effect of restoration in the study region is the improvement of lateral hydrological connectivity and thus more frequent inundation, so-called "hot moments" (McClain et al., 2003). In our models, more frequent and thus higher nutrient input into floodplains leads to higher absolute nutrient retention (Newcomer Johnson et al., 2016; Noe et al., 2019) because of higher accumulation rates of N and P (Noe and Hupp, 2005) and greater removal of reactive nitrogen with increasing load (Jordan et al., 2011). Frequent inundations with less destructive power are important, because N removal efficiency (%) is reported to decrease with higher N load (Fisher and Acreman, 2004; Bernot and Dodds, 2005; Venohr, 2006; Jordan et al., 2011). Similar findings, though less pronounced, are described for TP retention (%) in wetlands (Reddy et al., 1999; Fisher and Acreman, 2004). Because of its ability to be released, not only with increasing incoming load, but with increasing duration of input, phosphorus retention efficiency in floodplains may decline (Fisher and Acreman, 2004).

In combination with connectivity and nutrient load inputs, Newcomer Johnson et al. (2016) showed in an extensive review that nutrient retention in floodplains could be enhanced through restoration, leading to increased water surface area and increased hydraulic residence time. In both models, discharge is a determinant for inundated area, days of inundation and incoming nutrient load. The highest retention in the statistical model is found in frequently connected areas with high nutrient load inputs, following rising patterns of the hydrograph. On the other hand, the highest retention rates found by the semi-empirical model occur in flat topographies with high input loads [e.g., Regelsbrunn (3)], where area increases disproportionately faster compared to the discharge, hence reducing HL and flow velocity. Maaß and Schüttrumpf (2019) also model more effective sedimentation in restored, lowered floodplains than in restored, elevated rivers. Saunders and Kalff (2001) and Craig et al. (2008) confirm that low flow velocities increase retention through longer water-sediment contact time, which is responsible for denitrification and sedimentation. Under current conditions (CUR) inundation happens less frequently, but if it does happen, the area is larger on average. In contrast, under higher connectivity levels, inundation happens more frequently, leading to reduced average areas but longer inundation periods of far more days. This indicates the importance of small inundation events with low HL for effective nutrient retention and further underlines the importance of improved lateral hydrological connectivity of the whole floodplain, not only selected side arms, as the main goal of floodplain restoration. Furthermore, prioritizing reconnection of larger side arm systems creates synergies of high retention potential with the provision of habitat for protected and endangered rheophilic communities (Funk et al., 2013, 2019).

In summary, increasing connectivity and its consequences for retention is estimated differently by the two models, but generally leads to higher retention, in answer to our second research question.

How Much Connected Floodplain Area Do We Need to Reduce Nutrient Loads in the Upper Danube River by 1%?

We considered a total of 3,200 ha of floodplains that can be inundated with a probability of once every 30 years, making up one-third of the DFNP. This is the lowest probability found in Flood Hazard Maps showing inundation of all the floodplains already considered. With an average inundation area of 481 ha (wet) and 282 (dry), which we would call a very well-connected floodplain, the semi-empirical model calculated for the ALL scenario a river load reduction of 0.07–0.1% for NO_3-N and 0.05–0.07% for TP. This seems to be very little and would not be detectable in the river. However, we analyzed a stretch of only 30 km and argue that the floodplain area is very small compared to the river size. Thus, we ask the question: How much well-connected floodplain area would be needed to achieve a nutrient retention of 1% of the yearly transported river load? A one-percent decrease in river load would already be detectable and within an achievable range in the light of our modeled retention efficiencies.

From our model results, we can conclude an areal retention rate of up to 334 (dry)−400 (wet) kg NO_3-N ha^{-1} yr^{-1} and 7 (dry)−9 (wet) kg TP ha^{-1} yr^{-1}. A river load of 199,000 t dissolved inorganic nitrogen and 6,700 t TP is reported by ICPDR (2002). To achieve a retention of 1% of the river load in a wet year, we would need 4,975 ha for NO_3-N and 7,444 ha for TP. As we stated above, only 15% of the DFNP is flooded on a regularly basis, which would then result in a floodplain area 10.4 and 15.5 times larger than the DFNP. Alternatively, on a 100 km river stretch we would need a floodplain that is 0.5 km wide on each side for NO_3-N and 0.75 km for TP. In the dry year, the Danube transported 119,015 t DIN and 2,699 t TP (ICPDR, 2003). The area required to remove 1% of this load is 3,563 ha for NO_3-N and 3,856 ha for TP. Considering an average inundated area of only 9%, an area of about 12.6 and 13.7 times the DFNP is required for a 1% removal of NO_3-N and TP.

We suggest increasing reconnection not only through side arm connection but also by allowing overbank flow, which inundates the entire floodplain complex during frequent floods with lower water levels (annual floods). This increases river-floodplain interactions and might lead to higher sedimentation and phosphorus and N-enriched sediment deposition (Maaß and Schüttrumpf, 2019; Noe et al., 2019). Despite the clear evidence that the re-establishment of hydrological pulsing increases denitrification and decreases emissions of greenhouse gases (Mitsch et al., 2008; Welti et al., 2012), we are aware that nutrient retention in restored floodplain areas is a complex topic and that the potential for phosphate release from soils of floodplains with restored wetland hydrology is a large concern. Although some PO_4-P release processes might occur after floodplain reconnection (**Figure 2**; Aldous et al., 2007; Schönbrunner et al., 2012), over the long run positive net retention after restoration will appear (Owens and Walling, 2002; Noe and Hupp, 2005; Venterink et al., 2006; Wassen and Olde Venterink, 2006; Anderson and Mitsch, 2007; Noe et al., 2019).

Based on these considerations, we can answer our third research question and confirm that the measures planned in the ALL scenario will not be enough to retain a significant amount of nutrients (1% threshold). Only when reconnection at low flow conditions leads to very frequent inundation of the floodplain area as a whole could a significant amount of river nutrient load be retained in the DNFP. Finally, knowing that floodplain restoration may increase the multi-functionality of these ecosystems worthy of protection, it should still be our major goal to manage water quality primarily through reduction of punctual and diffuse nutrient emissions into river systems rather than filtering out pollutants afterwards.

CONCLUSION

So far, only four side arm systems in the DFNP were partially reconnected to different degrees, resulting in no noticeable reduction of nutrients transported in the Danube River. Even though the two models were built upon different backgrounds, hydrological connectivity has shown to be the common main driver determining the amounts of nutrients to be retained by the floodplains. From our results, we conclude that if more area were frequently inundated by reconnecting all proposed side arms, an increased reduction in transported nutrient load could be achieved. To achieve a retention of 1% of the total load, 10–15.5 times more re-connected floodplain area is necessary. Frequent inundations are a prerequisite not only for effective nutrient retention through denitrification and sedimentation, but also for typical floodplain habitat provisioning, and could positively influence the multi-functionality of floodplains.

By applying two fundamentally different models, we were able not only to generate a more comprehensive understanding by elucidating common driving factors, but also to point out general or specific limitations to modeling nutrient retention, including reduced data availability and the detailed description of extreme events. Whereas, the strength of the semi-empirical model is the calculation of nutrient retention on a larger scale and during a wider range of discharges, the statistical approach is able to represent the current retention functions in more detail on a smaller scale. Overall, it was our aim to quantify the current state and the achievable potential of the DFNP in light of nutrient retention and floodplain restoration. We could show for the first time that the effect of complete reconnection of side arms leads to higher nutrient retention than sole flooding events in an extreme wet year without better connectivity—but the investigated floodplain stretch is still too small to considerably reduce nutrient loads in the Upper Danube.

Due to the complexity of river floodplains, quantification of nutrient retention potential remains challenging, but is an important management issue. With our results, we contribute to a better understanding of this ecosystem service, which helps to tailor future restoration programs to the needs of nature and society.

DATA AVAILABILITY STATEMENT

Data are available upon request from the authors or at following publicly accessible databases: https://ehyd.gv.at/, https://www.eea.europa.eu/data-and-maps/data/natura-10/natura-2000-spatial-data, https://wasser.umweltbundesamt.at/h2odb/, https://maps.wisa.bmnt.gv.at/hochwasser, http://www.cmsaf.eu/pum.

AUTHOR CONTRIBUTIONS

SN set up the semi-empirical model, wrote the first draft of the manuscript, carried out the formatting and created the maps (**Figures 1**, **6**) as well as **Supplementary Tables 3–5** and **Supplementary Figures 1, 3**. MT developed the statistical model supported by TH, wrote the section on the statistical model as well as the management scenarios, carried out the literature research on nutrient retention values in floodplains, and created **Figures 2–5**, and in the **Supplementary Tables 1**, **2**, **6, 7** and **Supplementary Figures 3**, **4**. SN and MT jointly created **Tables 1–3**. TH developed the design of this model comparison and made available the data on measurements. EB-K initially launched the BEDOM project and contributed to sections 1 and 4. All authors contributed to the manuscript revision and read and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2020.00074/full#supplementary-material

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Effect of Hydrological Connectivity on the Phosphorus Buffering Capacity of an Urban Floodplain

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Floodplains can perform nutrient buffering functions and therefore influence the riverine nutrient dynamics depending on the extent of the hydrological connectivity. This work focused on quantifying the adsorption/desorption potential of a degraded floodplain of the Danube River (Lower Lobau) based on sediment characterization (grain size distribution, organic content, and P-fractions) and sediment type-specific P-adsorption via batch experiments. We established an adsorption/desorption budget model with a high temporal and spatial resolution. With this model, we identified spatial patterns related to hydrology and calculated the phosphorus-buffering capacity of permanent and temporary floodplain water bodies. Sediment characteristics were defined by the distance to the inflow area and the hydrological connectivity of the floodplain water bodies. The main factor for the concentration of total phosphorus (P_{tot}) in the sediments was the grain size distribution. P_{tot} was 10 times higher in silt-dominated sediments compared with gravel-dominated sediments. Inorganic phosphorus (P_{inorg}) ranged between 36 and 90%, depending on the organic content of the sediments. Both the adsorption and the desorption potential of soluble reactive phosphorus (SRP) were highest in large, frequently connected water bodies and were strongly controlled by hydrology. The total adsorption potential of the floodplain was up to 40 times higher in wet years (e.g., 2002) than in dry years (e.g., 2003), when floodplain water bodies were connected less frequently to the main channel of the Danube. Up to 75% of the adsorbed SRP was desorbed and released into the water column after periods of connection. Consequently, SRP adsorption directly reduced the P-load in the Danube River main channel. The adsorption/desorption mechanisms worked as a buffering system by taking up the SRP imported during floods and releasing it over a longer period after the floods. This stimulated high primary production in the floodplain water bodies and impacted the overall P-retention of the floodplain.

Keywords: phosphorus adsorption, equilibrium phosphorus concentration, floodplain, Danube, phosphorus adsorption and desorption, hydrological connectivity

INTRODUCTION

Floodplains are highly productive habitats (Tockner and Stanford, 2002; Mitsch and Gosselink, 2015) and of crucial importance for nutrient dynamics and retention in riverine landscapes (Hoffmann et al., 2009; Noe and Hupp, 2009). Lateral hydrological exchange processes between the main channel and the floodplain water bodies are both sources and drivers for biogeochemical cycling (Amoros and Bornette, 2002; Junk and Wantzen, 2004). These processes do not only control the floodplain water quality, but they also affect downstream riverine and marine ecosystems (Billen et al., 1991). In functionally intact river–floodplain systems, discharge fluctuations determine the hydrological connectivity and the exchange and storage of matter across the floodplain, thereby controlling the net impact of floodplains on the river water quality (Reddy et al., 1999; Van der Lee et al., 2004).

Phosphorus plays a central role in the biogeochemical cycling in floodplains (Wolf et al., 2013) and river systems (Records et al., 2016; Weigelhofer et al., 2018). The availability of soluble reactive phosphorus (SRP) in floodplains is controlled by a variety of internal biotic and abiotic processes, such as, e.g., assimilation by organisms, organic matter mineralization, and adsorption/desorption processes at the sediment/water interface (Noe et al., 2019). However, unlike other standing water bodies, floodplains are also subject to frequent temporally and spatially restricted inputs of river water. These inputs facilitate the exchange of chemically different water sources and the creation of chemical gradients between the water column and the floodplain sediments, thereby stimulating various abiotic and biotic processes, such as, e.g., SRP adsorption and desorption (Froelich, 1988; Borggaard et al., 2005).

Adsorption originates from diverse geochemical and physical processes, which lead to the fast and usually reversible phosphorus fixation to sediment particles (REF). Adsorption reactions can buffer water column SRP concentrations and increase the overall SRP availability in floodplain water bodies (Mainstone and Parr, 2002; James and Barko, 2004). The adsorption or desorption potential can be determined by analyzing the equilibrium phosphate concentration (EPC_0) (House and Denison, 2000; Dunne et al., 2005; Yoo et al., 2006). This EPC_0 represents the SRP concentration in the water column where no adsorption or desorption takes place. Under conditions with higher SRP concentrations in the overlying water column than the EPC_0, the sediments have the potential to take up SRP from the water column. If the SRP concentration is below the EPC_0, the sediments can act as a source of phosphate (Taylor and Kunishi, 1971; House and Denison, 2000; Jarvie et al., 2006). Many factors, which determine the adsorption capacity of the sediments, may change during floods, such as, e.g., the particle size, the concentration of amorphous or less crystalline iron and aluminum oxides, the pH, and the oxygen content (Withers and Jarvie, 2008; Records et al., 2016). Thus, hydrological connectivity is a key factor for SRP adsorption processes in floodplain water bodies.

In addition to abiotic processes, phosphorus can also be bound in the sediments in organic form due to assimilation by autotrophic and heterotrophic microbes or accumulation of dead plant material from macrophytes or riparian vegetation (Fisher and Acreman, 2004; Watson et al., 2019). Part of the organic bound P is released back to the overlying water column as SRP through microbial mineralization processes (House, 2003; Ahlgren, 2006; Kleeberg et al., 2008; Palmer-Felgate et al., 2011). Like P adsorption, P assimilation and mineralization are influenced by environmental factors, such as levels of dissolved oxygen and temperature.

However, river engineering measures have reduced the hydrological connectivity of floodplains worldwide (Tockner et al., 2010). Along the Upper Danube, up to 90% of the former floodplain areas have disappeared due to river regulation, large-scale land-use changes, and terrestrialization processes (Tockner et al., 2009; Hein et al., 2016). Initially, the floodplain Lower Lobau was part of the braided Danube River system, where transport processes dominated river–floodplain interactions. In contrast, storage and internal processes were limited to peripheral zones. Nowadays, due to large-scale regulations of the Danube River, the Lower Lobau presents a floodplain forest with water bodies of varying degrees of hydrological connectivity, which are connected via a downstream opening in the flood protection dike (Preiner et al., 2018). The decoupling of the floodplain and the main channel changed floodplain processes fundamentally, as internal processes gained in importance. With hydrological connectivity as the main driver of the SRP availability in the floodplain of the Lower Lobau (Weigelhofer et al., 2015), phosphorus adsorption/desorption mechanisms may play an important role in the P retention and floodplain primary production.

The main objective of the present study was to analyze the impact of the hydrological connectivity on adsorption/desorption patterns and the buffering capacity of the floodplain Lower Lobau in a high spatial and temporal resolution. We measured standing stocks of five different phosphorus fractions to quantify phosphorus allocation in the floodplain water bodies (n = 162) and relate them to hydrological connectivity and other abiotic conditions of the water bodies. We classified the sediments and determined the EPC_0 of the different sediment types. We set up a segment based model with a high spatial resolution, which combined the EPC_0 with estimated daily water SRP concentrations in the floodplain water bodies for the period 1999–2019. The model was used to identify hydrologically driven patterns of the adsorption/desorption potential and the SRP buffering capacity of the floodplain.

MATERIALS AND METHODS

Study Sites

The Lower Lobau is a floodplain of the Danube River, located on the left river bank at the eastern border of Vienna (river kilometer 1908–1918) (Funk et al., 2013). It is composed of an approximately 10 km long main side-arm, which is subdivided by check dams and natural fords into a chain of connected basins, accompanied by isolated pools and temporary water bodies (**Figure 1**). The floodplain is connected to the main

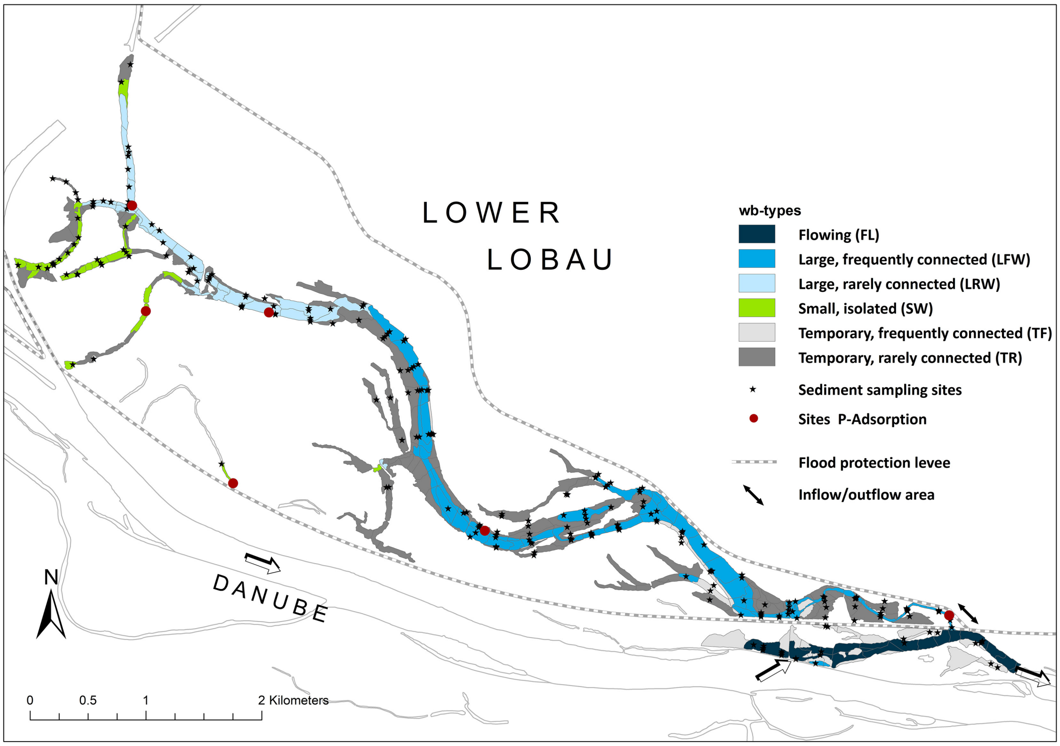

FIGURE 1 | Study area Lower Lobau (area: 1,480 ha), sediment and water column sampling sites, and sites where adsorption/desorption experiments were done are shown. Arrows indicate inflow/outflow areas of the floodplain.

channel of the Danube River via back-flooding through a 10-m wide opening of the flood protection levee at the downstream end of the floodplain. With increasing water levels in the main channel of the river, large parts of the main side-arm and larger areas of the floodplain become connected and inundated. Groundwater tables are low due to drinking water abstraction for the supply of the city of Vienna. Groundwater input to surface water bodies is, therefore, negligible, and the inundation of the floodplain is instead seen as groundwater recharge (Danielopol et al., 1997). At Vienna, the Danube is a ninth order river, characterized by an alpine regime with highly variable patterns. For the study, we defined the hydrological connectivity of the floodplain water bodies as the average number of days per year, where a surface water connection with the main channel of the Danube is established. At the mean discharge of 1,930 m^3s^{-1}, which correlates to the mean water level of 142.41 m a.s.l. (MW, Austrian River Authority, gauge at Wildungsmauer), the floodplain is disconnected from the main channel. A surface water connection of the floodplain water bodies with the main river channel is established at water levels above 143.02 m a.s.l. This level was exceeded on 75 days per year on average in the period 1999–2019. Therefore, the hydrological connectivity of the various floodplain water bodies ranged from 75 days per year in the most downstream parts of the main side-arm adjacent to the inflow to 9 days per year in the upstream regions of the main side-arm. Isolated ponds were connected less than 2 days per year on average at water levels above 146 m a.s.l. We used the water body types defined by Weigelhofer et al. (2015) for the Lower Lobau (LFW-large frequently connected water bodies, LRW-large rarely connected water bodies, SW-small, isolated water bodies) in this study and added three more types FL, TF, and TR. While LFW, LRW, and SW are all back-flooded, FL (flowing) water bodies are characterized by a unidirectional flow from upstream to downstream during surface water connection (connection level 142.7 m a.s.l., exceeded on 106 days per year). The types TF (temporary, frequently connected) and TR (temporary, rarely connected) represent temporary water bodies with different connectivity. We defined TF or TR as areas adjacent to FL and the main side channel (LFW, LRW), which are inundated only during floods (TF: connection level 146 m a.s.l., exceeded on 1.6 days per year; TR, connection level 146.5 m a.s.l., exceeded on 0.8 days per year on average in the period from 1999 to 2019). TF and TR are only wetted as long as the water level of the main channel is higher than the connection level.

Sampling Design

Monitoring data of the Lower Lobau between 2005 and 2014, provided by the Municipal Authorities of Vienna (MA45), were integrated into the present study.

Limnochemical data of water samples were collected from 2005 to 2014. Sampling was performed four times per year between 2005 and 2008 and in monthly intervals between 2009 and 2014. Additional sampling with a higher frequency was done during three floods in 2009, 2012, and 2013 at nine sites (n = 63–87 per site; Weigelhofer et al., 2015). Sediments were sampled between 2008 and 2010 in the main side-arm, in isolated water bodies, and also in temporary water bodies (total n = 142) to cover the full gradient of hydrological connectivity within the floodplain (**Figure 1**).

Sediments Characteristics

Sediment samples were taken following cross-sections from a boat or, in shallow water, from the ground with a Gilson-Corer (65 mm diameter). The upper 5-cm layers of three samples per spot were mixed and used for the analysis. The depth of the fine sediment layer was measured with a U-profiled bar. In the lab, grain size distribution (silt < 0.2 mm, sand 0.2–2 mm, gravel > 2 mm) was determined by sieving the dried sediments (70°C, until constant weight) followed by combustion (450°C, 4 h) to define the organic content (OC) of each size class. Before drying, we took subsamples to analyze nutrient concentrations of the sediments. We determined four phosphorus fractions (triplicates per sample)—total phosphorus (P_{tot}), inorganic phosphorus (P_{inorg}, HCL extraction), loosely sorbed phosphorus (P_{sol}, NH_4Cl extraction), and reductive soluble phosphorus (P_{red}, dithionite extraction)—according to Ruban et al. (2001). Organic phosphorus (P_{org}) was calculated as the difference between P_{tot} and P_{inorg}.

Previous studies carried out in the Donau-Auen National Park (Welti et al., 2012) showed a strong relation of grain-size distribution and OC of the sediments with processes like denitrification and respiration. For that reason, we categorized the sediments based on the predominating grain-size class in "gravel-dominated," "sand-dominated," "silt-dominated," and a category with more or less equal shares of the size classes ("mixed"). The categories were then split up into two subcategories based on their OC (below or above the average OC of each group (**Table 1**).

Adsorption and Desorption Experiments

We determined EPC_0 for the different sediment types in the laboratory via batch equilibrium experiments (Froelich, 1988; House, 2003; Jarvie et al., 2005). The analysis was done in triplicates, and the average values were used for further calculations. Ten grams of fresh sediments were incubated in 50-ml deionized water enriched with KH_2PO_4 (0, 0.1, 0.3, 0.5, 1, 5 10, 25, 50, 75, and 100 mg P L^{-1}). Sediment samples were shaken at 20°C in the dark for 24 h. After the incubation, the extract was centrifuged (3,000 rpm, 15 min). SRP concentrations of the supernatant (P_{eq}) were analyzed spectrophotometrically with a continuous flow analyzer (CFA, Systea Analytical Technology) following the molybdenum blue method (APHA, 1998). The amount of adsorbed SRP per gram sediment was calculated as

$$P_{sorb} = \frac{(P_{ini} - P_{eq}) \cdot V}{w_{sed}} \; (\mu g \; g \; DW^{-1})$$

with P_{sorb} as adsorbed SRP (μg g DW^{-1}), P_{ini} and P_{eq} as initial and equilibrium SRP concentrations in the water (μg L^{-1}), respectively, V as the volume of the solution (L), and w_{sed} as dry weight of the sediments (g).

We plotted P_{sorb} against P_{eq} and fitted a two-component Langmuir isotherm (Barrow, 1978) using a least-squares method (SPSS version 18.0):

$$P_{sorb} = \frac{C_{max1} P_{eq}}{(K_{d1} + P_{eq})} + \frac{C_{max2} P_{eq}}{(K_{d2} + P_{eq})}$$

where C_{max1} and C_{max2} were the adsorption maxima of the two Langmuir components, and K_{d1} and K_{d2} were adsorption parameters. The maximum P adsorption capacity was calculated as the sum of C_{max1} and C_{max2} (Manning et al., 2006).

The EPC_0 was calculated as the x-intercept of these adsorption curves.

After removing the supernatant of the adsorption experiment, 25 ml of deionized water was added to the sediment pellets (soil:solution ratio of 1:100) to determine the desorption of the freshly adsorbed SRP (Lair et al., 2009). The tubes were shaken for 1 h and centrifuged. The SRP concentrations (P_{desorp}) of the supernatants were analyzed, as described earlier. The desorption procedure was repeated three times. The percentages of desorbed SRP were averaged, multiplied by 24 to obtain a desorption potential per day, and related to P_{sorb} to estimate the sediment-specific potential desorption rates as a percentage of the freshly adsorbed SRP per day.

Upscaling

We applied segmentation to the whole floodplain area (number of segments: 326) based on hydro-morphological differences and different macrophyte coverage. Each segment was assigned a sediment category and a water body type to calculate and upscale the adsorption/desorption potential. We set up a model for 20 years (1999 to 2019) to quantify the influence of hydrology on the adsorption/desorption potential of the floodplain.

Hydromorphological data like depth, water area, volume, and flow velocity were computed by a steady-state hydrodynamic surface water model (Baart et al., 2010). We divided the water bodies of the Lower Lobau, which had defined hydrological connectivity, roughly into three depth categories (0–0.5 m, 0.5–1.5 m, and >1.5 m) and used macrophyte coverage to refine it into 326 segments (ArcGIS 10.4, ESRI). Macrophyte coverage was gained from aerial images (Federal Office of Metrology and Surveying [BEV]) by manually encircling macrophyte-covered areas divided in floating leaf plants, emerged and submerged macrophytes. We cross-checked with samples taken in the area (unpublished report, Systema GmbH). If different life forms were located within the same depth category of a water body, we separated them into different segments. If areas with high coverage and low coverage were in the same depth class of a water body, we also separated them into different segments. Macrophyte coverage of a segment was calculated as the sum of areas covered by each life form divided by the total area of the segment.

The segments, therefore, represented subareas of permanent or temporary water bodies, which were different from the adjacent segments in their hydro-geomorphology or the coverage

TABLE 1 | Categorization of sediments into eight types according to their prevailing grain-size and their organic content (OC).

	n	Silt (%)0–0.2 mm	Sand (%)0.2–2 mm	Gravel (%) > 2 mm	OC (%)
Gravel-dominated—low OC	4	4.2 ± 4.4	11.5 ± 5.0	84.3 ± 8.6	0.1 ± 0.1
Gravel-dominated—high OC	9	5.2 ± 4.2	15.6 ± 3.8	79.2 ± 4.4	3.0 ± 1.5
Sand-dominated—low OC	7	7.9 ± 3.7	87.0 ± 4.0	5.2 ± 6.3	0.8 ± 0.6
Sand-dominated—high OC	5	16.8 ± 5.6	78.0 ± 8.6	5.2 ± 5.4	12.4 ± 11.9
Mixed—low OC	19	31.6 ± 14.1	33.3 ± 14.0	35.2 ± 22.5	3.2 ± 3.1
Mixed—high OC	8	38.1 ± 11.9	32.7 ± 13.7	29.2 ± 18.0	14.9 ± 6.4
Silt-dominated—low OC	55	78.8 ± 16.4	17.3 ± 14.6	3.9 ± 5.7	7.4 ± 2.7
Silt-dominated—high OC	28	76.2 ± 15.3	17.1 ± 12.1	6.6 ± 8.3	19.0 ± 8.3

of macrophytes. The segments were defined as areal base units for the calculations of the standing stocks of different phosphorus fractions and the upscaling of the adsorption/desorption potential (**Supporting Information**, **Supplementary Figure 1**). The median area of the segments was 6,184 m^2 with a range from 248 to 42,759 m^2.

Sediment characteristics of each segment were defined by the characteristics of the samples taken within a segment or of the closest sampling sites within the same water body. If two or more sediment sampling sites were located within the same segment, we checked the variability of grain size distribution, OC, and P-fractions and either used average values or refined the segments in the case of high variability. Sediment categories (based on the dominant grain-size and the OC) were assigned to each segment to allow the application of adsorption/desorption patterns (with EPC_0 curves) and to upscale it to the water body and floodplain scale. Water bodies were composed of 1–30 segments depending on their size. Although sediment types of segments were different within a water body, the limnological conditions were assumed to be constant for water bodies because they were mostly driven by surface water connection with the main channel. SRP concentrations in the Danube main channel usually are higher than in the water bodies of the Lower Lobau. The nutrient availability in the main side-arm of the Lower Lobau is strongly determined by the hydrological situation (Weigelhofer et al., 2015). We defined SRP concentrations for the six different water body types and two different hydrological conditions: "flood," which referred to a state of surface water connection with the main channel of the Danube, and "no-flood," based on monitoring data from 2005 to 2014 (Municipal Authorities of Vienna, MA 45) and described in detail in Weigelhofer et al. (2015). For every waterbody type, we defined connectivity levels by analyzing water levels measured in the river main channel and within different parts of the floodplain (water level data 2008–2011, Municipal Authorities of Vienna, MA45). We calculated average SRP concentrations by water body (and therefore by segment) and hydrological situation (**Table 2**). This enabled us to link the main channel water level (Austrian River Authority, gauge at Wildungsmauer) directly with SRP concentrations in the floodplain water bodies for the period 1999 to 2019.

Finally, each segment had assigned (i) a sediment category, which determined sediment characteristics, the standing stock of sediment phosphorus fractions, and the potential for SRP adsorption or desorption (based on EPC_0), and (ii) a water body type, which defined the SRP concentrations in the water column for each hydrological condition: flooded and not connected to the main channel of the river. We assumed homogeneous conditions of water and sediment within the segments.

We calculated the adsorption potential according to a modified version of Lair et al. (2009) for the period 1999 to 2019.

$$P_{sorb} = \left[C_{\max 1} \cdot \frac{(SRP - EPC_0)}{(K_{d1} + (SRP - EPC_0))} + C_{\max 2} \cdot \frac{(SRP - EPC_0)}{K_{d2} + (SRP - EPC_0)} \right] \cdot f_{Sed}$$

where SRP was the SRP concentration in the overlying water column, EPC_0 was the determined phosphate equilibrium concentration, and C_{max1}, C_{max2}, K_{d1}, and K_d were adsorption parameters. f_{Sed} was a factor to convert the potential from mg kg^{-1} to g m^{-2}. We assumed that the upper 5 cm of the sediments was involved in adsorption/desorption processes and used bulk densities for silt-, sand-, and gravel-dominated sediments, according to Smith and Wheatcraft (1993) (**Table 3**).

Adsorption took place when the SRP concentration in the water was higher than EPC_0, which usually was during periods of connection. After surface water connection periods (flood conditions), the adsorbed SRP was the basis for the estimation

TABLE 2 | Connectivity levels (cl), average hydrological connectivity, and SRP concentrations of water bodies (wb) with different hydrological connectivity compared with Danube River concentrations (D) for two hydrological situations—flood and no-flood—as a basis for upscaling.

wb	cl (m a.s.l.)	Connectivity (days per year)	SRP flood (μg L^{-1})	SRP no-flood (μg L^{-1})
D	NA	365	20.6 ± 5.2 (*n* = 12)	18.0 ± 11.7 (*n* = 59)
FL	142.7	106 ± 50.1	18.8 ± 10.7 (*n* = 42)	4.87 ± 7.2 (*n* = 41)
LFW	143.0	76.5 ± 42.6	14.2 ± 14.3 (*n* = 54)	0.8 ± 0.6 (*n* = 87)
LRW	144.5	10.6 ± 9.6	6.4 ± 5.7 (*n* = 20)	0.7 ± 1.5 (*n* = 189)
SW	145.5	2.8 ± 3.7	5.7 ± 4.2 (*n* = 4)	42.1 ± 77.5 (*n* = 77)
TF	146.0	1.6 ± 2.8	14.2	NA
TR	146.5	0.8 ± 1.9	6.4	NA

Concentrations (± standard deviation) are in μg L^{-1}. Concentrations of adjacent water bodies were assigned to temporary water bodies (TR, TF). Danube River (D) concentrations. Connectivity is the average number of days per year (period 1999–2019), where the water level of the main channel exceeded the connectivity level of a water body.

TABLE 3 | Concentration of P-fractions per sediment type; units in mg kg^{-1}.

(mg kg^{-1})	*n*	P_{tot}	P_{inorg}	P_{org}	P_{red}	P_{sol}
Gravel-dominated—low OC	4	46.0 ± 31.3	41.4 ± 33.6	4.6 ± 7.6	3.0 ± 3.1	0.2 ± 0.1
Gravel-dominated—high OC	9	149.9 ± 51.2	54 ± 12.3	95.9 ± 49.6	18.8 ± 4.3	1.6 ± 1.7
Sand-dominated—low OC	7	235.5 ± 126.4	216.7 ± 121.4	18.8 ± 22.2	14.0 ± 5.9	0.7 ± 0.4
Sand-dominated—high OC	5	218.8 ± 66.9	168.9 ± 77.4	49.9 ± 44.5	22.1 ± 15.8	2.6 ± 3.3
Mixed—low OC	19	275.1 ± 109	203.3 ± 94.5	71.9 ± 75.8	21.0 ± 12.5	2.7 ± 4.3
Mixed—high OC	8	357.1 ± 216.6	174.5 ± 96.4	182.6 ± 146.4	37.2 ± 29.1	6.9 ± 12.1
Silt-dominated—low OC	55	507.4 ± 199.4	322.6 ± 121.4	184.8 ± 108.6	50.8 ± 38.8	2.2 ± 2.5
Silt-dominated—high OC	28	529.0 ± 202.0	256.7 ± 88.8	272.3 ± 167.4	74.1 ± 69	2.7 ± 2.4

P_{org} was calculated as the difference between P_{tot} and P_{inorg}.

of desorption processes. Based on the sediment-specific potential desorption rates, we calculated stepwise desorption from day-to-day. It also accounted for changes in the desorption potential as a response to decreasing adsorbed SRP amounts.

Statistics

We performed multivariate adaptive regression splines (MARS, R-package earth, Milborrow et al., 2019) using the techniques from Friedman (1991) to analyze how general parameters of floodplain hydrology, sediment characteristics, and macrophyte cover affected the distribution of phosphorus fractions in the sediment. We used the hydrology of the water bodies (permanent or temporary, hydrological connectivity), the relative share of different sediment grain size classes (silt: <0.2 mm, sand: 0.2–2 mm, and gravel: >2 mm), the OC of the sediments, and the macrophyte coverage as basic data. MARS is a form of non-parametric regression analysis, which can be seen as a generalization of stepwise linear regression that integrates non-linearities and interactions between variables automatically (Hastie et al., 2017). MARS creates subsets of terms describing all included variables (forward pass). The following backward pass then reduces the number of terms by using generalized cross-validation that allows to compare the performance of different model subsets and choose the best performing model with the lowest residual sum-of-squares (RSS). The predictive power of the selected models was calculated analogously to R^2 as (1-RSS)/TSS, with TSS as total sum-of-squares. The used R-package conducts basic checks for collinear terms (Milborrow et al., 2019) and performs well even when collinearity is present (Dormann et al., 2013).

RESULTS

Sediment Characteristics

The hydrological connectivity to the main channel drove sediment characteristics in the Lower Lobau. The amount of imported suspended solids increased with increasing connectivity of the water bodies. The fine sediment layer was significantly higher in water bodies near the inflow than in more distant areas of the floodplain, with a maximum depth of up to 270 cm. With increasing distance to the inflow, the OC of the sediments increased, whereas grain sizes generally decreased. Sand-dominated and mixed sediments characterized the parts of the main side-arm close to the inflow area, the adjacent flooding areas by silt-dominated sediments with low OC (**Figure 2**). In the middle and upstream parts of the side-arm (LFW, LRW), silt-dominated or mixed sediments with low or high organic matter content were found. Silt-dominated sediments characterized isolated waterbodies. In water bodies with flowing conditions (FL), sediments were dominated by gravel and sand with low OC.

Phosphorus concentrations in the sediments strongly depended on the predominating sediment type of a water body. The highest levels of P_{tot} were found in silt-dominated sediments (529 ± 202 mg kg^{-1}) and the lowest in gravel-dominated sediments (46 ± 31 mg kg^{-1}) (**Table 3**). The organic phosphorus fraction was between 7% in sediments with low organic matter content and 52% in sediments with high organic matter content. The smaller the average sediment grain size was, the higher were the concentrations of reductive soluble phosphorus (P_{red}). The amounts of P_{red} ranged between 3.0 ± 3.1 mg kg^{-1} in gravel-dominated sediments and 74 ± 69 mg kg^{-1} in silt-dominated sediments. The maximum relative share of P_{red} was 13% in silt-dominated sediments with high OC. P_{sol} was considerably lower in sediments with low OC than in sediments with high OC with a maximum relative share of 1.1%.

In summary, P_{tot} in water bodies with prevailing flowing conditions was mainly composed of P_{inorg}, showing low concentrations of P_{red} and P_{sol} (**Figure 3**). P_{tot} was higher in the other water body types and also showed a higher variability there. The lower the connectivity was, the lower was the fraction of P_{inorg} and the higher was the fraction of P_{red}. P_{sol} was low in all water bodies.

The predictive power of the MARS models for the different phosphorus fractions was between 0.68 and 0.8 (**Table 4**). Explaining variables were the relative shares of the various sediment grain-sizes, the hydrological connectivity, macrophyte coverage, and the permanent or temporary character of a water body. The highest effect of connectivity was found for the distribution of P_{sol}.

Phosphorus Adsorption/Desorption Potential

EPC_0 was highest for the silt-dominated sediments (8.5 μg L—^{1}) and lowest for gravel-dominated sediments (3.2 μg L^{-1}) and mixed sediments with low OC (2.1 μg L^{-1}) (**Table 5**).

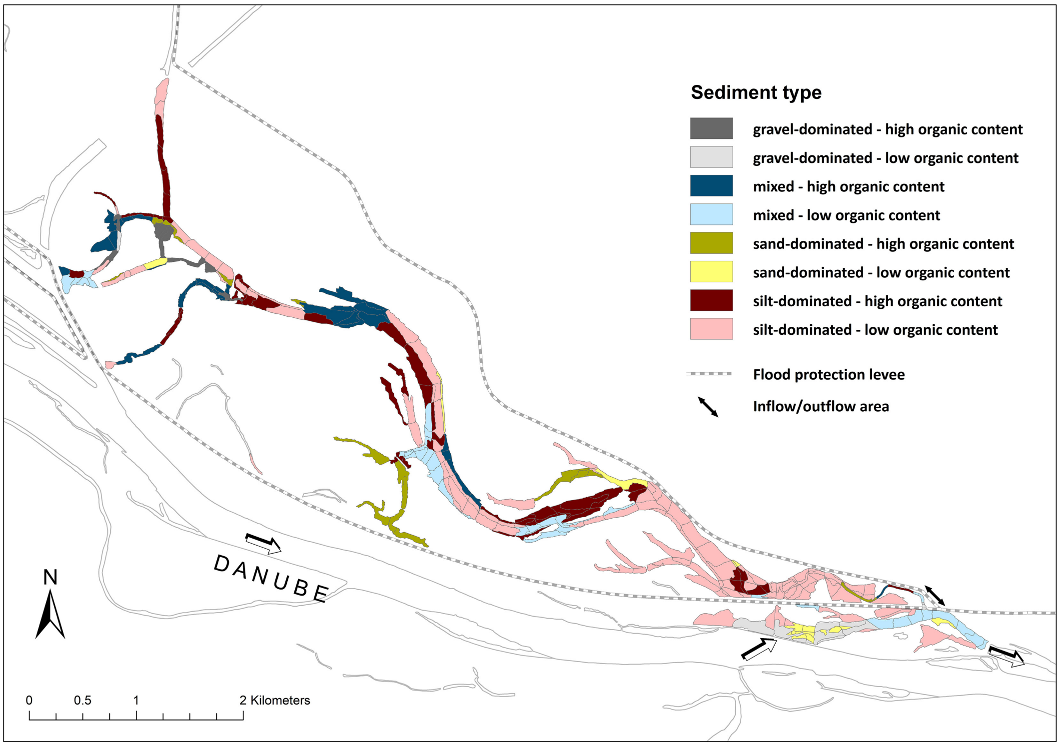

FIGURE 2 | Distribution of the predominating sediment types in the Lower Lobau.

Depending on the location of the water bodies and the predominant sediment type, the adsorption/desorption potential was calculated for flood and no-flood situations. Surface water connection with the main river channel was usually established for short periods. During this period, nutrients were imported into the floodplain, whereby the SRP concentrations decreased with distance to the inflow. At sites where the level of SRP in the water was higher than EPC0 of the particular area, sediments had the potential to act as a sink for SRP (**Figure 4**). The adsorption potential increased with increasing differences between the SRP concentrations and the EPC_0. Therefore, the phosphorus adsorption potential was higher in the downstream parts of the floodplain than in the upstream parts during connection with the main river channel. Isolated water bodies were characterized by SRP concentrations exceeding the EPC_0 during disconnection.

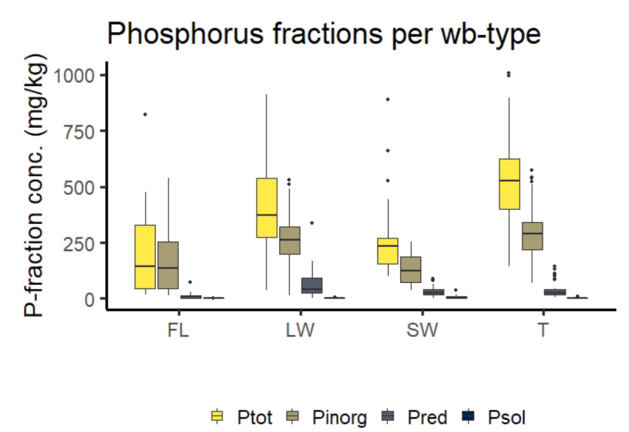

FIGURE 3 | Distribution of P-fractions in different water body types - FL, LW (including LFW and LRW), SW, and temporary water bodies (TF and TR).

bd, bulk density; C_{max} and K_d are adsorption parameters of the fitted two-compound Langmuir curve. Desorption as a percentage of adsorbed P per day.

After periods of connection, SRP concentrations in the water column rapidly decreased (**Supporting Information**, **Supplementary Figure 2**). At water SRP concentrations below the EPC_0, phosphate was potentially desorbed from the sediments to the water column, and the sediments changed from a sink to a source for SRP.

Upscaling of the Adsorption/Desorption Potential

We analyzed water level characteristics of the Danube main channel for the period from 1999 to 2019, summarizing the days of flooding conditions and the number of floods for the studied water body types, and simulated adsorption/desorption patterns (**Figure 5**). FL was connected during 106 ± 50 days per year on average in the period from 1999 to 2019 (**Table 2**). In FL, flood conditions were associated with flow velocities higher than 0.5 m s^{-1} and low hydrological retention. Therefore, water SRP concentrations in FL were similar to the concentrations

TABLE 4 | Results of multilinear regression for P_{tot}, P_{inorg}, P_{red}, and P_{sol} for the water body types MH, LW (LFW and LRW), and SW with the significant determining factors.

Predictive power	Variables	$n_{subsets}$	rss
P_{tot}			
0.78	Fraction of silt	19	100.0
	Macrophyte coverage	18	56.3
	Fraction of sand	18	56.3
	Fraction of gravel	17	49.8
	Organic content	16	43.7
	Permanent/temporary	13	30.8
	Hydrological connectivity	10	23.1
P_{inorg}			
0.80	Fraction of sand	20	100.0
	Organic content	19	64.7
	Fraction of silt	19	64.7
	Permanent/temporary	18	57.1
	Hydrological connectivity	16	40.4
	Macrophyte coverage	11	28.7
P_{red}			
0.71	Fraction of silt	21	100.0
	Macrophyte coverage	20	67.9
	Organic content	19	60.6
	Hydrological connectivity	18	55.3
	Fraction of sand	14	39.3
P_{sol}			
0.68	Hydrological connectivity	20	100.0
	Macrophyte coverage	19	81.4
	Fraction of silt	18	71.5
	Permanent/temporary	10	22.8
	Fraction of gravel	5	7.4

$n_{subsets}$ is the number of model subsets that include the variable, and RSS is the normalized residual sum of squares and shows the relative importance of the variables.

in the Danube during connection. Besides, the higher flow velocities resulted in the occurrence of gravel-dominated or mixed sediments, with low adsorption and desorption potential (**Table 5**). LFW was connected to the main channel at 76 ± 42 days per year. The connection increased the water levels of LFW, resulting in flow velocities lower than 0.05 m s^{-1} in most parts of the water bodies and inputs of SRP from the river. The sediments were mainly silt-dominated and showed a high potential for SRP adsorption (**Table 5**).

The adsorption/desorption dynamics in LRW were similar to the ones in LFW, but the average hydrological connectivity was only 10 ± 9 days per year. Therefore, adsorption phases were short and less intense because of SRP concentration and, consequently, the difference between SRP and EPC_0, were much lower than in LFW (**Table 2**). In SW, P dynamics were generally different from the other water bodies. Water SRP concentrations were higher than in the other parts of the floodplain and the main channel of the Danube during disconnection (**Table 2**), which theoretically would facilitate a high potential for SRP adsorption. However, as the SRP concentrations remained high in these water bodies during disconnection, we assume that other SRP release mechanisms, like reductive phosphate release, superimposed the adsorption/desorption processes. Connection during floods resulted in a decrease of SRP concentrations due to dilution.

The hydrological connection of a water body with the Danube main channel and the import of nutrients resulted in a general increase in the SRP adsorption potential of the sediments, outbalancing the desorption potential. It resulted in an annual positive adsorption/desorption balance. Only in the year 2003, which was characterized by low water levels, the P-desorption potential was higher than the adsorption potential, and the annual balance was negative. The highest annual net adsorption of the entire floodplain, with an average water surface area of 137.5 ha, was calculated for the exceptionally wet year 2002 (3,274 kg SRP per year). A net release of SRP of the whole floodplain area was only found for the dry year 2003 (−344 kg SRP per year) (**Figure 5**). The average adsorption/desorption potential for the period from 1999 to 2019 was 751 kg SRP per year, showing overall net adsorption of SRP.

DISCUSSION

The present study underlines the high importance of phosphorus adsorption and desorption processes in river floodplains. The fluctuations of the main channel water level determined the adsorption and desorption processes of phosphate to the sediment on both the short- and the long-term. It influenced the availability of SRP in water bodies with different connectivity levels and, thereby, the SRP balance of the Lower Lobau floodplain.

TABLE 5 | Phosphorus equilibrium concentrations (EPC_0) for the studied sediment types.

Sediment type	bd_sed kg m^{-3}	EPC_0 μg L^{-1}	C_{max1} mg kg^{-1}	K_{d1}	C_{max2} mg kg^{-1}	K_{d2}	Desorption %
Gravel-dominated—low OC	2.1	3.2	20.2	18.9	21.9	18.9	5.6
Gravel-dominated—high OC	2.1	3.2	20.2	18.9	21.9	18.9	5.6
Sand-dominated—low OC	1.9	6.7	149.7	0.4	144.2	0.42	1.1
Sand-dominated—high OC	1.9	6.7	149.7	0.4	144.2	0.42	1.1
Mixed—low OC	1.8	2.1	108.9	0.02	438.3	0.65	3.7
Mixed—high OC	1.8	5.7	59.2	0.2	421.1	64.5	8.6
Silt-dominated—low OC	1.4	4.7	96.9	0.02	380.8	0.2	9.7
Silt-dominated—high OC	1.4	8.5	21.6	0.07	388.6	10.6	28.1

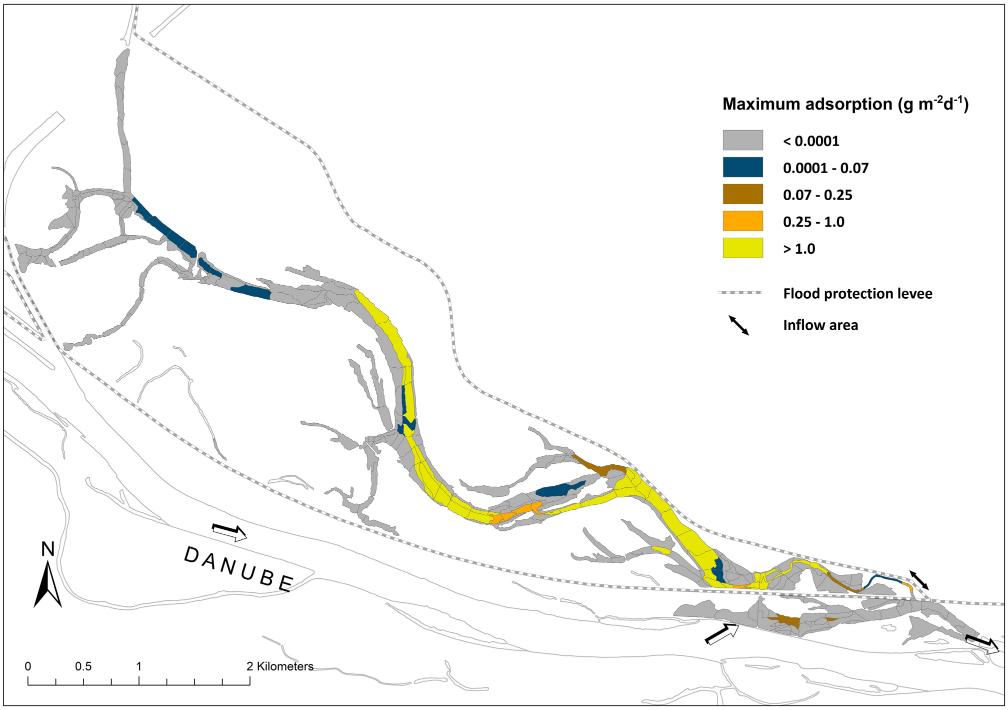

FIGURE 4 | Maximum SRP adsorption potential in different floodplain water bodies under flooding conditions (in g m^{-2} d^{-1}).

Relevant Processes in Phosphorus Cycling in Water and Sediments

Prior studies have shown that the hydrology is a reliable driver for phosphorus availability in the floodplain Lower Lobau (Reckendorfer et al., 2013; Weigelhofer et al., 2015). Danube water imports (average SRP concentration during floods: $20.6 \pm 5.2\ \mu g\ L^{-1}$) into the main side-arm of the floodplain result in a decreasing gradient of water column SRP concentrations in the floodplain water bodies, determined by their distance to the inflow area and their connection level. Due to the fast turnover rates, peak concentrations of water column SRP decrease within 2–3 days after the flood peak in the main side-arm (Weigelhofer et al., 2015; **Supporting information**, **Supplementary Figure 3**). Similar observations have been made by House et al. (1995), who reported a fast initial reaction of P-adsorption under oxic conditions, with about 60% uptake in the first half-hour.

Various mechanisms of phosphate removal were studied in floodplains, such as, e.g., assimilation by autotrophic and heterotrophic organisms, interactions with the sediment, and output to the main channel (Noe et al., 2019). Despite the high importance of these processes for the phosphorus cycling, in general, we think that biotic uptake played a minor role in the removal of the imported P in the Lower Lobau due to decreased phytoplankton densities during flooding (Weigelhofer et al., 2015). Instead, we assume that adsorption is a major removal pathway in this floodplain system, whereby a large part of the water column SRP imported during floods is already adsorbed in the upper sediment layers of LFW and a minor part in LRW. Within a few days after floods, SRP declined to concentrations below EPC_0 of the sediments, which potentially enabled the desorption of SRP. The implemented EPC_0 method included the adsorption or desorption of easily soluble phosphate under idealized conditions and was therefore calculated as adsorption or desorption potential. SRP adsorption or desorption in the field depends on both large- and micro-scale characteristics and conditions of the sediments. For example, diffusive boundary layers that indicate the change from oxic to anoxic conditions in the sediment could inhibit or slow down SRP diffusion from the pore water to the water column (Golterman, 2004).

After floods, SRP concentrations were consistently low and below EPC_0 in all water bodies except SW. Other studies showed increasing algal biomass and total phosphorus concentrations in the Lower Lobau water bodies after floods, especially in more isolated sections (Reckendorfer et al., 2013; Weigelhofer et al., 2015). We attribute this release to the desorption of the previously adsorbed SRP, leading to the observed phytoplankton peaks after floods.

Effects of Surface Hydrological Connection on the Adsorption/ Desorption Potential

To be able to set up an SRP adsorption/desorption balance for the floodplain, we assumed constant sediment characteristics and conditions throughout the study period. It enabled us to use a segment based model with a high spatial resolution to upscale adsorption/desorption patterns of SRP at floodplain scale. As shown, adsorption/desorption potentials were strongly determined by the hydrological connectivity of the water bodies. It was also indicated that water bodies with higher hydrological

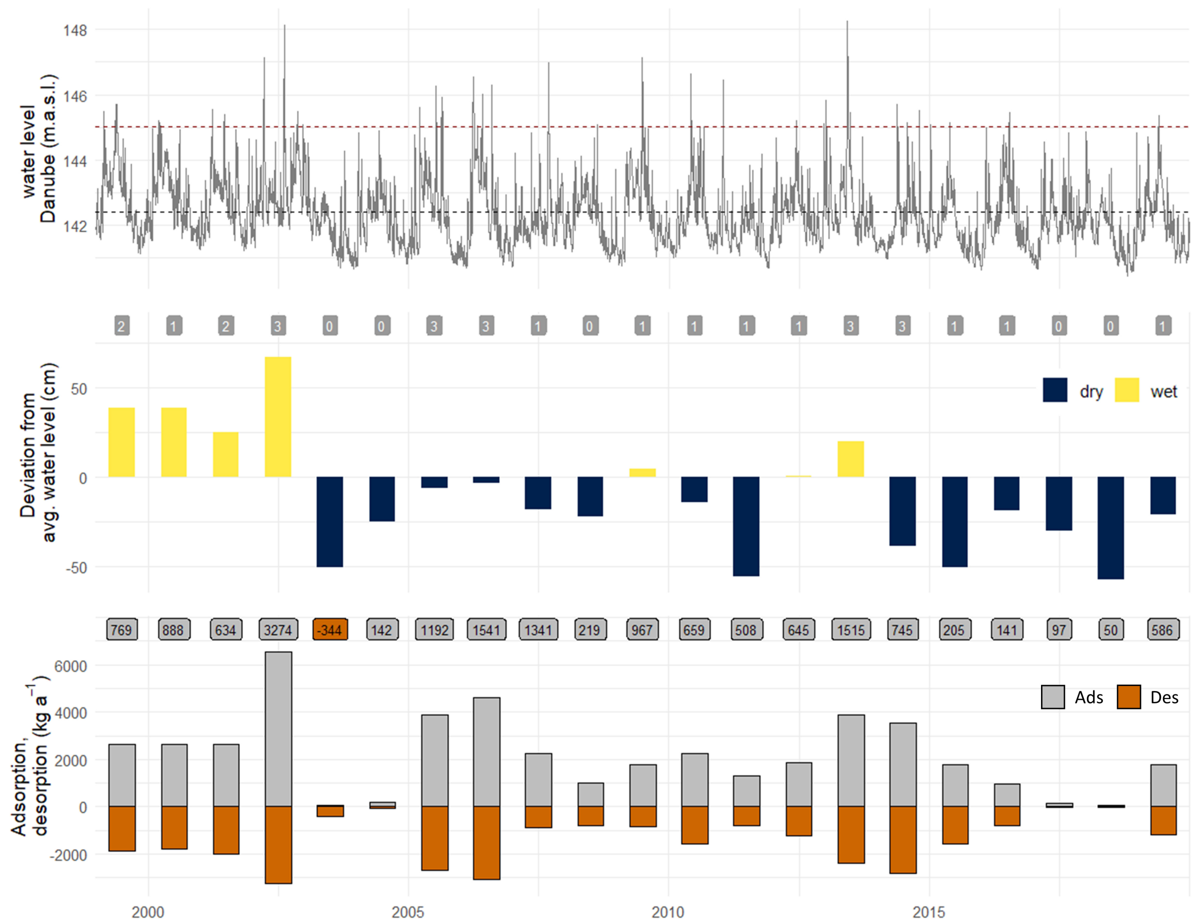

FIGURE 5 | Riverine water level and corresponding adsorption/desorption potential of all floodplain water bodies from 1999 to 2019. Water level of the main channel of the Danube; dashed line—mean water level (MW2010, KWD 2010). Number of floods per year is indicated (gray boxes). Deviation from average water level calculated as the difference between the average water level per year and the mean water level of the Danube (MW 2010, KWD 2010). Adsorption/desorption potential of the whole floodplain per year; labels indicate net adsorption (gray) or release (orange) of SRP are shown in boxes.

connectivity showed much higher potential for SRP adsorption if the sediments were not gravel-dominated, such as in FL. About 65% of the calculated adsorption potential occurred in LFW (**Table 6**) due to the high SRP concentrations during connection periods and the mainly silt-dominated sediments. In other water bodies, only minor P-adsorption and -desorption potential was indicated. A large portion (about 75%) of the adsorbed SRP in LFW was released gradually in the periods after floods (**Table 6**). The calculated desorption potential can, therefore, be described as the buffering capacity of the floodplain. About 30% of the annual adsorption potential was attributed to temporary water bodies (T), inundated only during floods. We calculated the potential based on the sediment characteristics and the corresponding EPC_0. Other studies (Schönbrunner et al., 2012; Dieter et al., 2015) reported that repeated drying and wetting resulted in an elevated phosphorus release from the sediments. These processes were not included in our calculations and may outmatch the considered adsorption processes. As temporary water areas were inundated only for short periods (about 1 week during floods), the desorption potential was low, and the adsorbed SRP was removed from the water column for more extended periods.

The overall buffering capacity of the floodplain water bodies was mainly determined by large, frequently connected water bodies (LFW). The main reason was the higher and more frequent SRP inputs and the large area compared with other water body types. Furthermore, in these water bodies, mostly silt-dominated and mixed sediments with low OC were found,

TABLE 6 | Average adsorption/desorption potential of SRP per year in the period 1999–2019 (in kg ha^{-1} per year) per water body type (wb).

wb	Area (ha)	Adsorption (kg ha^{-1} per year)	Desorption (kg ha^{-1} per year)
FL	20.7	2.0 ± 0.6	-0.3 ± 0.1
LFW	63.1	29.5 ± 21.9	-22.3 ± 15.6
LRW	27.2	0.7 ± 0.4	-0.4 ± 0.3
SW	9.9	0.9 ± 1.1	-0.5 ± 0.3
T	16.6	40.6 ± 22.7	-0.4 ± 0.5

which had the highest capacity for SRP adsorption and, therefore, also for desorption. The buffering mechanism of SRP had a crucial impact on the phosphorus availability in the floodplain water bodies after floods. It was of high importance for the algal primary production, resulting in algal peaks after floods (up to 45 μg Chl-a L^{-1} in LFW, compared with about 10 μg L^{-1} before floods, Weigelhofer et al., 2015).

Further hydrological decoupling of the Lower Lobau floodplain from the main river channel, as predicted by Hohensinner et al. (2008), will result in a reduction of water bodies and a decline of connection periods. This will, in turn, lead to a decrease in the adsorption potential, the buffering capacity, and the retention of phosphorus in the floodplain. The re-establishment of floodplain-typical hydrodynamics (connection at low water level; 141.1 m a.s.l.) could completely change the P dynamics within the floodplain and the floodplain–main channel interactions. It includes a changing availability of SRP due to the higher nutrient import from the main channel and altered sediment characteristics and, therefore, a changed adsorption potential. We estimated that the lateral channels of the main side-arm with non-flowing conditions would show the most dynamic adsorption/desorption patterns. Because of the increased water SRP concentrations due to continuous inputs from the Danube main channel, the desorption potential would also decrease. Although the buffering function of the sediments would be primarily limited to backwater areas, the overall phosphorus retention of the floodplain could be higher than under current conditions because of the increased area of water bodies and the more dynamic water level fluctuations. Besides, increased SRP concentrations in the main side-arm would result in higher phytoplankton primary production (Amoros and Bornette, 2002; Preiner et al., 2008) and can increase the overall P-retention of the floodplain.

CONCLUSION

Under the current conditions, river–floodplain interactions in the Danube floodplain Lower Lobau are reduced to short periods of connection during increased riverine water levels. Hydrology has a temporal but also a very distinct spatial component. While flooding controls the exchange with the main river channel, the location and morphology of the floodplain water bodies determine the degree and duration of this connection. Based on the SRP dynamics in different water bodies, we could show that the hydrology strongly affects the net adsorption/desorption potential of the floodplain with a vast impact on the overall role of the floodplain for the P dynamics. The SRP adsorption in the floodplain has the potential to reduce the SRP load of the Danube main channel by SRP retention. The floodplain sediments can act as a buffering system by taking up high amounts of SRP during floods and releasing parts of the adsorbed P time-delayed over a more extended period within the floodplain water bodies. This had a crucial impact on phosphorus availability in the floodplain water bodies and is of high importance for the primary production in the floodplain water bodies after flood events.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

SP: conceptualization, funding acquisition, project administration, investigation, data curation, formal analysis, and writing – original draft. EB-K: conceptualization, investigation, data curation, formal analysis, and writing – review. BP: data curation, formal analysis, and writing – review. GW: conceptualization and writing – review. TH: conceptualization, funding acquisition, project administration, supervision, and writing – review. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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Response of Submerged Macrophyte Growth, Morphology, Chlorophyll Content and Nutrient Stoichiometry to Increased Flow Velocity and Elevated CO_2 and Dissolved Organic Carbon Concentrations

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It is expected that climate change will cause more frequent extreme events of heavy precipitation and drought, changing hydrological conditions in riverine ecosystems, such as flow velocity, evapotranspiration (drought) or runoff (heavy precipitation). This can lead to an increased input of terrestrial organic matter and elevated levels of dissolved organic carbon (DOC) and CO_2 due to degradational processes in water. Consequences for submerged macrophytes, as essential organism group, are still poorly understood. The combined effects of changing flow velocity, DOC and CO_2 have not been studied before, so this was tested in a racetrack flume experiment on the macrophyte *Berula erecta* using a trait-based approach. The plants were exposed to two different flow velocities, two DOC concentrations and two CO_2 concentrations in a full factorial design. Apart from individual dose-response tests, two climate change scenarios were tested: a wet scenario simulating heavy precipitation and runoff with high flow velocity, high DOC and CO_2 concentrations and a dry scenario simulating evapotranspiration with low flow velocity, high DOC and high CO_2 concentrations. Growth rate, biomass, morphology, chlorophyll and nutrient content (C, N, and P) were measured. *B. erecta* responded strongly to both scenarios. Biomass and the relative growth rate increased and stems were shorter, especially in the wet scenario, and vegetative reproduction (the number of stolons) decreased. In both scenarios, the N content was lower and P content higher than in conditions without climate change. It can be concluded that climate change effects, especially shading by DOC, strongly influence macrophytes: macrophyte abundance will probably be negatively affected by climate change, depending on the macrophyte species and abundance of epiphytic algae. This may have consequences for other components of the aquatic ecosystem.

Keywords: aquatic plants, *Berula erecta*, climate change, carbon dioxide, brownification, humic substances, flow velocity, multiple stressors

INTRODUCTION

As a result of human-induced climate change, worldwide precipitation patterns are altering. In Europe, for example, the frequency of heavy precipitation events is increasing in winter, whereas there is an increased risk of drought in summer at the same time in some regions (Hoegh-Guldberg et al., 2018). If temperatures increase by 1.5°C, it has been predicted that heavy precipitation intensity (annual maximum 5-day precipitation) increases by at least 5–10% in many parts of Europe, whereas precipitation may decrease by 5–15% in some periods, especially in the Mediterranean area (Jacob et al., 2018). Because precipitation is an important driver of changes in river discharge (Dai et al., 2009), more extremes in discharge can be expected in the future, which can profoundly affect water quality and riverine ecosystems (van Vliet et al., 2013). Aquatic macrophytes play a key role in those ecosystems as they affect nutrient cycling and sedimentation (Clarke, 2002), oxygen dynamics (Uehlinger et al., 2000) and organise stream structure and functioning (Schoelynck et al., 2012b).

Macrophytes can be affected in several ways by changing river discharge. Firstly, aquatic macrophytes are directly affected by changes in river discharge. Dry periods with slow flowing or standing water can lead to warmer water and a lower water level with more eutrophic conditions including high algae growth and relatively more fish, and in some cases more saline conditions; leading to a decline of submerged macrophytes (Short et al., 2016). When discharge and flow velocity are high, macrophytes can break or uproot due to increased pulling forces acting on the plants (Schutten et al., 2005). Hydrodynamic stress caused by increased flow velocity can also affect plant physiology: photosynthesis can decrease by 30–60% (Madsen et al., 1993). Macrophytes can adapt to hydrodynamic stress by changing their morphology. There are two strategies: the first strategy is stress avoidance, which involves becoming more streamlined or smaller, so this affects plant biomass. The second strategy is stress tolerance, which involves increasing resistance to breakage by increasing their cross-sectional area and forming stronger tissue (Puijalon et al., 2011), for example by increasing their silica content (Schoelynck et al., 2012a). Altered plant biomass and nutrient stoichiometry can indirectly affect other organisms that depend on macrophytes.

Secondly, changing precipitation patterns can affect the amount of organic and inorganic carbon in water. From 1990 an increase in dissolved organic carbon (DOC) concentrations in surface waters has been observed, especially in Europe and North America (Monteith et al., 2007), which often leads to an increase in water colour called "brownification" (Kritzberg and Ekström, 2012). This is probably caused by a complex interaction of different factors, but two main mechanisms have been proposed: due to better regulation of sulphate pollution in the atmosphere, atmospheric acid deposition decreased which caused higher soil organic matter solubility (Pagano et al., 2014). The second mechanism is the effects of climate change: with increasing temperature and increased atmospheric carbon dioxide (CO_2) concentrations, more terrestrial organic matter is produced and with increased precipitation intensity this material can be flushed into rivers (Pagano et al., 2014). The flux of terrestrial carbon to inland waters is 5.1 Pg C year^{-1}, and this is increasing with 0.3 Pg year^{-1} (Drake et al., 2018). On the other hand, drought can be a driver of DOC as well: when the water level is lowered, in some cases more aerobic conditions are created which can stimulate the production of DOC (Porcal et al., 2009). Increased DOC concentrations in the water can have several effects on macrophytes. DOC from terrestrial sources like tree leaves often mainly consists of humic substances that give the water a brown colour (Sachse et al., 2005) and may thus be a main driver for brownification. Moreover, it is expected that as a result of climate change more DOC will consist of humic substances in the future (Creed et al., 2018). Humic substances can directly negatively affect macrophytes as they diminish light availability to primary producers (Karlsson et al., 2009; Choudhury et al., 2019) and reduce macrophyte colonisation depth (Chambers and Prepas, 1988). Moreover, some humic substances may directly affect macrophytes by entering the plant's cells and causing damage by production of reactive oxygen species (Grigutytė et al., 2009) or by interfering with photosynthesis (Pflugmacher et al., 2006). Even though DOC may cause a major threat to macrophytes, research about the magnitude of the problem and the exact effects on macrophytes is still limited (Reitsema et al., 2018).

Upon degradation, DOC can also be a source of CO_2 (Sobek et al., 2005). Mainly due to the high quantity of carbon entering from terrestrial soil or wetlands the world average CO_2 concentration in rivers and streams is 3100 ppm (Raymond et al., 2013), which is substantially higher than the concentration of 400 ppm in the atmosphere. Despite the fact that riverine CO_2 concentrations are relatively high, a further rise is expected in the future (Sobek et al., 2005; Phillips et al., 2015). DOC degradation is one of the mechanisms behind this, together with a reduced CO_2 efflux from the water as a result of higher atmospheric CO_2 concentrations, caused by a rise in CO_2 emissions (Phillips et al., 2015). It is difficult to predict future CO_2 levels in freshwater ecosystems because the exact factors controlling aquatic CO_2 concentrations and their response to climate change are not yet well understood. Moreover, current CO_2 and total inorganic carbon levels in rivers are highly variable and can depend on the catchment (Iversen et al., 2019), and location within the river (Maberly et al., 2015). As a consequence, it is hard to predict future CO_2 levels and how freshwater organisms will respond (Hasler et al., 2016). Research on the effects of CO_2 mainly focusses on marine ecosystems, where the resulting ocean acidification is relatively well studied (Boyd et al., 2016). Studies looking at the effects of elevated CO_2 concentrations on freshwater macrophytes observed increased plant growth rates under high CO_2 concentrations (Eusebio Malheiro et al., 2013; Dülger et al., 2017; Lv et al., 2019), increased biomass production (Hussner et al., 2016), and an increase in root:shoot ratio (Madsen et al., 1996; Hussner et al., 2016; Dülger et al., 2017). Moreover, the nitrogen (N) content of macrophyte tissue was found to be lower (Dülger et al., 2017; Hussner et al., 2019), the phosphorus (P) content was higher (Yan et al., 2006), chlorophyll content was lower (Madsen et al., 1996; Dülger et al., 2017), their dry matter content higher (Eusebio Malheiro et al., 2013) and specific leaf area (SLA) lower (Madsen et al., 1996).

Although the separate effects of varying flow velocity, increased DOC and increased CO_2 concentration have been studied before, their combined effects have not. However, macrophytes will probably be affected by a combination of different climate change effects. Often, complex ecological drivers like climate change are simplified in experiments (Knapp et al., 2018), so by testing the interactions between three factors a more realistic situation can be approached. This is important because contrasting results may be expected for the different factors that are tested. Macrophytes exposed to high DOC concentrations may remain smaller (Szmeja and Bociąg, 2004), whereas macrophytes exposed to high CO_2 concentrations may produce more biomass (Hussner et al., 2016) and show more clonal growth (Yan et al., 2006). Larger plants may be more vulnerable when flow velocity increases (Puijalon et al., 2011). Studying multiple aspects of climate change may result in more accurate predictions about how macrophytes may respond to climate change.

This study aims to test how macrophytes respond to flow velocity, DOC, CO_2 and their interactions. Besides individual dose-response tests, the effects of two climate change scenarios were tested: a wet scenario with high flow velocity, high DOC and high CO_2 concentrations, and a dry scenario with low flow velocity, high DOC and high CO_2 concentrations. A trait-based approach was used with analysis of growth rate, morphology, biomass allocation, chlorophyll production and C, N and P content of the plant. We hypothesised that in both scenarios plants would produce more biomass, especially more reproductive biomass like stolons, and that they would have a lower N and chlorophyll content and higher P content due to the increased CO_2 concentration. In contrast, we hypothesised that DOC would partially counteract the effect of elevated CO_2 due to shading, resulting in decreased plant growth. We also hypothesised that the stems would be shorter and thicker in the wet scenario as an adaptation to hydrodynamic stress. Lastly, we hypothesised that there would be interaction effects between flow velocity, DOC and CO_2 concentrations, due to the contrasting effects they can have as described in earlier paragraphs.

MATERIALS AND METHODS

Plant Material

In this experiment *Berula erecta* (Hudson) Coville (Apiaceae) was chosen as model species, since it is a sub-cosmopolitan species that can grow in many different lotic and lentic freshwater habitats (de Belair and Lansdown, 2013), and it is not a floating species, which makes it relatively vulnerable to the effects of climate change (Short et al., 2016). *B. erecta* is a homophyllous amphibious species, but at the sampling location it grew only submerged. Although many macrophyte species can take up two forms of inorganic carbon [bicarbonate (HCO_3^-) and CO_2], *B. erecta* can only take up CO_2 (Sand-Jensen et al., 1992), so we expected that this species would respond strongly to changes in CO_2 availability. Young plants were collected in the Fischa River in Austria close to the village of Pottendorf (47.91° N, 16.39° E). Plants of similar size were selected with initial dry mass of 0.11 ± 0.06 g. This was determined on 12 representative individuals that were not used in the experiment: from those 12 plants fresh and dry weight was measured and the conversion factor between fresh and dry weight was used to estimate dry weight of the experimental plants, based on their fresh weight. 384 plants (48 pseudo replicates per treatment) were each placed in $9 \times 9 \times 10$ cm square pots filled with 0–2 mm grain size cleaned river sand (commercially bought: Cobo gardens, Niel, Belgium) and with a layer of gravel on top to prevent erosion of the sand.

Experimental Design

The experiment was carried out in a greenhouse at the University of Antwerp (Belgium), where the plants were exposed to the natural day/night cycle. Plants were divided over four 400×120 cm racetrack flumes, in a 155×36 cm test section with a water height of 44 cm. Tap water was used [initial nutrient concentrations: 0.002 mg L^{-1} phosphorus (PO_4^{3-}-P), 0.03 mg L^{-1} ammonium (NH_4^+-N), 0.002 mg L^{-1} nitrite (NO_2^--N), and 2.308 mg L^{-1} nitrate (NO_3^--N)] and temperature was kept constant at 18°C. After 19 days of acclimatisation the plants in two flumes were exposed to higher flow velocity (0.4 m s^{-1}) and the other two flumes to low flow velocity (0.04 m s^{-1}), measured with a Valeport 801 ElectroMagnetic Flowmeter at 5, 10, 15, and 20 cm above the sediments in the middle of the flume, at 10 cm left from the middle and at 10 cm right from the middle, afterward the average was calculated. Moreover, CO_2 gas from a commercial bottle was added to two flumes with an airstone at approximately 2 L h^{-1} (gas pressure 2 bar). Gas flux was regulated with a Skalar GT1355 Sho-Rate G flowmeter. This resulted in four different treatments: high CO_2 (1000 ppm) with high flow velocity (HC-HF), high CO_2 with low flow velocity (HC-LF), low CO_2 (400 ppm) with high flow velocity (LC-HF), and low CO_2 with low flow velocity (LC-LF). The experiment was done between May 19, 2017 and July 24, 2017 without any added DOC (low DOC or LD treatment) and the experiment was repeated the year after between May 24, 2018 and July 31, 2018, this time DOC was added to all treatments (high DOC or HD treatment), see **Figure 1** for experimental setup. Solar radiation on the roof of the greenhouse was measured and in 2017 the total amount of radiation received during the experiment was 4.32 MW m^{-2} (224 W m^{-2} d^{-1}) and in 2018 this was 4.65 MW m^{-2} (237 W m^{-2} d^{-1}).

DOC

In this study it was decided to use leaf and peat leachate as DOC source. In some other studies artificial humic acid is used, but when we tested this material it did not dissolve well and only resulted in low DOC values that did not correlate with the amount of artificial humic acid added to the water. DOC was created in two tanks of approximately 2000 litres of water. To each tank, four 100 L bags of leaf litter (a mix of *Fagus sylvatica* L. and *Quercus robur* L.) and 30 L of peat (commercially bought: Aveve) was added. This was done on the 25th of May (the second day of the experiment). The tanks were covered with cloth to prevent photodegradation of the DOC. On day 21, 30, and 54 of the experiment, approximately 200 L of DOC-water was

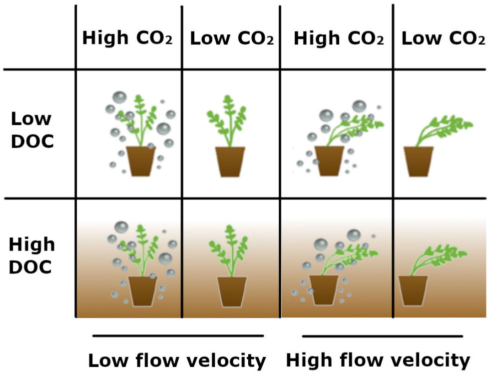

FIGURE 1 | Schematic overview of the experimental setup. The experiment was carried out in four flumes with each their own combination of treatments: high CO_2 × low flow velocity, low CO_2 × low flow velocity, high CO_2 × high flow velocity, and low CO_2 × high flow velocity. This experiment was then repeated with the same treatments, but this time DOC was added to all flumes.

added to each flume after being filtered through muslin cloth, in order to establish a DOC concentration of 5 mg C L^{-1}. In total, eight different treatments were tested (one flume per treatment), with the LD-LC-LF treatment as "no climate change scenario," and the HD-HC-HF and HD-HC-LF treatments as two climate change scenarios; in both scenarios increased CO_2 and increased DOC were tested, with heavy precipitation and drought being simulated in the HF and LF scenario, respectively. The other five treatments help in understanding the relative contribution of the three tested aspects of climate change to the response of the macrophytes.

Water Quality Measurements

The concentration of CO_2 in the water was measured continuously with a Pro-Oceanus Digital Mini CO_2 probe which alternated between the flumes. In addition, pH was measured weekly on approximately the same time of the day (early afternoon) (multiline F/set-3 multimeter) Alkalinity was measured four times during the experiment (SAN++, Skalar, Breda, Netherlands). Nutrient concentrations in the water were measured on day 6, 20, 50, and 67 of experiment 1 and on day 12, 26, 40, 54, and 68 of experiment 2; water samples were filtered with 0.45 μm filters (Chromafil® Xtra MV-45/25, Macherey-Nagel, Düren, Germany) and the concentration of PO_4^{3-}-P, NH_4^+-N, NO_2^--N, NO_3^--N was measured (SAN++, Skalar, Breda, Netherlands). The concentration of DOC was measured on day 6 (first experiment) and day 6, 12, 22, 26, 33, 40, 47, 54, 61, and 68 (second experiment). In order to measure DOC quality a sample from the DOC stock (see earlier paragraph) was filtered with a 0.45 μm filter and subsequently the sample was characterised by LC-OCD (liquid chromatography – organic carbon detection) (Huber et al., 2011). With this technique different size class fractions can be determined: biopolymers (large molecules like polysaccharides and proteins), humic substances (humic and fulvic acids), building blocks (oxidation products of humics) and low molecular weight neutrals and acids.

The effect of DOC on photosynthetically active radiation (PAR) availability was measured as well. On two clouded days, plastic transparent 5 L buckets (diameter 19 cm, height 20 cm) were filled with water from each flume and another bucket was filled with tap water in order to be able to compare to a control. A light sensor (MQ-210 Apogee underwater quantum PAR meter) was mounted to a frame to keep the sensor in the same position in all buckets. The frame was put in the middle of each bucket and the amount of PAR was measured. PAR availability was measured in buckets to avoid effects of shading from the macrophytes, the lid of the flume and the roof of the greenhouse. Additionally, a light profile was made in each flume in the middle of the test section by measuring PAR at every 5 cm, starting at the bottom.

Plant Growth and Morphology Measurements

Before planting on day 1, the total fresh mass (roots and shoots together) was determined for each individual. On day 1, 28, 46, and 67 (experiment 1) and day 1, 30, 47, and 68 (experiment 2) all plants were measured: number of stems and leaves, length and stem diameter of the longest stem, number of stolons (if visible) and the number of stems and leaves on the new ramets were counted (all are non-disturbing measurements). After harvesting the plants, stems, leaves and roots were separated and weighed fresh, and after drying the plant material for 48 h at 70°C the dry mass was determined. Before drying the samples, a subsample of 10 randomly chosen plants from each treatment was selected. The leaves of those plants were separated from the stems and photographed on a white background, after which the surface area of the leaves was calculated using the image processing programme ImageJ.

During the experiment periphytic algae started growing and covered the inner walls of the flumes and parts of the macrophytes. The algae were removed from the macrophytes twice by carefully taking them off the leaves by hand (see **Supplementary Figure S1**), but often started growing again within a few days. The amount of algae growing in the flumes was not quantified, but on pictures that have been taken it can be seen that in the treatment with high DOC there appear to be more algae growing in the flumes than in the treatment with low DOC (**Supplementary Figure S1**). The dissolved CO_2 pattern in the water also suggests that there were more algae in the high DOC treatment, as the day-night fluctuations were more pronounced than in the low DOC treatment (**Supplementary Figure S2**), despite a lower plant biomass.

Chlorophyll Analysis

From the subset of 10 plants per treatment used for the leaf surface area calculations, approximately 150 mg of fresh leaf material was ground with 80% acetone and quartz sand. The sample was centrifuged once at 4000 rpm and twice at 3000 rpm, after which the chlorophyll content (a, b, total and carotenoids) was determined spectrophotometrically. The samples were kept in the dark on ice during the extraction. The absorbance of the samples was measured at four different wavelengths (710, 663.2, 646.8, and 470 nm) which were used to calculate chlorophyll according to the following formulas (A_x = absorbance at specific wavelength):

$$Chl_a = 12.25 * (A_{663.2} - A_{710}) - 2.79 * (A_{646.8} - A_{710})$$
$$Chl_b = 21.5 * (A_{646.8} - A_{710}) - 5.1 * (A_{663.2} - A_{710})$$
$$Chl_{a+b} = 7.15 * (A_{663.2} - A_{710}) - 18.71 * (A_{646.8} - A_{710})$$

$$\text{Total carotenoids} = \frac{1000 * (A_{470} - A_{710}) - 1.82 * \left(Chl_a - 85.02 * Chl_b\right)}{198}$$

The rest of the subsample plant material was dried in the same way as the other material and the dry weight was

TABLE 1 | *F*-values of the three-way ANOVA tests and *z* values of the generalised linear models of growth and morphological parameters (*n* = 48).

	CO_2	Flow	DOC	CO_2*Flow	CO_2*DOC	Flow*DOC	CO_2*Flow*DOC
Number of stems	−12.96***	−3.44***	9.89***	ns	ns	ns	ns
Number of leaves	178.69***	0.19	61.51***	0.11	17.41***	0.11	9.49**
Length longest stem	163.81***	51.14***	12.03***	19.01***	95.30***	23.43***	ns
Diameter longest stem	133.80***	20.91***	131.70***	5.72*	7.33**	5.88*	9.86**
Dry mass total	379.93***	4.08*	234.89***	0.019	21.69***	2.73	5.32*
Leaf stem ratio	11.19***	5.88*	57.26***	ns	37.66***	ns	ns
Root shoot ratio	0.17	9.96**	60.97***	0.11	70.79***	1.76	8.01**
Number of stolons	−8.40***	−4.00***	8.49***	ns	ns	ns	ns
Average stolon length	−2.97**	−3.27**	9.22***	2.57*	−4.15***	2.33*	−3.07**
Total stolon length	−2.97**	−3.27**	12.31***	2.57*	−6.33***	1.35	−2.37*
Relative growth rate	640.62***	25.60***	117.12***	7.81**	48.70***	4.71*	21.83***
Dry matter content leaves	1.83	9.45**	43.52***	4.83*	17.82***	11.88***	9.93**
Dry matter content stems	1.16	12.40***	48.53***	3.95*	18.15***	12.93***	7.55**
Dry matter content roots	−0.10	0.45	−2.03*	ns	ns	ns	ns

*Interaction effects that were not significant have been removed from the model (ns). Number of stems, number of stolons and average and total stolon length and DMCR have been tested with a GLM. Some variables have been transformed: number of leaves: $x^{1/4}$, length of the longest stem: $x^{1/2}$, stem diameter: $x^{1/2}$, dry mass total: $x^{1/15}$, leaf:stem ratio: $x^{1/2}$, root:shoot ratio: $x^{1/5}$, relative growth rate: 100 + $x^{1.1}$, dry matter content leaves and dry matter content stems: 1/x. Signif. codes: * < 0.05, ** < 0.01 *** < 0.001.*

TABLE 2 | *F*-values of the three-way ANOVA tests of morphological parameters, chlorophyll and nutrient stoichiometry parameters (*n* = 5–10).

	CO_2	Flow	DOC	CO_2*Flow	CO_2*DOC	Flow*DOC	CO_2*Flow*DOC
% N Leaves	107.68***	0.29	144.92***	ns	33.79***	ns	ns
% N Stems	539.56***	0.67	56.31***	ns	ns	ns	ns
% C Leaves	76.25***	0.96	5.05*	ns	ns	7.03*	ns
% C Stems	1.85	0.02	6.43*	8.31**	58.07***	8.05*	ns
C:N leaves	132.20***	4.57*	89.07***	ns	17.91***	ns	ns
C:N stems	221.05***	1.70	36.95***	ns	5.73*	ns	ns
% P leaves	0.14	3.24	38.14***	ns	ns	ns	ns
% P stems	3.68	2.61	235.58***	ns	ns	ns	ns
C:P leaves	0.28	3.75	24.35***	ns	ns	ns	ns
C:P stems	0.55	3.58	120.90***	ns	ns	ns	ns
N:P leaves	18.55***	2.68	9.49**	ns	ns	ns	ns
N:P stems	111.42***	0.93	56.32***	ns	ns	ns	ns
Total leaf area	87.07***	1.12	56.85***	5.51*	17.39***	ns	ns
Average leaf area	155.39***	0.84	9.55**	ns	41.59***	6.77*	ns
Specific leaf area	Na	2.47	5.28*	na	na	ns	na
Chlorophyll a	10.77**	0.91	0.92	7.40**	6.38*	4.37*	ns
Chlorophyll b	30.33***	0.15	4.50*	6.14*	ns	ns	ns
Chlorophyll a:b	19.45***	0.04	19.94***	ns	45.10***	ns	ns
Chlorophyll a + b	30.21***	0.07	ns	6.77*	ns	ns	ns
Carotenoids	32.68***	0.41	ns	7.30**	ns	ns	ns
Total plant chlorophyll	63.55***	0.027	28.22***	11.65**	28.48***	ns	ns

*Interaction effects that were not significant have been removed from the model (ns). Some variables have been transformed: % N leaves: x^{-1}, % N stems: logxˆ(0.8), % C leaves: log, % C stems: x^6, C:N leaves: $1/x^{1/2}$, C:N stems: $x^{1/2}$, % P leaves: x^2, C/P leaves: 1/x, C/P stems: log, N/P leaves: $\log x^{1/3}$, N/P stems: log, total leaf area: $x^{1/4}$, mean leaf area: log, SLA: x^2, chlorophyll B: log, chlorophyll A/B: x^2, total carotenoids and total plant chlorophyll: log. Signif. codes: * < 0.05, ** < 0.01 *** < 0.001.*

TABLE 3 | Omega squared values for the growth and morphological parameters (n = 48).

	CO_2	Flow	DOC	CO_2*Flow	CO_2*DOC	Flow*DOC	CO_2*Flow*DOC
Number of leaves	0.43	0.012	0.257	0.009	0.016	0.004	0.006
Length longest stem	0.205	0.113	0.308	0.014	0.069	0.016	0
Diameter longest stem	0.241	0.021	0.482	0	0	0	0.006
Dry mass total	0.4	0.006	0.458	0.001	0.006	0	0.002
Leaf stem ratio	0.002	0.012	0.049	0	0.087	0	0
Root shoot ratio	0.216	0.023	0.031	0.025	0.125	0.002	0.005
Relative growth rate	0.567	0.021	0.276	0	0.009	0	0.007
Dry matter content leaves	0.02	0.001	0.069	0	0.017	0.005	0.022
Dry matter content stems	0.032	0.005	0.069	0	0.023	0.011	0.016

TABLE 4 | Omega squared values for the morphological parameters, chlorophyll and nutrient stoichiometry parameters (n = 5–10).

	CO_2	Flow	DOC	CO_2*Flow	CO_2*DOC	Flow*DOC	CO_2*Flow*DOC
% N Leaves	0.759	0	0.139	0	0.037	0	0
% N Stems	0.824	0	0.085	0	0	0	0
% C Leaves	0.436	0.016	0.183	0	0	0.034	0
% C Stems	0.134	0	0.186	0.038	0.296	0.037	0
C:N leaves	0.804	0.005	0.099	0	0.021	0	0
C:N stems	0.892	0	0.039	0	0.005	0	0
% P leaves	0	0	0.411	0	0	0	0
% P stems	0.009	0.006	0.806	0	0	0	0
C:P leaves	0	0.04	0.305	0	0	0	0
C:P stems	0	0	0.689	0	0	0	0
N:P leaves	0.221	0.023	0.108	0	0	0	0
N:P stems	0.506	0	0.256	0	0	0	0
Total Area	0.401	0	0.413	0.009	0.03	0	0
Mean Area	0.271	0.002	0.451	0	0.089	0.013	0
SLA Total	na	0.085	0.19	na	na	0	Na
Chlorophyll a	0.207	0.062	0.006	0.052	0.04	0.029	0
Chlorophyll b	0.231	0.065	0.033	0.045	0	0	0
Chlorophyll a:b	0	0	0	0	0.393	0	0
Chlorophyll a + b	0.22	0.067	0	0.054	0	0	0
Carotenoids	0.251	0.019	0	0.06	0	0	0
Total plant chlorophyll	0.374	0.02	0.352	0.026	0.064	0	0

determined. Beside chlorophyll concentration, total chlorophyll content per plant was calculated by multiplying the total chlorophyll concentration with the total fresh weight of the leaves of each plant (as chlorophyll was measured in fresh biomass).

Plant Carbon, Nitrogen and Phosphorus Analysis

The dried plant material (leaves and stems separately) from each flume was combined into five samples (nine plants per sample), in order to have enough material for the analyses. Those combined samples were ground with an Ultra Centrifugal Mill ZM 200 (Retsch, Germany). The ground material was analysed for C and N content on a FLASH 2000 Organic Elemental Analyser, based on Flash Dynamic Combustion (Thermo Fisher Scientific, Waltham, MA, United States). P content was determined by acid digestion and subsequently measured on ICP-OES (iCAP 6300 Duo view, Thermo Fisher, Waltham, MA, United States).

Statistical Analyses

All statistical analyses were carried out in R statistics version 3.4.3. The effects of elevated CO_2, DOC and flow velocity on growth and morphology parameters, chlorophyll, C, N and P content (35 traits in total, **Tables 1**, **2**) were tested with a three-way ANOVA with type III sums of squares. Normal distribution of the residuals was tested with Shapiro–Wilk tests and checked visually with Q-Q plots, homogeneity was tested with Levene's tests, and if necessary, data were transformed to meet the assumptions. When significant, a Tukey HSD *post hoc* test was performed. Variables with count data (number of stems and number of stolons) were analysed with poisson regression and variables with a severe positive skew (average and total stolon length and leaf, stem and root dry matter content) were analysed with gamma regression. In order to test the relative importance of the treatments and their interactions omega squared (ω^2) was calculated, which shows the proportion of the variance that is explained by every treatment and interaction. Negative values were set to zero as it can be assumed that those values signify that the effect was negligible (Graham and Edwards, 2001). R package "sjstats" (Lüdecke, 2019) was used to calculate ω^2 values and the values were visualised with Venn diagrams. To test how the plants responded to the treatment over time a Principal Response Curve (PRC) was used, which is a special case of the Redundancy Analysis (RDA) and was developed by Van den Brink and Ter Braak (1999). This was done using the "vegan" (Oksanen et al., 2019) package in R. In a PRC plot the effect of the different treatments is shown over time, relative to a control treatment that has been assigned before the analyses. The control treatment that was chosen is the "no climate change" scenario, with low CO_2, low DOC and low flow velocity.

RESULTS

CO_2 and DOC Concentrations

The average CO_2 concentration in the HC-LD and HC-HD treatments was 1494 ppm ± 299 (62 ± 12 μM) and 1086 ppm ± 948 (45 ± 39 μM), respectively. In the LC-LD treatment it was 449 ppm ± 51 (19 ± 2 μM) and in the LC-HD treatment 183 ± 153 (8 ± 6 μM). The concentrations followed a day-night rhythm with the most pronounced fluctuations in the high DOC treatment (**Supplementary Figure S2**). The DOC added to the flumes had the following consistence: 72.6% humic substances, 11.64% neutrals with small molecular weight, 7.1% building blocks, 7.0% biopolymers and <5.5% acids with small molecular weight. The DOC concentration in the first experiment was very low (1.4 ± 0.3 mg L^{-1}), whereas in the second experiment, where DOC was added regularly, it reached a reasonably constant value of 5.9 ± 0.8 mg L^{-1}

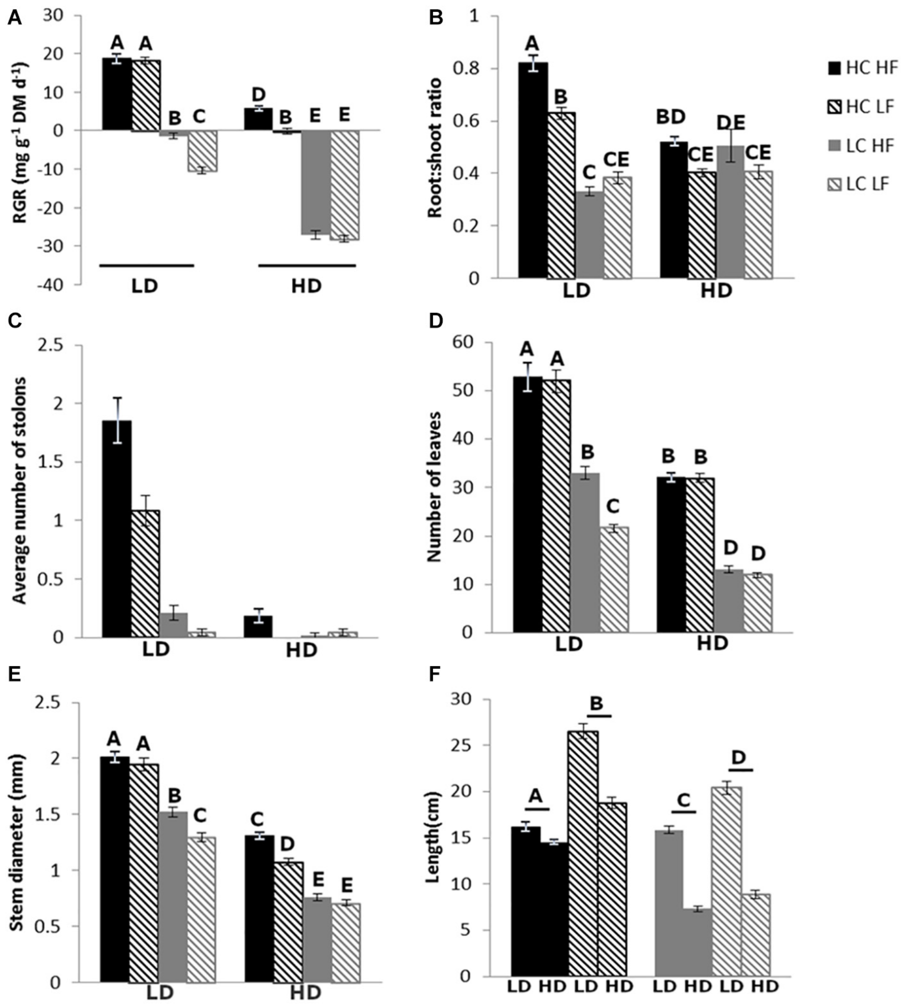

FIGURE 2 | Relative growth rate **(A)**, root:shoot ratio **(B)**, number of stolons **(C)**, number of leaves **(D)**, stem diameter **(E)**, and length of the longest stem **(F)**. The letters above the graph indicate significant differences ($p < 0.05$, $n = 48$), tested with three-way ANOVA. In panels **(A,B,D,E)** three-way interactions are shown, in panel **(C)** there were no interactions, just main effects of flow velocity, carbon and DOC, and in panel **(F)** a CO_2*Flow interaction.

(**Supplementary Figure S3A**). In the stock solution of DOC the amount of nutrients was relatively high, especially phosphate and ammonium. In a DOC solution of 5 mg C L^{-1} there was 0.29 mg L^{-1} phosphate (PO_4^{3-}-P) and 0.87 mg L^{-1} ammonium (NH_4^+-N). However, in the flumes the measured concentrations were far lower (**Supplementary Figure S4**), suggesting that nutrients were consumed rapidly.

Light availability was lower in the second experiment compared to the first; this ranged (average for all flumes) from 437.5 ± 28.5 μmol m^{-2} s^{-1} just below the water surface to 163 ± 22.7 μmol m^{-2} s^{-1} at the bottom of the flumes (**Supplementary Figure S3B**). PAR availability decreased with 23.8% in water with increased DOC concentrations (measured in a 20 cm deep bucket, see section "Materials and Methods"). For more details on water quality (pH, alkalinity and nutrients) see **Supplementary Information** "detailed results and discussion" and **Supplementary Figure S4**.

Effects of the Treatments and Interactions

Flow velocity, CO_2 and DOC all affected *B. erecta*. Out of the 35 traits measured, in 32 of them there was a significant effect of DOC, in 25 of them there was a significant effect of CO_2, in 13 traits a significant effect of flow, in 20 a significant effect of the CO_2*DOC interaction, in 14 a significant effect of the CO_2*flow interaction, in nine a significant effect of the flow*DOC interaction and in nine traits a three-way interaction (**Tables 1**, **2**). When looking at the relative importance of the treatments (omega squared values), in most cases DOC and CO_2 had the greatest effect, relative to the other treatments, followed by the CO_2*DOC treatment. Flow velocity and the other interactions had lower omega squared values in most traits (**Tables 3**, **4**).

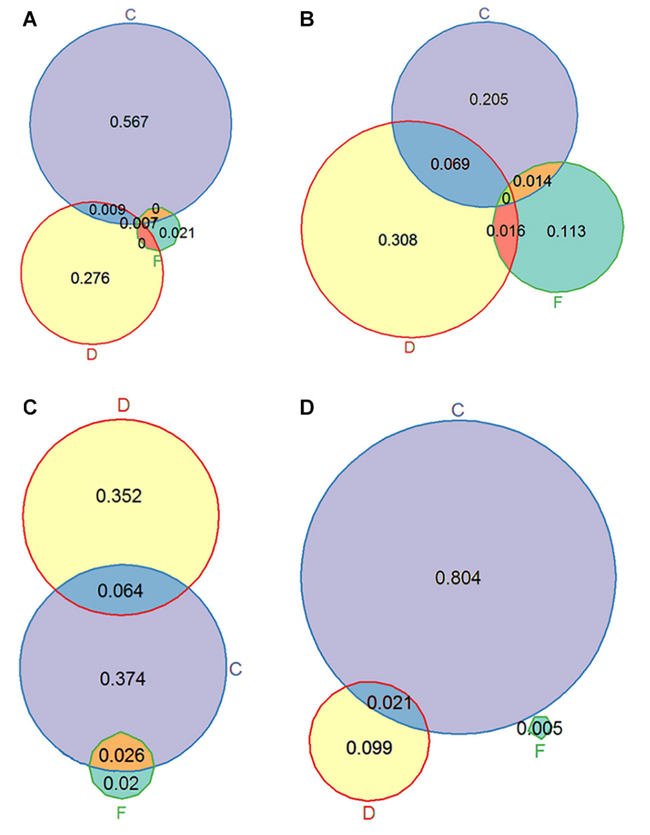

FIGURE 3 | Venn diagrams showing omega squared values representing the proportion of variance explained by CO_2 (C), flow (F), DOC (D) and their interactions for the variables relative growth rate **(A)**, length of the longest stem **(B)**, total plant chlorophyll **(C)** and leaf C:N ratio **(D)**.

Macrophyte Growth and Morphology

In the following paragraphs the main results will be highlighted, for a more detailed overview of the results, see **Supplementary Information** "detailed results and discussion". CO_2 and DOC had a pronounced effect on the relative growth rate (RGR) (**Table 3**) which was significantly higher in plants exposed to HC compared to LC and higher in LD compared to HD (**Figures 2A**, **3A**). Flow velocity had a smaller effect: plants growing under low flow velocity (LF) had a lower RGR than plants growing under high flow velocity (HF), but this was only significant in the LC-LD and HC-HD treatment (**Tables 1**, **2**). In nearly all LC and HD treatments the average RGR was negative. Biomass allocation was also affected by the treatments: the root:shoot ratio was mainly affected by CO_2, and to a smaller extent by the CO_2*DOC interaction (**Table 3** and **Figure 2B**). This can be seen in the LD treatment, where there is a positive effect of CO_2 on root:shoot ratio, whereas there is no CO_2 effect in the HD treatment. Moreover, the high flow, high CO_2 and low DOC treatments resulted in more and longer stolons (**Figure 2C**). In most morphological traits a positive effect of CO_2 and a negative effect of DOC was observed. This was most pronounced in the number of leaves (**Figure 2D** and **Table 3**). The number of stems, stem length, stem diameter (**Figure 2E**), total and average leaf area and total dry mass were also significantly more numerous or larger in HC and LD than in LC and HD conditions, SLA was also higher in the HD than the LD treatment.

Flow velocity had a smaller effect on plant morphology: plants exposed to HF had more leaves and more and thicker stems than plants growing under LF, but this was only significant in the LC-LD treatment (**Figures 2D,E**). In the LD treatment, leaves exposed to HF were smaller than leaves exposed to LF. However, in the HD treatment there was no effect of flow velocity (**Figure 4A**). The clearest effect of flow velocity was observed in the stem length, with the longest stems in the LF treatment (**Figures 2F**, **3B**).

Chlorophyll and Nutrient Stoichiometry

For chlorophyll a, chlorophyll b and total chlorophyll (a + b) concentration (mg g^{-1} FM) similar results were observed. Plants growing in the LC-HF treatment had a higher chlorophyll concentration than plants growing in other treatments (**Figure 4B**). When looking at the total chlorophyll content per plant, a different pattern was observed: plants exposed to HC appeared to have more chlorophyll than plants exposed to LC, and in the LD treatment they had more chlorophyll than in the HD treatment (**Figures 3C**, **4C**), as the plants in the HC-LD

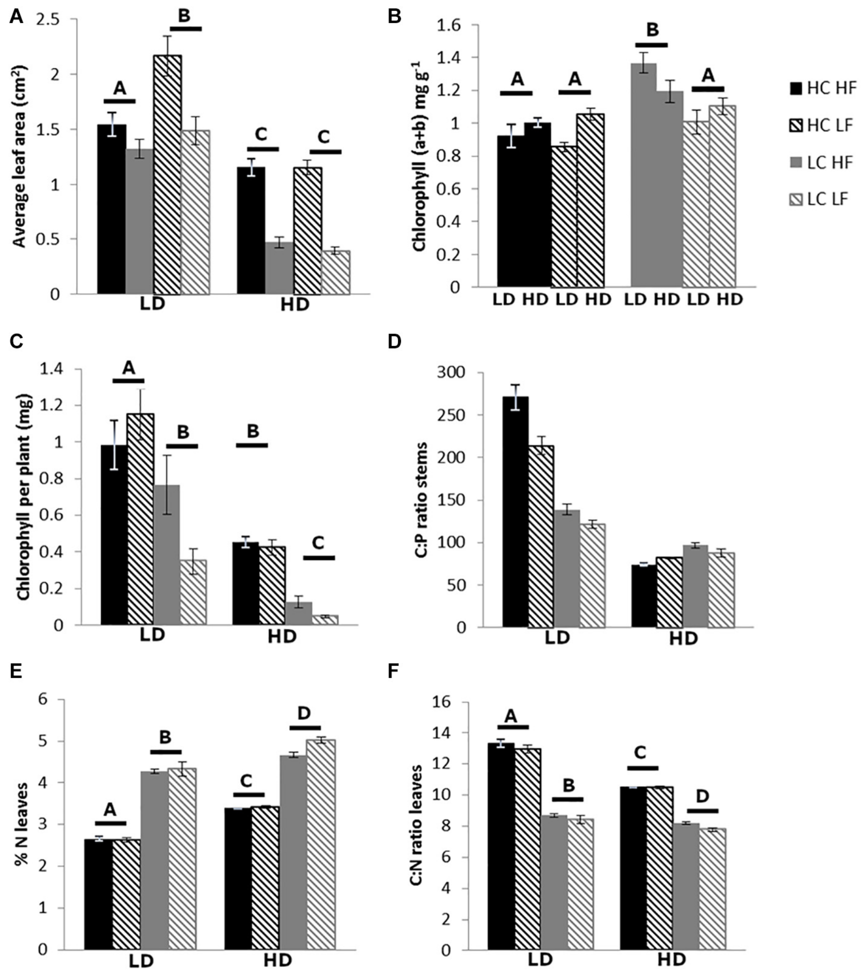

FIGURE 4 | Average leaf area **(A)**, total chlorophyll concentration **(B)**, total amount of chlorophyll per plant **(C)**, C:P ratio of the stems **(D)**, % N in the leaves **(E)**, and C:N ratio of the leaves **(F)**. The letters above the graph indicate significant differences ($p < 0.05$, n = 5–10), tested with three-way ANOVA. In panels **(A,C,E,F)**, CO_2*DOC interactions are shown, in panel **(B)** a CO_2*flow interaction and in panel **(D)** there were no interactions.

treatment had more biomass. The chlorophyll a: chlorophyll b ratio was higher in the LC than the HC treatment when plants were exposed to LD, but this was the other way around when plants were exposed to HD.

The DOC treatment affected every component of nutrient stoichiometry: in the high DOC treatment plants had higher N, C, and P concentrations than in the low DOC treatment; for P the differences were most pronounced, leading to lower C:P and N:P ratios in the HD treatment (**Figure 4D** and **Table 2**). The CO_2 treatment mainly affected plant N concentrations, which were lower in the HC than the LC treatment, resulting in higher C:N ratios in both leaves and stems (**Table 4** and **Figures 3D**, **4E,F**), especially in the LD treatment.

Differences Over Time

For eight plant traits that have been measured four times during the experiment a PRC diagram was made (**Figure 5**) to show how the traits developed over time. This was done for: number of leaves and stems (total, on the main plants and on the newly formed ramets at the end of the stolons), the number of stolons and the length of the longest stem. 30% of the treatment variance could be explained by the model ($F = 82.264$, $p = 0.001$). All plant traits had positive weights, indicating a positive relationship with the treatments in the diagram. This means that, especially toward the end of the experiment, all plant traits (especially the number of leaves) were favoured by most treatments except for the LC-LF-HD and LC-HF-HD treatments. The differences between the treatments become more pronounced toward the end of the experiment. While CO_2 and DOC had a relatively large effect, the effect of flow velocity was limited for the traits measured in this analysis.

DISCUSSION

In this study CO_2, DOC and, to a smaller extent, flow velocity (all potential effects of climate change) had strong effects on the growth and development of *B. erecta*, which is consistent with what was found in literature (Steinberg et al., 2006; McElarney et al., 2010; Cao and Ruan, 2015; Reitsema et al., 2020). Macrophytes that grew in the wet climate change scenario with increased heavy precipitation intensity (HD-HC-HF) had a higher RGR, more biomass, shorter stems, a higher root:shoot ratio, lower N content and higher P content than the plants growing in the no climate change scenario. The higher RGR and biomass production, especially belowground, seemed to be mainly caused by the increased CO_2 availability and this effect is also found in other studies (Dülger et al., 2017; Gufu et al., 2019). This effect is partly compensated by the negative effect of DOC on RGR and biomass production, which is probably caused by light limitation (Szmeja and Bociąg, 2004; Karlsson et al., 2009; Thrane et al., 2014), although DOC can also interfere with oxygen production (Pflugmacher et al., 2006) and cause oxidative stress (Steinberg et al., 2006). Additionally, the low, even negative, RGR in the HD treatment may have been caused indirectly by carbon limitation, besides the shading effect of elevated DOC. Measured CO_2 concentrations in the HD-HC treatment were lower than in the LD-HC, possibly caused by growth of epiphytic algae on the macrophytes (**Supplementary Figure S1**). *B. erecta* is an homophyllous amphibious plant that is unable to take up other forms of inorganic carbon than CO_2 and therefore it needs a high concentration of CO_2 to sustain photosynthesis (Nielsen, 1993).

The higher root:shoot ratio under HC has also been observed in other studies (Madsen et al., 1996; Yan et al., 2006; Hussner et al., 2016) and can be explained by root carbohydrate storage for overwintering (Dülger et al., 2017) and investment in clonal reproduction, which is regarded as a strategy to increase the plants' potential nutrient uptake (Yan et al., 2006). This last hypothesis seems to be most consistent with the results of the current study, as the stolons, which are used for clonal reproduction, were more numerous and longer in the LD-HC treatment.

In the HD-HC-HF scenario stems were shorter, and this may be explained by the plants' adaptation strategy to develop a more compact growth form in order to avoid hydrodynamic stress (breakage or uprooting), which has been observed in other research studying *B. erecta* (Puijalon et al., 2005). This idea is supported by the high root:shoot ratio in the HF treatment, which can be explained by the fact that roots enable plant anchoring (Schutten et al., 2005). The lower plant N content in the HD-HC-HF scenario seemed to be caused by the increased CO_2 treatment, which has been found in other studies as well (Titus and Pagano, 2002; Hussner et al., 2016). This may be explained by accumulation of carbohydrates under high CO_2 concentrations, leading to nitrogen savings (Dülger et al., 2017), although no evidence was found in the current study as the dry matter content in the leaves was similar under HC and LC and leaf C content was even smaller under HC compared to LC. The higher stem P content, which seemed to be caused by the high DOC treatment, is more difficult to explain. In literature the opposite is found: due to light limitation plants elongate their stems and in this structural tissue the relative amount of C is high and P is low (Su et al., 2016). In the current study P originating from DOC may explain the high P content. After adding DOC, a high P peak was observed in the water, whereas this was less pronounced for N (**Supplementary Figure S4D**).

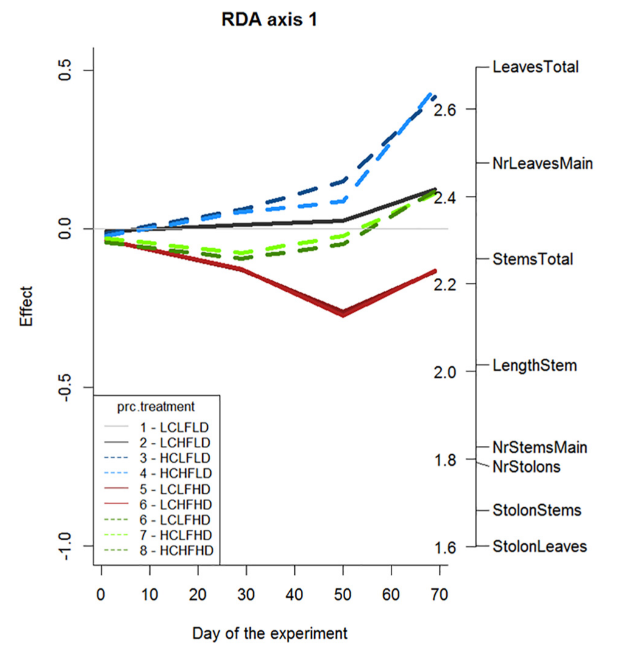

FIGURE 5 | Principal response curve (PCR) with the effects of the treatments on eight plant traits. On the right vertical axis the response variables are shown (number of stems and leaves on the main plant, stems and leaves that grew on the new ramets on the stolons, total number of stems and leaves, number of stolons and length of the longest stem) and their relative contribution to the observed pattern. The treatment with low CO_2 concentration, low flow velocity and a low DOC concentration is set as a reference situation (the horizontal grey line) and the effects of the other treatments are compared to this reference.

In the second climate change scenario with increased drought (HD-HC-LF) most of the results were comparable to the first climate change scenario with heavy precipitation (HD-HC-HF). The RGR was lower in the HD-HC-LF treatment, suggesting that there was a negative effect of increased boundary layers due to low flow velocity on biomass production (Westlake, 1967). However, the RGR was higher than in the no climate change scenario, suggesting that this negative effect of increased boundary layers was partially compensated by the increased CO_2 availability. The root:shoot ratio was smaller and stems were longer in the HD-HC-LF scenario compared to the HD-HC-HF scenario and were more similar to the no climate change scenario (LD-LC-LF), suggesting that flow velocity had a major impact on those morphological traits due to a stress avoidance response (see previous paragraph). With regard to nutrient stoichiometry, plants responded similarly to both climate change scenarios; flow velocity had a negligible effect on nutrient stoichiometry.

Most of the plant traits were strongly affected by CO_2. However, it should be taken into account that most rivers and streams are supersaturated with CO_2 (Raymond et al., 2013), so *in situ* concentrations are likely always higher than the ones used in this experiment. Aquatic CO_2 enhancement due to climate change may be relatively limited, and the effects on macrophytes less pronounced than in this experiment (Andersen and Pedersen, 2002). This means that the relative effects of flow velocity and DOC may be higher in natural situations. In this study, DOC had a negative effect on plant growth, but this is not observed for all macrophyte species: fast-growing potentially invasive species like *Hydrilla verticillata* (L. f.) Royle or *Elodea nuttallii* (Planch.) H. St. John show a positive growth response to DOC, due to accelerated growth rates under light limitation (Xu et al., 2018).

Although DOC is usually degraded in water by microorganisms, which results in CO_2 production (Sobek et al., 2005), this was not observed in this experiment: CO_2 concentrations in the LC treatment were lower in HD than LD conditions. Although additional tests confirmed that respiration increases when DOC is added to the water, in the flumes the extra amount of CO_2 was consumed fast. The macrophytes may have taken up this CO_2, but it is more likely that algae used the main part, as in general DOC had a negative effect on macrophyte growth and algae growth was more pronounced in the HD than the LC treatment. Moreover, the higher biomass of periphytic algae may also have caused additional shading (**Supplementary Figure S1**). A second factor to take into account concerning the HD treatment, besides periphytic algae growth, is that this treatment was done a year later than the LD treatment. Still, as the experiments were done in the same time of the year for an equal number of days, with equal constant water temperature, and a comparable amount of solar radiation we think that this difference was very small and did not significantly affect the results of this study.

Dissolved organic carbon also had a negative effect on vegetative reproduction: the number of stolons in the HD treatment is very low compared to the LD treatment. This may be explained by light limitation caused by brownification: although the effect of DOC on stolon formation has not been studied before, it has been found that there is a negative effect of water depth on stolon formation in *Vallisneria natans* (Lour.) H. Hara (Xiao et al., 2007), which suggests that in low light conditions, in this case caused by DOC, macrophytes produce fewer stolons. These results show why it is important to study multiple aspects of climate change in experiments, as different climate change aspects can have contrasting results, which makes it difficult to predict the response of macrophytes and the rest of the aquatic ecosystem.

To conclude, in this study it was found that *B. erecta* strongly responds to climate change. High flow velocity mainly affected plant morphology; stems were shorter and belowground biomass relatively larger. Biomass production was stimulated by CO_2 and limited by DOC, and there were strong interaction effects between those two stressors. As CO_2 has a large positive effect and DOC has a small negative effect on biomass production, compared to the control situation, one would expect a positive effect of the combination of CO_2 and DOC. However, in this study the combined effects of CO_2 and DOC are less positive than the sum of the two effects separately (a positive antagonistic effect) (Piggott et al., 2015). This means that elevated DOC concentrations can form a major reduction of performance in *B. erecta*, and this cannot be completely compensated by increased CO_2. Therefore, if DOC levels rise in the future, it can be expected that, depending on the macrophyte species and abundance of epiphytic algae, macrophyte biomass production and reproduction is negatively affected, and it can also indirectly influence ecological functions of the ecosystem, because macrophytes play an important role in riverine ecosystems. For example, a reduction in macrophyte biomass may imply reduced nutrient cycling between sediments and water column (Clarke, 2002), a reduction in dissolved oxygen (Carpenter and Lodge, 1986) and reduced diversity of macroinvertebrates and small fish (Camp et al., 2014). It is important that more studies investigate changes in the DOC and CO_2 concentrations, flow velocity and other parameters that will change due to climate change in rivers and how these changes correlate with macrophyte growth and the health of the ecosystem.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

All authors contributed to the study design, commented on previous versions of the manuscript, and read and approved the final manuscript. RR, JS, J-WW, and SP performed the material preparation, data collection, and analysis. RR drafted the first manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2020.527801/full#supplementary-material

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New Emphasis on Water Transparency as Socio-Ecological Indicator for Urban Water: Bridging Ecosystem Service Supply and Sustainable Ecosystem Health

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The perspective on water transparency changed since the early days of limnology from being a physical parameter of optical water property to an ecological indicator tracking algal turbidity due to eutrophication or an overall success of sustained lake restoration in the late 60ies to 80ies. In modern cities, where ecosystems are commonly deteriorated by man-made modifications, water transparency offers a great opportunity to the public to raise socio-ecological consciousness concerning urban green-blue spaces. We thus re-emphasize water transparency as a key indicator of multi-functional value when assessing an oxbow lake of the riverine floodplain in Vienna, the Alte Donau. Our study covers the eutrophication from 1987 to 1994 due to the inclusion of the riverine landscape in the urban area, the following lake restoration with an ecosystem shift from a nutrient-rich, algal-turbid water body to a nutrient-poor, clear-water macrophyte controlled system and the impact of global warming in recent decades. We used light attenuation profiles to identify depth layers of specific ambient light requirements for photosynthetic domains (phytoplankton and submerged macrophytes), and to interpret Secchi measurements. Here, we calculated the depth at 1% (minimum light requirements for phytoplankton growth as euphotic depth), 3% (minimum light requirements for macrophytes as maximum macrophyte colonization depth), and 12% (preferred light requirements for phytoplankton development) of surface ambient light. A Secchi disk water transparency of 1.5 m ("lake bottom view"), judged as good water quality by human perception, refers to mesotrophic conditions with a maximum colonization depth for macrophytes exceeding the mean lake depth in Alte Donau. Water clarity required for sustained macrophyte growth, in particular for favoring bottom-dwelling *Chara* meadows instead of tall-growing *Myriophyllum spicatum*, is

3.5 m Secchi depth and thus exceeds by far water clarity requested due to bathing aesthetics. Global warming, mirrored by an advanced warming in spring seems to favor significantly a higher yield of macrophytes mainly built up by *Myriophyllum* at the expense of the yield of algae. The prolongation of the summer period above 21°C, however, coincides with lowered Secchi transparency. Water visibility during the hot season thus seems to be slightly hampered against lake restoration efforts by global warming.

Keywords: urban green-blue space, recreational lake area, oxbow lake restoration, Secchi depth, threshold light requirement, phytoplankton, aquatic plants, climate change

INTRODUCTION

Recent acceleration of man-made ecosystem degradation (Crutzen, 2002; Steffen et al., 2011; Dalby, 2016) became most obvious in urban areas. The greatest threats to urban floodplain in Vienna are represented by simplification of the ecosystem structure due to canalization (Sanon et al., 2012; Haidvogl et al., 2013; Hohensinner, 2019), biodiversity loss (e.g., Tockner and Schiemer, 1997; Funk et al., 2009; Hein et al., 2016), and overusing natural systems for recreation purposes (e.g., Arnberger and Eder, 2012). Shortcomings of deteriorated surface waters were not only of concern from an ecological perspective but also raised social awareness in modern urban live. On the one hand, urban waters are at risk of being destroyed due to human impact on the other hand they are important for improving life quality in metropolitan areas (e.g., Naselli-Flores, 2008; Zimmermann-Timm and Teubner, 2019). Urban development thus recently gained an increasing awareness of the potential of green and blue infrastructure for the quality-of-life in densely populated areas. Aquatic ecosystems that originally were part of river floodplains in the vicinity of cities thus came to the fore of sustainable management practices (Funk et al., 2009; Sanon et al., 2012; Haidvogl et al., 2013; Preiner et al., 2018). They became more and more attractive serving by a multitude of cultural ecosystem services beneficial for quality-of-life in the city (Kazmierczak and Carter, 2010; Völker and Kistemann, 2011; Keeler et al., 2012; Dou et al., 2017; Hozang, 2018). Aesthetic satisfaction with nature in green and blue space experienced an increasing popularity contributing to higher awareness of life quality in urban areas (e.g., Smith et al., 1991, 1995a; Völker and Kistemann, 2011; Tajima, 2012; Kabisch, 2015; Kati and Jari, 2016; Dou et al., 2017; Lee, 2017; Angradi et al., 2018).

Despite the existence of a complex scientific assessment for urban waters (e.g., Karr, 1991; Dokulil and Teubner, 2002; Schneider and Melzer, 2003; Istvánovics et al., 2007; Hering et al., 2010; Janecek et al., 2018; Teubner et al., 2018b), human perception judging a good or sufficiently good status to be of high recreational value is often reduced to at least a single characteristic: the water transparency. The colloquial meaning of the term "good water quality" for Viennese is "a water body with high water transparency." When judging the suitability of an urban water body for multitude recreational use, the water transparency is often the primary optical criterion of human perception (Smith et al., 1991, 1995a; Michael et al., 1996; Wilson and Carpenter, 1999; Gibbs et al., 2002; Völker and Kistemann, 2011; Keeler et al., 2012; Angradi et al., 2018), followed by color (Smith et al., 1995b), and odor (Ginzburg et al., 1998; Chorus et al., 2000; Dokulil and Teubner, 2000; Paerl et al., 2001; Graham et al., 2010). In addition, aspects of urban landscape planning of water banks and associated green spaces enhancing nature aesthetics and better microclimate conditions play a further role (e.g., Bulkley and Mathews, 1974; Kazmierczak and Carter, 2010; Völker and Kistemann, 2011; Hozang, 2017; Lee, 2017). The perception of clear-water is further linked to hedonic values (e.g., West et al., 2016) as e.g., the believe in a pleasant and healthy environment. The trust in water clarity follows an intrinsic instinct to minimize health risk from unpleasant ill-making water as this came true for surface waters known from historical records when cities were rather seen as unhealthy places. The history of the role of polluted water and associated diseases for capital city Vienna are in detail described in Haidvogl (2019).

Measuring water transparency by disk visibility goes back to 1815, when it was adopted for measurements in the ocean and not lakes. This method yielded greater attention by the disk experiments published by Secchi (1866) (e.g., Aarup, 2002; Täuscher, 2015), i.e., just before the freshwater science epoch was initiated by Forel (1841−1912), who established limnology as a new branch of science in 1892 (Vincent and Bertola, 2012). Individual measurements of Secchi disk transparency in freshwaters may vary substantially from only few centimeters in hypertrophic riverine lakes (e.g., Teubner et al., 1999) to far more than 20 m in pristine alpine lakes (report of extreme high Secchi visibility of up to 26.5 m in the Alps; e.g., Tolotti and Cantonati, 2000; Tolotti, 2001).

In ecological research, measuring water transparency went beyond the physics of visibility of a water body and evolved into a tool for ecosystem assessment. It became of particular interest when eutrophication and the associated water turbidity due to algal blooms obviously deteriorated the ecosystems in the Anthropocene. Early trophic classification of lakes focused on the response of algal growth to the nutrient surplus by eutrophication, i.e., mainly phosphorus, which are well known as Vollenweider models (e.g., Vollenweider, 1968). Trophic classifications schemes by other studies were expanded to link an increasing amount of nutrient yield, such as algal biomass, with gradual deterioration of water clarity (e.g., Forsberg and Ryding, 1980; Nürnberg, 1996; ÖNORM M6231, 2001; Håkanson et al., 2005). In turn, in view of lake restoration, the sustainable increase of Secchi disk transparency – or also mentioned as water clarity – became the most well attributed value to water quality by human perception. It thus offered a key target indicating an overall success of lake restoration (e.g., Meijer et al., 1999; Hilt et al., 2006; Søndergaard et al., 2007; Gulati et al., 2008; Dokulil et al., 2018).

Although water transparency may differ among waters due to the natural color or inorganic seston, it is usually higher for ecosystems close to natural reference conditions hosting species assemblages that are characterized as reference biota. Such ecosystems are not strongly modified by man-made surplus of nutrients or other pollutants (man-made deterioration of water see e.g., Hupfer and Kleeberg, 2007; Dokulil and Teubner, 2011; Zimmermann-Timm and Teubner, 2019) so that their high transparency indicate a high degree of ecological integrity or ecosystem health from an ecological point of view (Karr, 1991; Dokulil and Teubner, 2002; Hering et al., 2010; Teubner et al., 2018b). Urban lake and river restoration today, however, does not end up with a good "water quality delivery" but focuses on securing a better "well-being" by providing valuable ecosystem services in particular if shared by socio-ecological awareness in cities. Even if the term Anthropocene was formulated as a warning of accelerated deterioration of ecosystems by recent human activities worldwide (Dalby, 2016), new attempts of "bettering the world" from regional to global scale are discussed. Thus, identifying ecosystem services generated in urban areas or in the vicinity of settlements has drawn increasing attention in recent time (e.g., Bolund and Hunhammar, 1999; Yigitcanlar et al., 2008; Sanon et al., 2012; Hein et al., 2016; Boyer et al., 2019).

The emphasis on water clarity in our study is exemplified for Alte Donau as it is the most well studied urban lake in the capital city of Austria, Vienna. The ecosystem faced dramatic changes mainly by losing its natural connectivity from the main river during river regulation from 1868 onward. The oxbow lake suffered from enhanced eutrophication from 1987 to 1994 due to the degradation of the riverine landscape into urban areas and global warming in recent decades. The growing public awareness of threats by eutrophication and global warming for providing reliable and sustainable provisioning of cultural ecosystem services (e.g., bathing, boating, and recreational fishing) called for a sustainable restoration of this Viennese oxbow lake in 1994. The progress of the restoration, which spanned more than 20 years and consisted of three main treatment periods characterized by various measures of sustainable restoration and ecological based activities, is summarized in Dokulil et al. (2018). We want to put here new emphasis on water transparency aimed at answering the question whether water transparency holds true as socio-ecological key indicator for Alte Donau. We want to understand how suffice the water clarity can be for identifying ecosystem services in view of (1) suitability for recreational use and (2) the overall success of sustained lake restoration. In addition, we will explore (3) the impact of global warming superimposing "water clarity mediated" ecosystem services.

MATERIALS AND METHODS

Site Description

The study area Alte Donau refers to the Vienna Basin, part of the northwest margin of the Pannonian Plain in Central Europe. The oxbow lake is located in the suburban area "Donaufeld" in Vienna, the capital of Austria (map and photos in **Figure 1**). The main characteristics of this urban lake given in **Table 1** includes information about location, genesis, morphometry, trophic state in 1987 and 1992−2019 as well as mean annual air temperature in the suburban and urban neighborhood. In addition, the restoration measures from 1995 to 2019 are summarized. Samples analyzing plankton biota and chemistry were taken in the two main impoundments at biweekly (to monthly) intervals. Further details are available about morphometry (Kum and Dokulil, 2018), chemistry (Donabaum and Riedler, 2018), phytoplankton (Teubner et al., 2018b), primary production (Dokulil and Kabas, 2018), zooplankton (Teubner et al., 2018a), macrophytes (Pall, 2018), fish (Waidbacher and Silke-Silvia Drexler, 2018), and urban planning (Hozang, 2018).

Measuring Water Transparency

Water transparency was regularly measured with a white Secchi disk at biweekly (to monthly) intervals from 1993 to 2019. Secchi depth (z_{Secchi}) measurements were conducted far from stands of underwater vegetation and thus relate to the "open water" of the lake. In order to extend this parameter to the early survey period (1987−1992), Secchi disk transparency was estimated based on Chl-*a* and TP measurements, which cover the period 1987−1995. This provides an overlap period of 3 years for deriving the relationship between Secchi disk reading and Chl-*a* and TP measurements.

In addition to regular Secchi disk transparency, the underwater light attenuation was retrieved from underwater light profile measurements of Photosynthetically Active Radiation (PAR) with a 4π quantum sensor (LI-COR) for 7 years (1995−2001), which covers the period between the restoration launching and first re-establishment of macrophytes. The mean vertical attenuation coefficient (k_{PAR}) is shown as mean values in **Table 2**.

The euphotic depth (z_{eu}), defined as the water layer from the lake surface (100% light) down to the depth of 1% underwater light intensity, where photosynthesis exceeds respiration, was calculated from the vertical k_{PAR} as follows:

$$z_{eu} = \frac{(\ln 100 - \ln 1)}{k_{PAR}} = \frac{4.605}{k_{PAR}}$$

Minimum light requirement for macrophytes refers to the mean of 2 and 4% of surface ambient light, according to Dennison et al. (1993) and Middelboe and Markager (1997), respectively. The maximum depth satisfying light requirements for macrophyte growth ($z_{macrophytes}$) at 3% underwater light intensity is calculated as:

$$z_{macrophytes} = \frac{(\ln 100 - \ln 3)}{k_{PAR}} = \frac{3.507}{k_{PAR}}$$

On calm days, summer phytoplankton biomass is often heterogeneously distributed along the vertical profile as long as

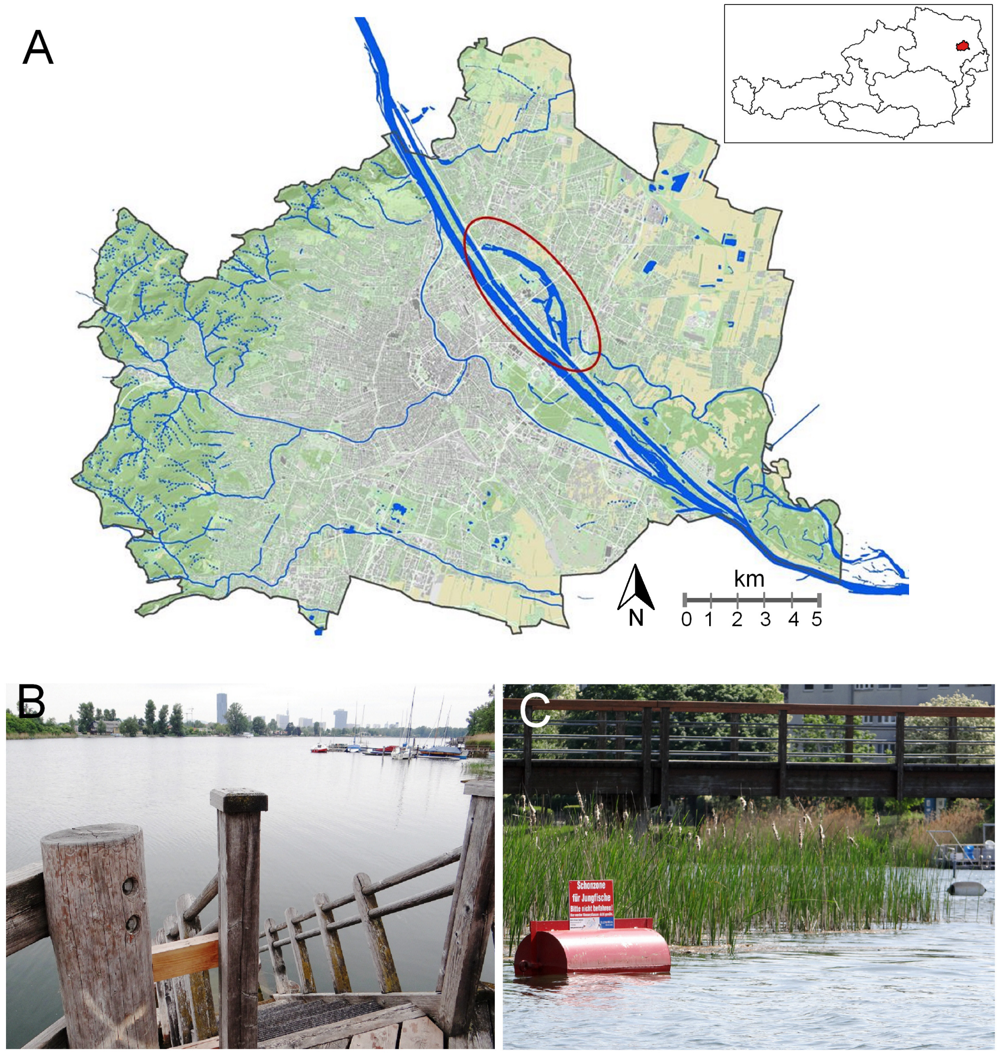

FIGURE 1 | Alte Donau- tightly coupled urban settlement and nature space. **(A)** Water city map Vienna. The ellipse indicates the oxbow-lake Alte Donau, in the close neighborhood of Neue Donau and the Danube River. Inset: Country map of Austria with Vienna (marked red). (Data source: City of Vienna – https://data.wien.gv.at; Inset: created using data from https://www.data.gv.at/katalog/dataset/bev_verwaltungsgrenzenstichtagsdaten150000). **(B)** Elongated impoundment shape due to the former main stretch of the Danube River. Reed belts (*Phragmites australis* in association with other reed belt plants) were re-planted on both banks. Use of cultural ecosystem services are indicated by boats and public wooden bathing platforms providing access to the open water for free. **(C)** Littoral area protected for young fish, close to a lake bank with urban settlements. Buoy reminds visitors by swimming or boat to stay away respecting nature. Sign with words "Schonzone für Jungfische. Bitte nicht befahren. Hier werden Wasserpflanzen nicht gemäht." **(B–C)** taken in 2015, from www.lakeriver.at.

no strong turbulences occur in the epilimnion. Particle clouds of summer phytoplankton in a rather narrow horizontal layer below lake surface build an epilimnetic maximum. This epilimnetic layer in mesotrophic lakes is most commonly found at a depth of 12% light intensity (Teubner et al., 2004). The depth of epilimnetic phytoplankton biomass peak ($z_{peak-phyto}$) is thus calculated as follows:

$$z_{peak-phyto} = \frac{(\ln 100 - \ln 12)}{k_{PAR}} = \frac{2.120}{k_{PAR}}$$

The factor f_{eu} with $f_{eu} = \frac{z_{eu}}{z_{Secchi}}$ can be used to retrieve euphotic depth from Secchi measurements by multiplying the factor with Secchi disk readings. Similarly, multiplying the factors $f_{macrophytes}$ and $f_{peak-phyto}$ with z_{Secchi}, the deepest layer for macrophyte growth $z_{macrophytes}$ (maximum colonization depth for macrophytes defined by 3% light availability) and the depth of peak phytoplankton $z_{peak-phyto}$ (depth of phytoplankton biomass peak layer defined by 12% light availability) is derived, respectively.

The percentage of surface ambient light at Secchi depth ($I_{Z_{Secchi}}$) is:

$$I_{Z_{Secchi}} = e^{(\ln 100 - k_{PAR} \times z_{Secchi})} = 100 e^{-k_{PAR} \times z_{Secchi}}$$

The decreasing z_{Secchi} due to increasing k_{PAR} in Alte Donau is described by the equation $z_{Secchi} = 1.40/k_{PAR}$ for individual

TABLE 1 | Main characteristics of oxbow lake Alte Donau in Vienna.

Characteristics	Lake Alte Donau (synonym Lake "Old Danube")
Location coordinates	48°14'9.26"N, 16°25'41.6"E
Altitude	157 m a.s.l. (adriatic)
Genesis	former main channel of River Danube, oxbow lake since cut-off in 1870−1875
Surface area	1.6 km^2
Volume	3.8×10^6 m^3
Maximum depth	7 m
Mean depth	2.5 m
Trophic lake characterization	1987: mesotrophic cyprinid fish dominated water basin with dense underwater macrophyte stands mainly of charophytes covering the whole bottom area (about 721 t dry mass), recreational use for bathing, boating and local fishery by Viennese population 1992−1994: hypertrophic cyprinid dominated lake without underwater macrophytes but heavy cyanobacterial blooms (e.g., *Cylindrospermopsis raciborskii*), algal turbid state 1995−2019: sustainable restoration management turned water quality back to mesotrophic clear-water conditions (see further Dokulil et al., 2018) by- re-establishing underwater macrophytes (mainly Myriophyllum spicatum, increase of Charophytes cover is still a target) and modified fish stocking in the yet cyprinid dominated water body, 1995-1999: restoration with chemical phosphate precipitation twice (RIPLOX-treatment), 2000-2006: re-establishment of macrophytes by periodical water level drawdown, 2007−2019: stable conditions with sustained dense macrophyte stands -attracting recreational use by measures of urban landscape planning, implementing a master plan
Annual air temperature Wien-Donaufeld*, suburb in Vienna (closest distance to Alte Donau 1.6 km, to River Danube 3.1 km) (mean 2005−2018)	11.6°C (10.3-12.7)
Annual air temperature Wien-Innere Stadt*, Vienna city centre (closest distance to Alte Donau 5.2 km, to River Danube 4.2 km) (mean 2005−2018)	12.5°C (11.1-13.5)
Difference in annual air temperature between Wien-Innere Stadt and Wien-Donaufeld	mean: 0.9°C (max: 1.1, min: 0.8)

**Data from ZAMG and Jahrbuch (2020).*

measurements (n = 131, R^2 = 0.55, p < 0.001) (c.f., Megard and Berman, 1989). Averaged values of optical properties as 1%, 3% and 12% surface light depths, factor predicting euphotic zone from Secchi depth, the percentage of ambient light at Secchi depth (%) and related parameters are shown in **Table 2**.

Statistical Treatment

Data in **Table 3** and **Figures 2–8** are based on the original dataset of biweekly sampling. However, as sampling was not always carried out in exactly 2-week intervals, available data were interpolated at daily resolution (Livingstone, 2003; Sapna et al., 2015) and were averaged afterward over a 2-week period (**Figure 3**). These bi-weekly data were then used to calculate annual averages (in **Figure 2** for Secchi, **Figure 4**). This avoids biases in the averages due to a more frequent sampling in summer and a relatively less frequent sampling in winter. Furthermore, the interpolated daily data were also used to retrieve the Julian day of onset about a certain value of water surface temperature (WT) and the length of the warm period, i.e., the number of days each year with WT above a certain value (data matrix for **Figures 5–8** and **Table 3**). Despite the normal distribution for most of the temperature data, the respective trends of the year-to-year variation were calculated as robust trend lines by non-parametric fitting according to Theil (1950) as described in Helsel and Hirsch (2002). These robust trend lines are applied to calculate the reliable slope of the year-to-year trends (**Figures 5A**, **6A**, **8** and **Table 3**), which are robust against outliers of unusual high or low values in the first or last year of observation. The statistical significance of the trends is calculated by Mann-Kendall tests using R (McLeod, 2015).

Most of the robust trend lines for the year-to-year variations of the length of warm period or for the earlier onset of passing a certain temperature value were statistically significant (black bars in **Figures 5A**, **6A**). Therefore, data were detrended before correlation analysis (anomalies used in **Figures 5B-D**, **6B–D**, **7**). Furthermore, significant robust trends were found for year-to-year variation of other parameters such as Secchi disk transparency, bathing visits per population, and thus anomalies were also calculated before analyzing the correlation of year-to-year variations between respective variables. The linearly detrending of time series data prior to correlation analysis is done to avoid spurious relationships, which might occur only due to the presence of significant trends.

Further, prior to the statistical correlation analysis shown in **Figures 5B–D**, **6B-D**, **7**, data were tested for normal distribution

TABLE 2 | Optical water properties as Secchi disk transparency (z_{Secchi}), the percentage of surface ambient light at z_{Secchi} ($I_{Z_{Secchi}}$) and the underwater light attenuation (k_{PAR}) satisfying light requirements for photosynthesis of phytoplankton and macrophytes and human perception to judge water suitability for bathing (satisfying water clarity for recreational aesthetics).

Category	(A) all	(B) Seasonal development				(C) Trophic lake classification scheme			(D) Human water-quality perceptions for bathing		
		Spring	Summer	Autumn	Winter	Oligo-trophic	Meso-trophic	Eu−trophic	z_{Secchi} > 1.55 m	z_{Secchi} 1.45−1.55 m	z_{Secchi} < 1.45 m
z_{Secchi} [m]	1.62	1.75	1.36	1.56	2.3	2.45	1.72	1.17	2.07	1.50	1.17
$I_{Z_{Secchi}}$ [%]	26	27	28	24	21	21	26	28	23	25	29
k_{PAR}[m^{-1}]	0.918	0.796	0.981	1.012	0.802	0.728	0.838	1.149	0.747	0.934	1.096
z_{eu} [m]	**5.35**	**6.04**	**4.93**	**4.82**	**6.2**	**6.62**	**5.72**	**4.18**	**6.33**	**5.02**	**4.40**
f_{eu}	3.45	3.58	3.65	3.24	2.99	3.05	3.42	3.62	3.17	3.35	3.78
$z_{macrophytes}$[m]	**4.08**	4.60	**3.75**	**3.67**	**4.83**	**5.04**	**4.36**	**3.19**	**4.82**	**3.82**	**3.35**
$f_{macrophytes}$	2.63	2.73	2.78	2.48	2.28	2.32	2.60	2.76	2.42	2.55	2.88
$z_{peak-phyto}$[m]	**2.47**	**2.78**	**2.27**	**2.22**	**2.92**	**3.05**	**2.64**	**1.93**	**2.91**	**2.31**	**2.03**
$f_{peak-phyto}$	1.59	1.65	1.68	1.49	1.38	1.41	1.58	1.67	1.46	1.54	1.74
Chl-*a* [µg L^{-1}]	10	7.5	11	12.5	5.9	3.1	7.7	17	6.6	11	13
n	131	38	43	37	13	11	82	38	55	16	60

Depth of surface ambient light at 1% refers to minimum light requirements of phytoplankton (euphotic depth, z_{eu}), at 3% to minimum light requirements of submerged macrophytes (maximum colonization depth, $z_{macrophytes}$) and at 12% referring to light required for phytoplankton optimum indicated by epilimnetic phytoplankton peak ($z_{peak-phyto}$) (see section "Materials and Methods"). Euphotic depth (z_{eu}) exceeds z_{Secchi} by the factor f_{eu} (more details in Kabas, 2004). Analogous factors for $z_{macrophytes}$ and $z_{peak-phyto}$ exceeding z_{Secchi} are $f_{macrophytes}$ and ($f_{peak-phyto}$), respectively. Mean values are shown for the whole data set ***(A)****, the four seasons* ***(B)*** *along three trophic states* ***(C)****, and for threshold of bathing aesthetics* ***(D)****. Further for* ***(C)*** *Trophic classification scheme refers to samples of chlorophyll-a (Chl-a) concentrations which were simultaneously taken when measuring z_{Secchi} and k_{PAR}, and applies here to ÖNORM M6231 (2001): oligotrophic: Chl-a < 4 µg L^{-1}, mesotrophic: 4 µg L^{-1} to 12 µg L^{-1}, eutrophic > 12 µg L^{-1}. Further for* ***(D)*** *To correspond water-quality perceptions for bathing (threshold of z_{Secchi} = 1.5 m according to Smith et al., 1991, 1995a), a narrow range of sampling dates with z_{Secchi} between 1.45 and 1.55 m is compared with those of higher and lower z_{Secchi}, respectively* ***(D)****. Depth [in m] of critical light requirements for phytoplankton and macrophytes growth are plotted in bold. Data based on mean values from biweekly to monthly measurements of z_{Secchi}, k_{PAR}, and Chl-a, in Alte Donau (1995−2001, n = 131).*

TABLE 3 | Lengthening of the period in time above a certain WT values (in number of days per decade) and time shift of the first day above a certain WT value (onset day shifted per decade) calculated from slopes of robust trend lines covering measurements from 1987 to 2019.

WT [°C]	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Lengthening of period [increasing nb of days per decade]	0	3.6	4.5*	4.6*	5.9**	5.8***	6.1***	5.4***	4.1**	5.4**	5.2*	6.5**	6.4**	6.6**	7.2**	8.7***	12.5***	14.7***	18***
Length of period in 1987 [nb of days]	245	245	227	220	203	196	184	176	169	158	149	136	122	104	94	79	53	35	7
Length of period in 2019 [nb of days]	256	257	243	237	226	216	206	196	183	176	167	158	144	133	120	109	97	87	71
Timing shift for onset [shift earlier per decade in nb of days]	−0.4	−1.8	−2.7	−3.2	−3.8*	−4.5**	−4.5**	−4.5***	−4.0**	−4.2***	−3.8**	−4.5**	−5.2*	−3.8	−3.5	−6.3*	−6.4**	−9.5***	−7.1*
Onset day in 1987 [JD]	63	76	86	93	100	105	105	116	118	122	126	116	135	140	147	159	164	176	175
Onset day in 2019 [JD]	61	70	76	81	86	89	89	100	104	108	112	100	117	126	135	137	142	175	149

The length in number of days (nb of days) and the onset day (Julian day) for 1987 and 2019 are derived from the first and the last value of these robust trend lines. WT values from 5°C to 23°C as in ***Figures 5****,* ***6****. Significance of trends are marked by *p < 0.05, **p < 0.01, ***p < 0.001; nb, number.*

and passed the Shapiro-test (Dunn and Clark, 1974) for satisfying Pearson correlation.

For analyzing climate response, the North Atlantic Oscillation (NAO) Index was used as climate signal since it represents a common proxy for studying the climate impact on aquatic ecosystems in the temperate zone (NAO station-based, from Hurrell, 2020 eds). A first testing of various seasonal NAO indices indicated the NAO signal for the period December – March (NAO_{DJFM}, see **Figures 5–7**) as most suitable. This winter climate signal does not vanish as fast as the NAO signal of later months or seasons (see, e.g., Blenckner et al., 2007; Dokulil et al., 2010); thus, it is suitable for unraveling the climate response in late spring-early summer in Alte Donau (see also Teubner et al., 2018b).

RESULTS

Urban oxbow lake Alte Donau is embedded in a naturally landscaped parkland. Visiting Alte Donau located in the suburban area of Vienna (**Figure 1A**), the manifold popular uses become obvious. Among the cultural ecosystem services provided recreational activities are common such as bathing in public baths or at publicly available wooden walkways along the lake banks

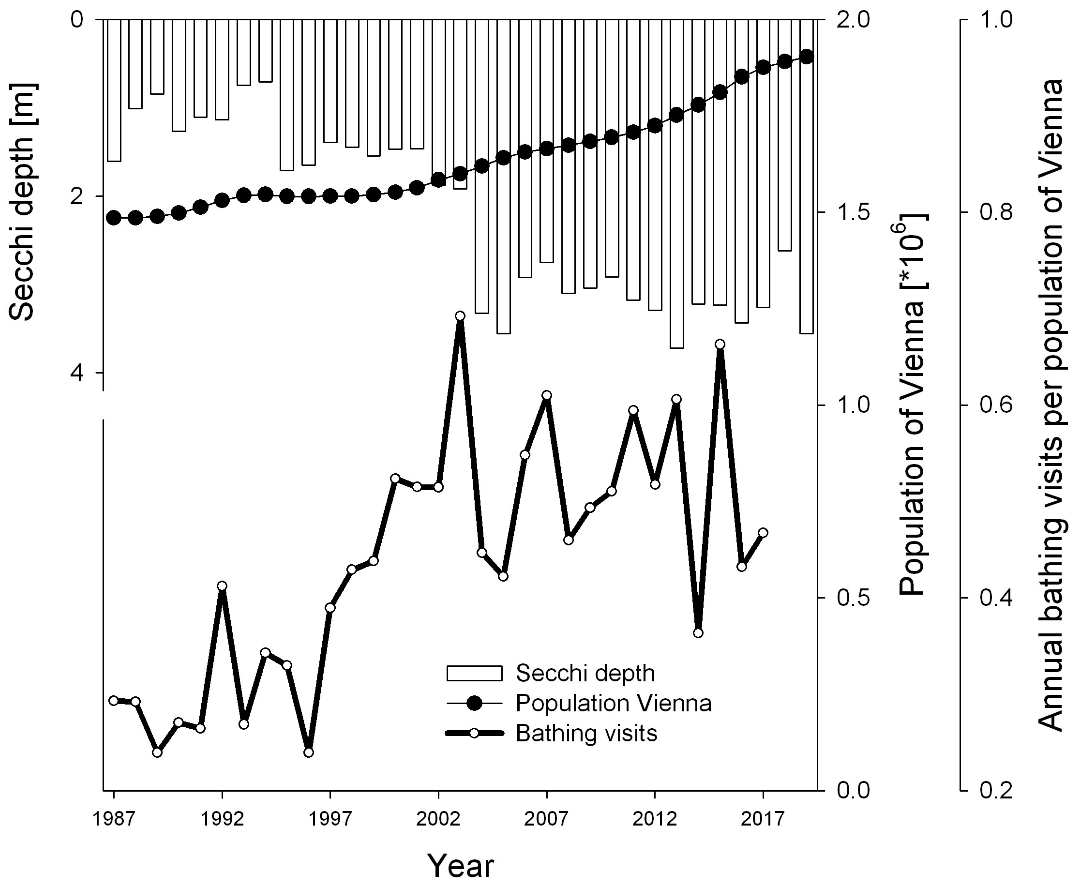

FIGURE 2 | Population development of capital city Vienna and water transparency as annual Secchi depth of Alte Donau for years 1987–2019. The number of annual bathing visits per annual population of Vienna are from 1987 to 2017 (data for population from www.statistik.at, for annual bathing visits from Hozang, 2017).

(**Figure 1B**), sport fishing, sport boating (rowers, sailors, and recreational fun boats), walking and cycling on the lake shore, visiting the playgrounds, recreational sport grounds, lawns and restaurants. Reed belts are naturally covering the shoreline or have been replanted (**Figure 1C**).

The population growth from 1.48 to 1.90 million inhabitants over the recent 33-year study period is shown in **Figure 2**. The highest numbers of bathing visits were observed in 2003 and 2015 (1.1 and 1.2 million, respectively), the lowest numbers in 1989 and 1996 (0.36 and 0.37 million, respectively; data from Hozang, 2017). The number of bathing visits per population of Vienna is displayed in **Figure 2**. These relative bathing visits also significantly increased from 0.29 in 1987 to 0.47 in 2017 following a robust increasing trend ($p < 0.05$). The water transparency, as represented by Secchi disk measurements, increased significantly over the 33 years of observation, with lowest annual means of 0.9 m and 1.0 m in 1993 and 1994, respectively (**Figure 2**). Starting in 1995, the first year of restoration, annual Secchi depth exceeded 1.5 m and increased further to highest values above 3.5 m from 2005 to 2016 and in 2019.

A water clarity corresponding to Secchi disk transparency of 1.5 m and higher is often considered as minimum threshold satisfying bathing aesthetics in view of human perception (Smith et al., 1991, 1995a). According to our observations in Alte Donau, a z_{Secchi} of 1.5 m corresponds to a penetration of 25% surface ambient light (**Table 2**). Applying this water clarity threshold of bathing aesthetics to Alte Donau, the corresponding chlorophyll-*a* concentration (Chl-*a*) would be about 11 $\mu g\ L^{-1}$ (**Table 2**) and thus refers to a water quality of the mesotrophic state (Chl-*a* limits indicating mesotrophic state refer to $>4\ \mu g\ L^{-1}$ and $<12\ \mu g\ L^{-1}$ according to ÖNORM M6231, 2001; see also Teubner et al., 2018b). According to **Table 2**, with $z_{Secchi} = 1.5$ m both the euphotic depth (z_{eu} = 5.02 m) and maximum colonization depth for macrophytes ($z_{macrophytes}$ = 3.82 m) would exceed the mean lake depth of 2.5 m in Alte Donau. On a calm day, we further could expect the optimum depth for phytoplankton growth at 2.3 m ($z_{peak-phyto}$ = 2.31 m).

While annual averages of Secchi disk transparency increased rather gradually throughout the years (**Figure 2**), individual measurements within the 27-year study period (1993−2019) varied strongly (**Figure 3**). Secchi depth was lowest at highly eutrophic to hypertrophic conditions with TP concentrations above 40 and 60 $\mu mol\ L^{-1}$ (**Figure 3**). Such nutrient-rich situation corresponded to concentrations of Chl-*a* above 24−35 $\mu g\ L^{-1}$. The period of nutrient enrichment associated with algal blooms was observed for the years 1993-1994, before

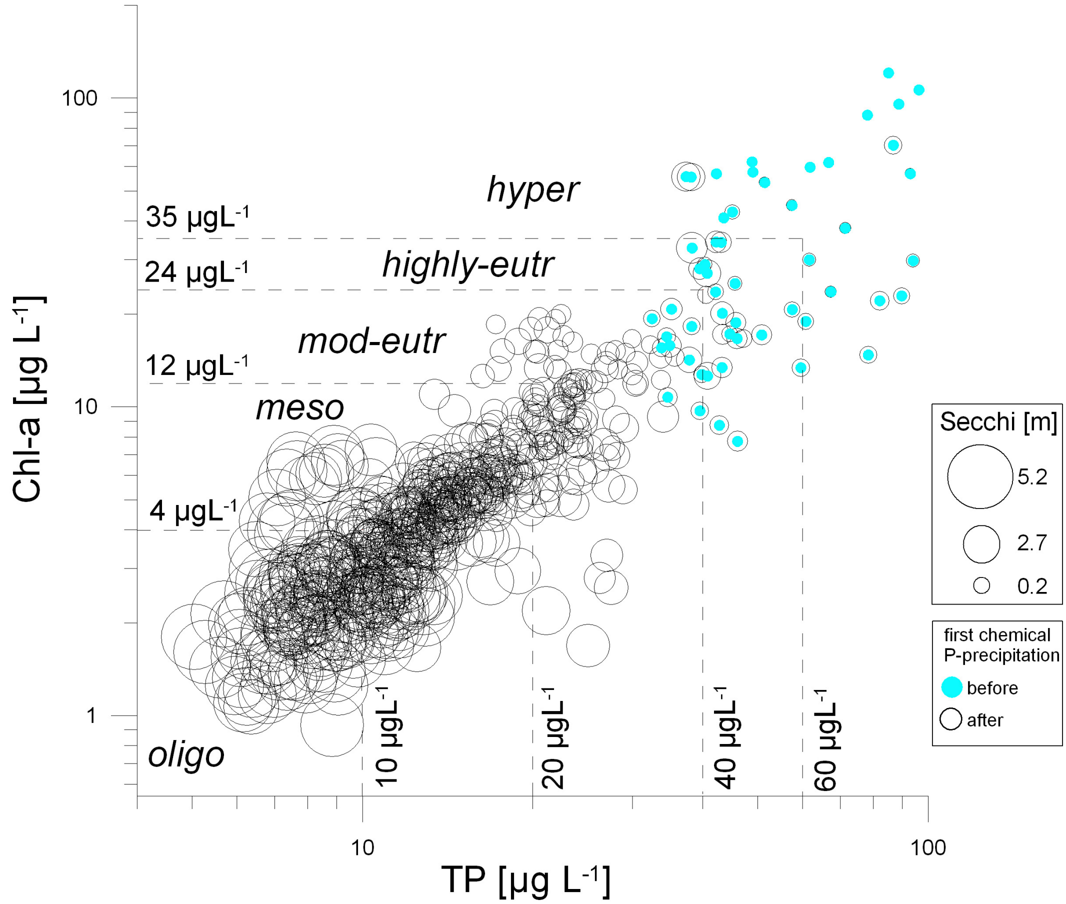

FIGURE 3 | Total phosphorus concentration (TP) versus algal biomass represented as Chlorophyll-*a* (Chl-*a*). The size of the circles indicates the Secchi disk transparency [m] ranging between 0.26 and 5.23 m. The scatter plot is based on biweekly data from 1993 to 2019, blue points indicate the nutrient-rich period before phosphate precipitation started, from January 1993 to April 1995.

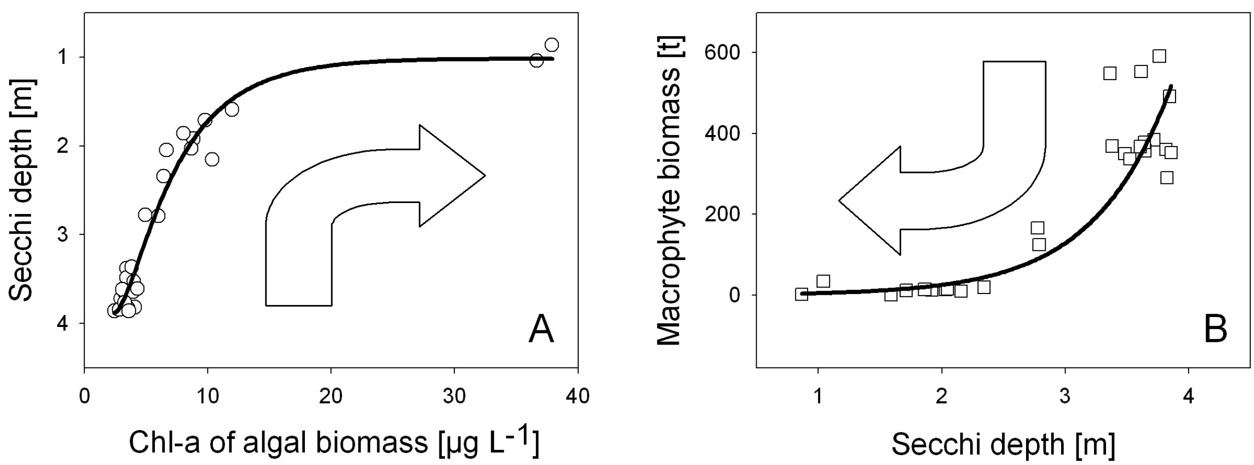

FIGURE 4 | The two sides of the same coin – the ecological perspectives of water transparency on photosynthetic organisms: Water transparency **(A)** as response function of phytoplankton biomass, where water turbidity decreases in the course of increasing algal biomass (measured as Chlorophyll-*a* in $\mu g\ L^{-1}$) and **(B)** as light utilization factor controlling the growth of underwater macrophytes biomass as dry weight in t for the whole lake **(B)**. Water transparency is indicated by Secchi depth. Annual data from 1993 to 2019 **(A)** and 1993 to 2018 **(B)**.

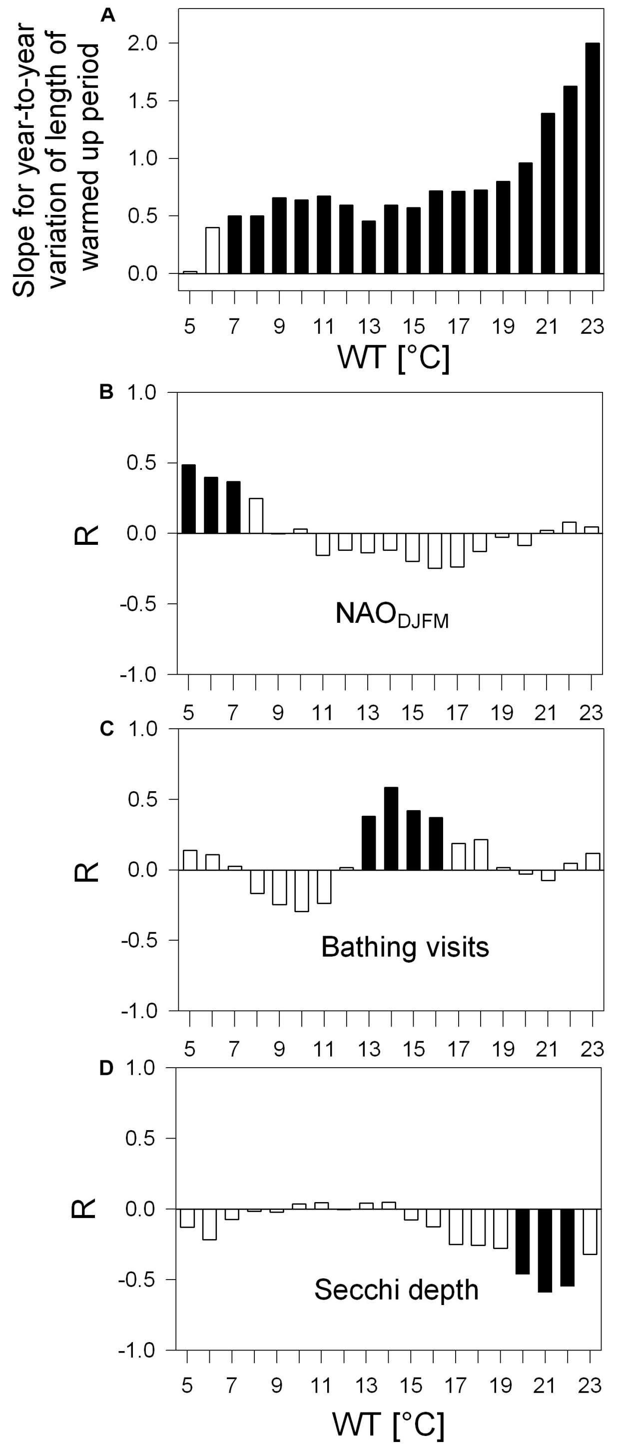

FIGURE 5 | Water surface temperature (WT) varying year-to-year, their trends (**A**, slopes) and relation to other parameters **(B–D)**, Pearson correlation coefficient R. **(A)** Bar-chart: Slopes of lengthening of periods above certain WT values, covering 33-year development above 19 discrete WT values ranging from 5°C to 23°C; all slopes are from robust trend lines proven to be statistically significant with $p < 0.05$ with the only exceptions for the WTs 5°C and 6°C, as indicated by white bars. For lengthening given in number of days see **Table 3**. **(B–D)** Correlograms: Correlation between detrended year-to-year *(Continued)*

FIGURE 5 | Continued
variation of the length of periods (above WTs 5°C to 23°C) and of NAO_{DJFM}-index **(B)**, of detrended bathing visits per population (**C**, original bathing visits displayed in **Figure 2**) and of detrended Secchi depth **(D)**. Black columns indicate statistically significant Pearson correlations with $p < 0.05$. Examples of most significant *R*-values in panels **(B–D)** are displayed in scatter plots (**Figures 7A–C**).

the lake restoration started. On the contrary, high values of Secchi disk transparency were associated with low concentrations of TP and of Chl-*a*. This situation of high water clarity mirrors the success of sustained restoration of Alte Donau, which consisted of phosphate precipitation in the planktonic zone in 1995 and 1996, followed by the sustained re-establishment of underwater macrophytes (timetable of restoration measures see **Table 1**; RIPLOX-treatment of phosphate precipitation see Donabaum and Dokulil, 2018; Macrophyte and reed-belt re-establishment see Pall, 2018; Pall and Goldschmid, 2018; for sustained fish management see Waidbacher and Silke-Silvia Drexler, 2018).

The two sides of ecological perspectives for water transparency are shown in **Figure 4** and refer to data from 1993 onward in Alte Donau. With an increase in phytoplankton corresponding to an increase in Chl-*a* concentrations up to about 10 $\mu g\ L^{-1}$, the Secchi depth linearly decrease (**Figure 4A**). Further increase of phytoplankton density, which potentially contributes to self-shading by algae, leads to approaching a minimum Secchi depth of 1 m (1.02 m and 0.86 m), the lowest annual mean values of Secchi disk transparency in the open water body measured in Alte Donau. In turn, water transparency stimulates growth of underwater macrophytes (**Figure 4B**). Massive exponential growth, which leads to establishing an underwater macrophyte biomass of about 300 t and more (macrophytes in dry weight of the whole lake area), is observed in Alte Donau when annual Secchi depth is 3.5 m or even higher (**Figure 4B**).

This annual mean threshold of 3.5 m Secchi disk transparency was exceeded first from autumn to winter in 2001.

In following years of successful re-establishment of submerged macrophytes (mainly angiospermic species as *Myriophyllum spicatum*) with more than 300 t biomass yield in the whole lake per year, i.e., 2004—2019, water transparency was on average higher than 3.5 m for more than the half year (average 189 day a year, 52% days a year, range: 13—75%). Considering only the first half of the year, Secchi disk transparency was on average exceeding a depth of 3.5 m on 115 days (63% days a half year, range: 23—75%, January—June). Referring to spring, it was 66 days (on average 71% days in springtime, range 23—92%, March to May). During mesotrophic state before eutrophication of Alte Donau, when dense charophyte meadows were observed (791 t per lake per year) which were co-occurring with cyprinid fish assemblages, the median Secchi disk transparency measured in June was 3.41 m (Löffler, 1988). Re-assessing this Secchi disk transparency from the late 80ies, the values for 2004 to 2019 were on average 199 days a year (54% of days a year), 122 days the first half of the year (67% of days from January to June), and 70 days in spring (76% of days from March to May). The mean Secchi disk transparency was 3.5 m in June from 2004

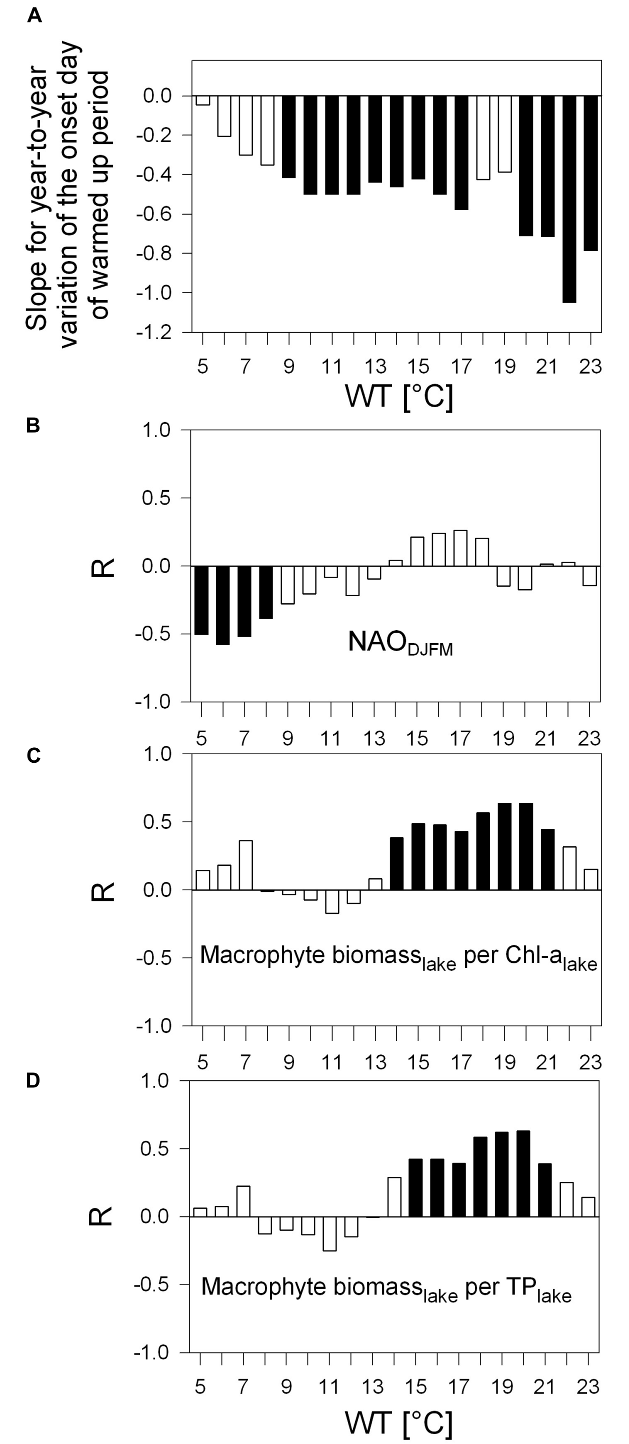

FIGURE 6 | Same as for **Figure 5** with **(A)** as bar-chart and **(B–D)** as correlograms, but in panel **(A)** with slopes for the first day above a WT values from 5°C to 23°C (JD of the onset). **(B–D)** Correlograms for Pearson correlation between detrended year-to-year variation of JD onset shown in panel **(A)** and the NAO$_{DJFM}$-index **(B)**, detrended ratio of macrophyte biomass (per lake) to Chl-*a* (per lake, **C**) and detrended ratio of macrophyte biomass (per lake) to TP (per lake, **D**). Black columns indicate $p < 0.05$. Examples of most significant *R*-values in panels **(B–D)** are displayed in scatter plots (**Figures 7D–F**); JD, Julian day.

to 2019 (range: 2.5—4.5 m). Thus, water transparency during both mesotrophic states, i.e., in the late 80ies (Löffler, 1988) and after chemical restoration 2004 to 2019 (Pall, 2018; Pall and Goldschmid, 2018) agree so far, but the composition and yield of macrophyte assemblage differed a lot, as it was twice the yield (1) and instead of dense stands of angiospermic species a meadow of charophytes (2) in the late 80ies.

Optical water properties in **Table 2** are described for various ranges of Secchi disk transparency (z_{Secchi}) and underwater light attenuation (k_{PAR}). The percentage of surface ambient light at Secchi depth ($I_{Z_{Secchi}}$) for individual measurements (n = 131) ranges from 7% to 43%. The mean z_{Secchi} of 1.62 m corresponds to a visibility of 26% surface ambient light (**Table 2A**). $I_{Z_{Secchi}}$ is highest in summer (28%) followed by spring (27%) and lowest in winter (21%) (**Table 2B**). $I_{Z_{Secchi}}$ also increases with trophic state, is lowest under oligotrophic (1%) and highest under eutrophic (28%) conditions (**Table 2C**).

The factors used for multiplying z_{Secchi} to retrieve euphotic depth (z_{eu}), maximum macrophyte colonization depth ($z_{macrophytes}$) and depth of the epilimnetic peak of phytoplankton biomass ($z_{peak-phyto}$) vary over a wide range during the seven-year study (see methods). For individual measurements (n = 131), z_{eu} exceeds z_{Secchi} by a factor (f_{eu}) varying between 1.77 and 5.45 (mean 3.45, **Table 2A**). Analogous, concerning $z_{macrophytes}$ and $z_{peak-phyto}$, the factors $f_{macrophytes}$ and $f_{peak-phyto}$ vary between 1.35 — 4.15 (mean 2.63, **Table 2A**) and 0.81 — 2.51 (mean 1.59, **Table 2A**) for exceeding z_{Secchi}, respectively. Seasonal mean values of these three factors, displaying the ratio or soundness between Secchi disk readings and underwater light attenuation measurements, do not vary stochastically but follow a pattern with highest means in summer and lowest means in winter (**Table 2B**). When categorizing water transparency measurements according to the trophic classification scheme (**Table 2C**), the mean values of these factors increase with trophy, i.e., are lowest for the oligotrophic and highest for eutrophic state. The variation of these factors thus relies on phytoplankton biomass, which was simultaneously measured during this investigation: relatively small ratios between a depth of 1%, 3%, and 12% of surface ambient light to Secchi disk readings, i.e., high values of the factors f_{eu}, $f_{macrophytes}$, and $f_{peak-phyto}$, were observed when phytoplankton biomass was low (low mean Chl-*a* for winter and for oligotrophic state, see **Table 2**). In turn, largest factors were found when phytoplankton was high, i.e., during peak season in summer and under eutrophic conditions.

The z_{Secchi} of 3.5 m is derived as a critical threshold for macrophyte growth (**Figure 4**). It refers to z_{eu} = 12 m and $z_{macrophytes}$ = 9.1 m, exceeding both the maximum depths of water basins (for mesotrophic state f_{eu} = 3.42; $f_{macrophytes}$ = 2.6, **Table 2C**). Further, the corresponding depth for $z_{peak-phyto}$ = 5.5 m exceeds by far the mean depth of 2.5 m ($f_{peak-phyto}$ = 1.58, **Table 2B**).

Global warming is issued in **Figures 5–8**, focusing on trends of year-to-year variation of water surface temperature (WT) in correspondence to the NAO climate signal. In addition, the response of long-term development of WT on bathing visits, Secchi disk transparency and macrophyte development is depicted.

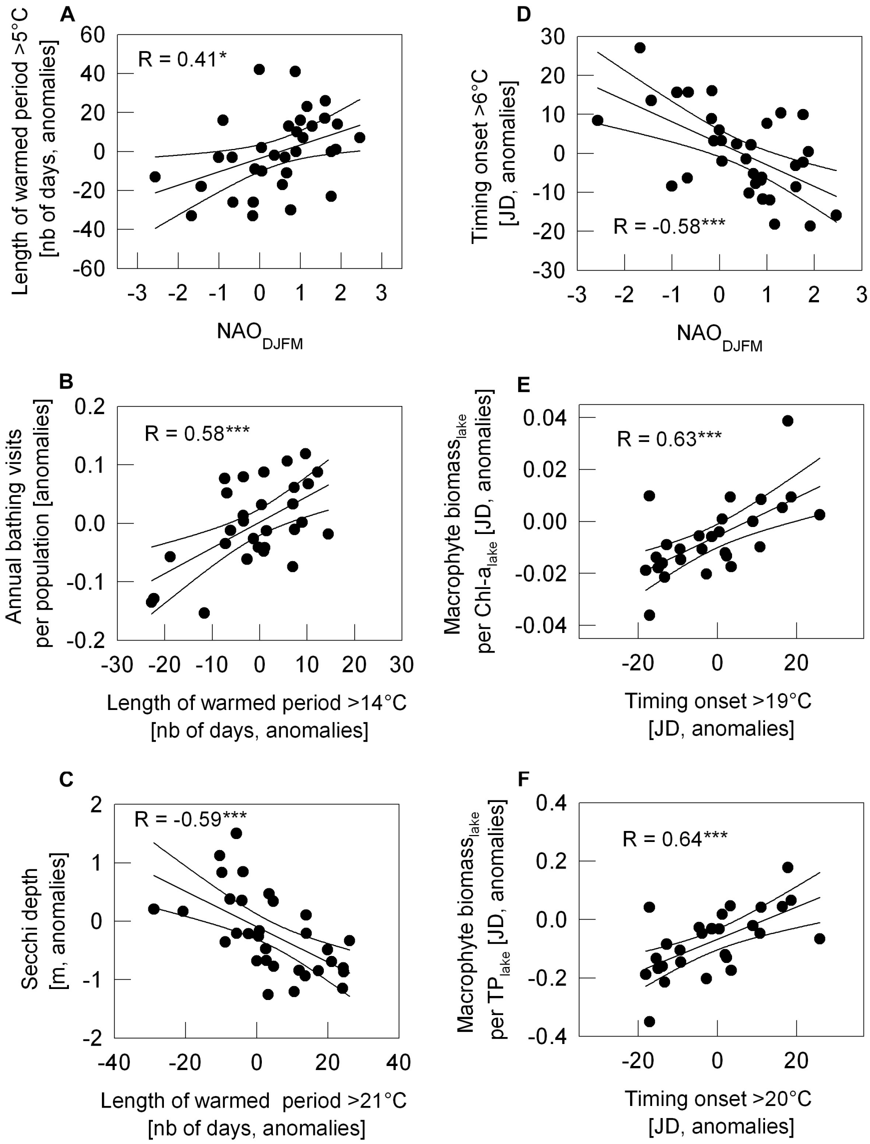

FIGURE 7 | Relation between year-to-year variation of the length of warm period number of days, **(A–C)** or of the onset of warming period (JD, Julian day; **D–F**) and year-to-year variation of NAO climate signal or further parameters indicating ecosystem status as scatter plots. NAO_{DJFM} against the length of warmed period above 5°C in panel **(A)** and the onset > 6°C in panel **(D)**. Length period > 14°C against annual bathing visits per population in Vienna **(B)**; Length of period > 21°C against mean Secchi depth during bathing season June–August **(C)**; First day a year with WT > 19°C against the ratio of macrophyte biomass (per lake) to Chl-*a* (per lake) **(E)**; First day a year with WT > 20°C against the ratio of macrophyte biomass (per lake) to TP **(F)**. With exception of NAO, all data as anomalies (see section "Materials and Methods"). R for Pearson correlation coefficient, significance of correlation is marked by $^{*}p < 0.05$ and $^{***}p < 0.001$.

The number of days above a certain WT value was used to analyze the length of the warm period for each year (**Figure 5**). Within the range of warmed water above 5°C to 23°C, a positive trend was found with the exception of WT of 5°C. The trends were statistically significant for the range of WTs from 7°C to 23°C and thus verify warming of surface water for 247 to 243 days per year along the 33-year study. Up to a WT of 19°C, the slope gradually increased (**Figure 5A**), indicating a modest lengthening of the warming period of about 4 to 7 days per decade (**Table 3**). With a WT value of 20°C and further of 21°C, 22°C, and 23°C, the slope increased more progressively (**Figure 5A**), mirroring the prolongation of the warm water period above these four values by 9, 12, 15, or 18 days per decade (**Table 3**). While in year 1987 half of the year was above 11°C (184 days), in year 2019 half of the year was above 13°C (183 days, **Table 3**). The detrended year-to-year variation of warm water above WTs 5°C, 6°C, and 7°C relates significantly to the year-to-year variation of the North Atlantic Oscillation climate index for winter (NAO_{DJFM}) (**Figure 5B**). The correlograms further show mainly the significant positive coincidence between year-to-year variation of the lengthening of warmed period above 13°C–16°C and of the annual variation

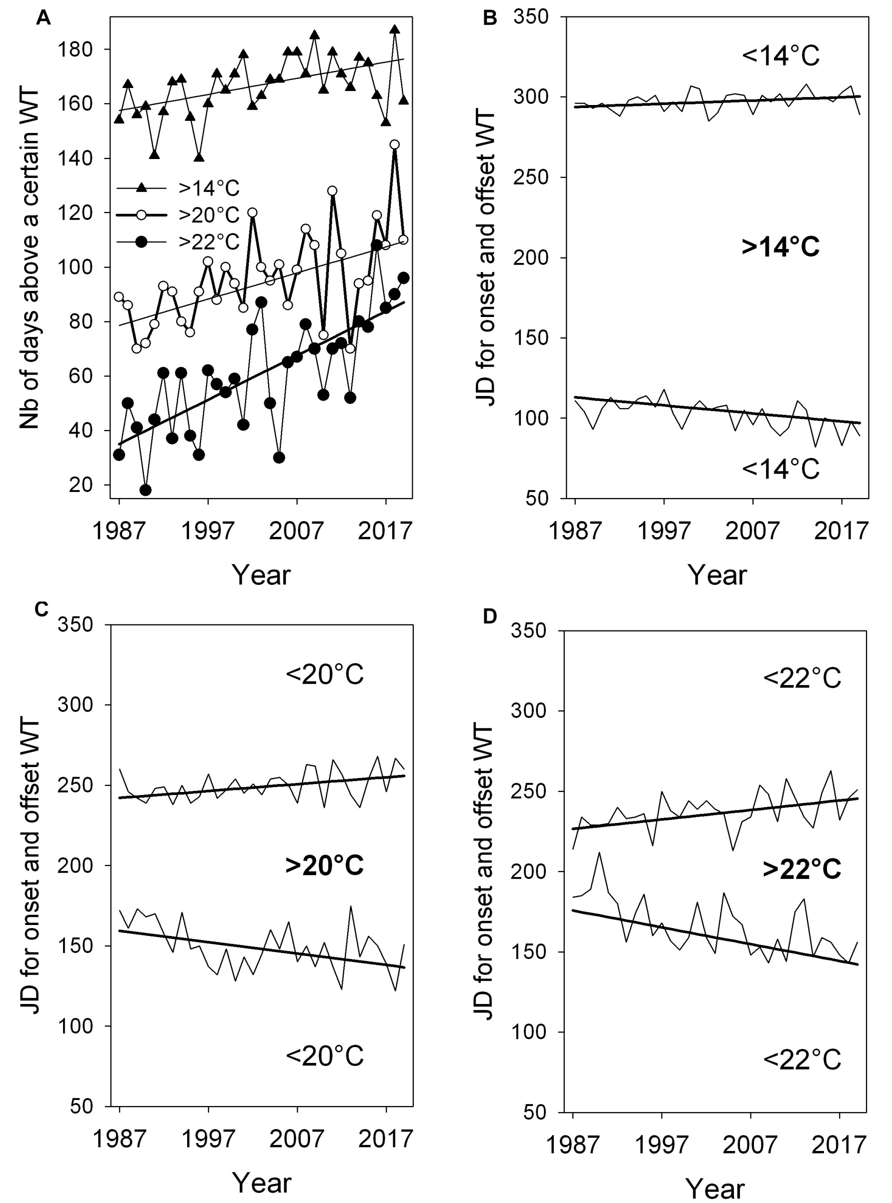

FIGURE 8 | Lengthening of the warm period above three WT values indicated by significant positive slopes of trends with +0.59** for WT > 14°C, +0.96*** for WT > 20°C and +1.63*** for WT > 22°C **(A)**. Days of onsets and offsets of the three WTs in panels **(B–D)**. The negative trend slope for onset days in mid spring or early summer is –0.46*** for WT > 14°C, –0.71* for WT > 20°C, and –1.05*** for WT > 22°C. Slope for the offset in late summer or autumn is +0.2* for WT < 14°C, +0.43* for WT > 20°C and +0.59* for WT < 22°C. Significance of robust slopes with $^{*}p < 0.05$, $^{**}p < 0.01$, and $^{***}p < 0.001$, Year-to-year time series from 1993 to 2019. The number of days for lengthening period and time shift for onset days above 11°C, 14°C, and 22°C see **Table 3**.

of bathing visits per population (**Figure 5C**). A prolonged warm period above 20°C, 21°C, and 22°C refers to lowered mean Secchi disk transparency for the bathing season (**Figure 5D**) (with the exception of the NAO-index, all time series data in **Figures 5B–D** were linearly detrended prior to correlation analysis, see "Materials and Methods").

According to robust slopes in **Figure 6A**, the first day passing the different WT values tends to occur progressively earlier. The earlier warming is statistically significant for onsets of 9°C to 17°C and 20°C to 23°C during the 33-year study. Intra annual earlier warming onsets above 5°C to 8°C coincide inversely with annual variation of winter NAO index (**Figure 6B**). Further, the first day above a WT value from 14°C to 21°C and 15°C to 21°C (timing of the onset days see **Table 3**: from Julian day 108 in mid-April to JD 164 in mid-June) corresponds significantly to the macrophyte biomass increase relative to Chl-*a* and TP, respectively (**Figures 6C, D**) (with the exception of the NAO-index, all time series for the onset in **Figures 6B–D** were linearly detrended prior to correlation analysis, see "Materials and Methods").

Most significant relationships from **Figures 5**, **6** are displayed in scatter plots in **Figure 7**. NAO positive years coincide with years of an extended warm phase above 5°C (**Figure 7A**) and reaching earlier the temperature above 6°C (**Figure 7D**). In turn, NAO negative years refer to years with a shortened period above 5°C and delayed onset of water temperature above 4°C. With a prolongation of the warm period above 14°C, the number of bathing visits per population increases (**Figure 7B**). The prolongation of warm period above summer WTs, such as 21°C shown in **Figure 7C**, relates most significantly to lowered Secchi depth averaged over the bathing season. With an earlier onset of warming phase above 19°C and 20°C, macrophyte biomass increases significantly relative to Chl-*a* or TP in the lake (**Figures 7E,F**) and thus seem to trigger high water transparency. Steep warming trends during extreme hot summer (WT 22°C and 23°C), however, neither seem significantly to favor further macrophyte increase relative to Chl-*a* or TP nor to enhance further water transparency in Alte Donau (**Figures 5**, **6**).

The time series and robust trend lines for the length of annual warm period above WTs of 14°C, 20°C, and 22°C, including temporal shifts of the onset and offset of these warm periods are shown in **Figure 8**. When comparing WTs above 14°C, 20°C, and 22°C, a progressive lengthening of the warm period, indicated by slopes of robust trends, is found from 14°C to 22°C (**Figure 8A** and **Table 3**). The lengthening of the annual warm period is mainly due to a pronounced earlier onset of warm period above 14°C, 20°C and 22°C in spring and early summer, rather than to a moderate delay of cooling in late summer and autumn (**Figures 8B–D**).

DISCUSSION

The restoration of degraded urban ecosystems, as it could be exemplified here for Alte Donau, can increase the quantity of ecosystem services per capita in densely populated areas. With the successfully restoration of Alte Donau (Dokulil et al., 2018), this urban oxbow lake became a life-enriching natural asset in Vienna again. Sustained restoration was meant to meet the goal of "maintaining the valuable water ecosystem features and excellent local recreation opportunities" as stated in Hozang (2017). Water clarity captures great attention as the most relevant socio-ecological indicator for the former floodplain riverine system that is now integrated into modern city life, as it can provide condensed information on: (1) the potential for recreational use of urban blue-green space; (2) the status of overall success of sustained restoration and ecosystem health; and (3) the ecosystem vulnerability against the superimposed global warming trend, accelerated in man-made age.

Water Clarity Attracts Recreational Values Enhancing Ecosystem Services

According to a questionnaire survey about city lake park Alte Donau with 1023 respondents in Vienna (2015 to 2017), which faced restoration at stable conditions with sustained dense macrophyte stands, five key issues were identified (Hozang, 2017). Highest priority was perceived for water quality by local resident visitors and business owners of boat rentals, restaurants and public baths, thus underlining the water quality awareness outlined by other socio-economic studies (e.g., Michael et al., 1996; Wilson and Carpenter, 1999; Gibbs et al., 2002; Lee, 2017). Respondents in Vienna were highly satisfied with the improved water quality and thus acknowledged lake restoration in general. The Secchi disk transparency of Alte Donau at the time of the questionnaire survey in Vienna was already stabilized according to the clear-water state associated with sustained macrophytes (annual means ranged between 3.4 m and 3.8 m). It thus exceeded by far the 1.5 m minimum threshold of bathing aesthetics, and also a higher Secchi disk transparency of 2.75 m indicated for satisfying 90% of respondents for perceiving a water clarity suitable for bathing according to questionnaire surveys by Smith et al. (1991, 1995a). Accordingly, when judging further improvement of water quality, water clarity did not represent an issue. Instead, underwater-macrophyte cutting was perceived to be important by visitors but also owners of public baths, boat rentals and restaurants with access to the lake banks, to restrict excessive biomass development of tall-growing macrophytes. Floating plant fragments on the water surface were perceived as causing nuisance (see also below target issue to replace *Myriophyllum spicatum* by charophytes). Secondly, 70% of the respondents considered near-natural lake banks as important elements for the preservation of selected littoral areas, although the free accessibility to the water edge for other areas had top priority. Despite the overall high priority of water clarity and presence of stable macrophyte stands, which indicates an attitude toward nature, deficits in a deeper understanding of the ecosystem Alte Donau and of ecological criteria for natural banks were striking. The other three key issues perceived as important for visiting Alte Donau were concerns about (3) bathing and boating, (4) the high recreational value of the whole area including meadows in the park, which finally (5) led to an improved quality-of-place for local residents. Around 88% of the bathing visitors of Alte Donau used public bathes (paying an admission fee for lido), the remaining visitors used public swimming areas for free. In the latter case, access to the water edge is provided through meadows or public wooden piers and platforms with bathing ladders in-between the reed belt (Hozang, 2017). Thus, the park around the lake Alte Donau, which underwent a comprehensive planning in parallel to lake restoration (Masterplan Alte Donau in Hozang, 2018), is also freely accessible as green space all year. According to the urban development plan (Mittringer et al., 2005), the green-blue infrastructure of Alte Donau contributes to the natural capital of Vienna in mainly two ways. On the one hand, the near natural lake is valued as natural asset aimed at bridging aspects of compact settlement in the city and green space of high ecological quality. On the other hand, recreational services mediated by water clarity concern also human health which are mitigated by urban heat island effects in Vienna (e.g., Roetzer et al., 2000; Matzarakis et al., 2010; Žuvela-Aloise et al., 2014). In general, spaces with high evapotranspiration (Sánchez-Carrillo et al., 2004; Gunawardena et al., 2017; Wu et al., 2019), such as the littoral reed belt of natural or near natural lakes, where annual evapotranspiration can exceed annual evaporation of the open lake surface (e.g., Herbst and Kappen, 1999), are most effectively improving microclimate. In this view, urban recreational services mediated by water clarity go by far beyond satisfying bathing aesthetics. Green-blue spaces in cities are thus in general higher rated by people than green spaces alone (White et al., 2010).

Water Clarity in View of Sustainable Restoration Measures and Ecosystem Health

Deterioration of freshwaters concerns ecologists worldwide. Sophisticated methods rely on biota integrity, using indicator species for assessing water quality and ecosystem health (Karr, 1991; Dokulil and Teubner, 2002; Schneider and Melzer, 2003; Padisák et al., 2006; Teubner et al., 2018b; Rücker et al., 2019). In case of eutrophication, however, i.e., when man-made surplus of nutrients is the sole relevant human impact, sustained increase of water clarity is the main target of restoration (e.g., Gulati et al., 2008). Water clarity is thus understood as "valued attribute" for judging the water quality (Håkanson et al., 2005; Peeters et al., 2009; Keeler et al., 2012). It enables a high degree of predictability of ecosystem health because it describes water quality simultaneously in view of two important aspects, i.e., the availability of nutrients pointing in the direction of potential phytoplankton development (indirect effect on water clarity) and the ambient light climate (direct effect on water clarity). Thus, water clarity mirrors the extent of nutrient surplus, that in turn triggers photosynthetic growth, yielding biomass on the one side, and the access to ambient light along the water column required for growth of primary producers, on the other side. These two aspects of water clarity are in particular relevant for shallow aquatic ecosystems, as exemplified here for the oxbow lake Alte Donau. With the reduction of the phosphorus-pool following the lake restoration, phytoplankton growth became limited and phytoplankton biomass drastically declined leading to an increase in water clarity. With the improvement of water clarity, submerged plants spontaneously grew from residual fragments (Dokulil et al., 2018). This switch between alternate stable states, represented by nutrient-rich algal-turbid state and water plant dominated clear-water state (e.g., Scheffer et al., 1993; Cristofor et al., 2003; Søndergaard et al., 2010; Hilt, 2015; Phillips et al., 2016), is well known in aquatic sciences and is seen as a cornerstone in lake restoration (e.g., Carpenter and Cottingham, 1997; Hilt et al., 2006; Søndergaard et al., 2007; Gulati et al., 2008; Jeppesen et al., 2012).

Underwater light climate is most commonly measured with Secchi depth readings (e.g., Forsberg and Ryding, 1980; Nürnberg, 1996; Giardino et al., 2001; ÖNORM M6231, 2001), but can also be determined by light attenuation along depth profiles. The latter is often used in case of "lake bottom view" (e.g., Meijer et al., 1999), i.e., Secchi disk transparency exceeds the lake depth (e.g., Löffler, 1988). The measure of underwater light attenuation further suits better for turbid water bodies where steep profiles of light attenuation are expected (e.g., Dokulil, 1975; Katalin et al., 2009). The exponential attenuation of irradiance with depth relies on light absorption and light scattering, i.e., depends mainly on the water color and on the characteristics of seston particles (e.g., Löffler, 1988; Koenings and Edmundson, 1991; Zimmermann-Timm, 2002). Secchi transparency and underwater light attenuation in our study, calculated within seasons or within boundaries of trophic classification scheme and thresholds of human perception for bathing aesthetic, mirror basically the background of a certain chlorophyll content. Whatever the factor predicting 1%, 3%, and 12% surface ambient light or light intensity at Secchi depth was, high values were associated with high Chl-*a*. Chlorophyll-*a* is the principal light harvesting pigment of primary producers and commonly used as rough estimator of phytoplankton biomass. Chl-*a* accounts with 0.50% to wet weight phytoplankton biomass in Alte Donau (Teubner et al., 2018b). In addition to light absorption by phytoplankton, these biotic particles contribute to underwater light scattering (e.g., Kirk, 1975; Bricaud and Morel, 1986). As our study on Alte Donau covers four seasons over years accomplishing the lake restoration from hyper- to a meso- oligotrophic state, optical properties of this lake are as variable as found in a multi-lake study. The wide range of surface ambient light at Secchi depth in Alte Donau agrees with the variation from 0.8 to 36.3% among different lake types by Koenings and Edmundson (1991). Further, the factor f_{eu} which is commonly used to predict $z_{eu}$by z_{Secchi}, ranged widely among seasons and boundaries of trophic states (i.e., between 3.0 and 3.8) in Alte Donau, as confirmed by other studies (Montes-Hugo et al., 2003). Compared with Alte Donau, the ratio z_{eu}/z_{Secchi} was even higher in the shallow, mesotrophic but turbid soda Lake Neusiedl, where it ranged from 3.5 to 6.0 for individual measurements (mean: 4.6, Dokulil, 1979), and lower in the deep mesotrophic alpine Mondsee (range 1.3−4.9, mean: 2.7, $n = 26$, 1999−2000, Teubner and Dokulil, unpublished data). Dokulil (1979) further reported mean ratios ranging from 1.3 to 5.0 for 26 mainly lake sites worldwide, Padial and Thomaz (2008) between 1.8 and 2.6 for subtropical reservoirs and floodplain lakes. These results underscore that Secchi disck readings need to be calibrated against exponential light attenuation in specific lakes and seasons, when they are used to predict optical properties relevant for the biota, such as the euphotic depth (1% of surface ambient light), the maximum colonization depth of macrophytes (3% of surface ambient light; cf. Middelboe and Markager, 1997; Dennison et al., 1993), and the optimum depth of epilimnetic phytoplankton growth (12% of surface ambient light, Teubner et al., 2004).

Both photosynthetic lake assemblages, phytoplankton and macrophytes, basically require the same nutrients and light sources when sharing the same habitat. Each of them includes a bunch of organisms that often are not taxonomically linked to each other. Phytoplankton communities include eukaryotic algae and prokaryotic cyanobacteria. Besides common physiological features for photosynthetic autotrophs, some algae such as cyanobacteria and cryptophytes rely on light absorption at specific wave-lengths, which is different from most eukaryotic species. For many cyanobacteria, but also for some bacillario- and ochrophytes, mixotrophy, in addition to autotrophic photosynthesis, is an alternative or obligate pathway of nutrition. Both, structural aspects (e.g., specific pigment pattern, different ways of nutrition) and physiological strategies (e.g., coping with ambient light and nutrients by optimizing resource utilization, acclimation), allow a balanced phytoplankton growth along the light attenuation gradient which may also result in different phytoplankton species inhabiting different layers in the water column (Klausmeier and Litchman, 2001; Greisberger and Teubner, 2007; Salmaso and Padisák, 2007; Zohary et al., 2010; Dokulil and Teubner, 2012; Mantzouki et al., 2016). In Alte Donau, the contribution of cyanobacteria to total phytoplankton varied strongly over the 22-year study period and was highest under nutrient rich conditions as described in detail in Teubner et al. (2018a).

Submerged macrophyte assemblages inhabiting lakes cover again taxonomically different species. They include vascular plants, charophytes (stoneworts, brittleworts) and bryophytes (Lacoul and Freedman, 2006), which exclusively rely on photosynthesis and are commonly anchored to the lake bottom. The different types of growth forms (e.g., near bottom rosettes, tall-growing with caulescent branches, canopy formations on water surface) also allow macrophytes to utilize underwater light at different layers in the water column (for inventory of about 40 macrophyte species in Alte Donau see Pall, 2018; Pall and Goldschmid, 2018).

It is common for both assemblages, phytoplankton (e.g., Wall and Briand, 1979; Kohl and Nicklisch, 1988) and submerged macrophytes (e.g., Chambers and Kalff, 1985; Dennison et al., 1993; Middelboe and Markager, 1997), that requirements for optimal growth under ambient light can vary from group to group and from species to species. Nevertheless, both assemblages often colonize mainly at certain depth layers. In the case of phytoplankton, epilimnetic community (dominated by strict photosynthetic organisms, with less mixotrophic species) avoids the near surface layer due to stress by too high light intensity (PAR and also UV radiation) and builds up maxima at 12% of surface ambient light (Teubner et al., 2004). In deep lakes, in addition to the epilimnetic peak at 12% surface light, metalimnetic phytoplankton (often in combination with mixotrophy) can develop below the euphotic zone, at 0.1 to 1% of surface ambient light (e.g., Walsby and Schanz, 2002; Zotina et al., 2003; Teubner et al., 2004; Greisberger and Teubner, 2007; Dokulil and Teubner, 2012; Yankova et al., 2016). The epilimnetic peak is most relevant for shallow lakes such as Alte Donau. An epilimnetic layer of about 10−14% of surface ambient light (12% of surface-ambient light for lake growth optimum, Teubner et al., 2004) expands vertically the water transparency, but narrows to only few centimeters if water transparency is very low. At high water transparency, this layer of optimal growth is far from the lake surface, but is very close to the top under high turbidity. High water clarity is associated with diverse but low number of phytoplankton species (often measured by low Chl-*a* at low TP) and often relates to an increase in biodiversity and integrity, as discussed above.

Conversely, under hypertrophic conditions that are associated with mass-development of phytoplankton, only few phytoplankton groups develop, and in particular cyanobacteria that are known for their potential of blooming and of producing toxins, thus damage ecosystem health and inhibit recreational use (Teubner et al., 1999; Chorus et al., 2000; Dokulil and Teubner, 2000; Graham et al., 2010; Mantzouki et al., 2016; Scherer et al., 2017; Dokulil et al., 2018). Their single cells, filaments or aggregates dramatically enhance underwater light attenuation by self-shading along the whole water column. Thus, shading acclimated cyanobacteria are abundant during mixing in spring while other cyanobacteria that are protected by UV-shield can form dense scums near the surface during stratified conditions in summer. Phytoplankton assemblages dominated by cyanobacteria are commonly scarcely diverse, as only few species can survive in an extreme habitat in terms of low light and surplus of nutrients, which indicate low ecosystem integrity. Thus, in view of lake assessment by phytoplankton, water clarity indeed provides an indicator for ecosystem health.

Water clarity is also used as reference for ecosystem quality when referring to macrophytes (Van Nes et al., 2002; Nõges et al., 2003; Feldmann and Nõges, 2007; Köhler et al., 2010; Søndergaard et al., 2010). For plants, the bottleneck for successful colonization is germination. Since light commonly acts as signal to start seasonal spreading or growing (e.g., Penfield et al., 2005; Chen et al., 2008; Nelson et al., 2010), which is also relevant for macrophytes (Ozimek, 2006; Tuckett et al., 2010), early seedling development and leaf-out during spring depends on certain thresholds of light availability. With water level draw-down of 25 cm for only few days in March to May, the light signal for stimulating vernal growth is enhanced and thus can trigger leaf-out and shoot development of submerged macrophytes even in deeper layers of the littoral zone (Pall, 2018; Pall and Goldschmid, 2018). In other studies, the clear-water phase, which is referring to lake phenology and describes the period when water clarity temporarily increases to "lake bottom view" for a few days (at least in shallow lakes) due to grazing of phytoplankton by zooplankton, also seems to be important for macrophyte succession starting in spring (Van Nes et al., 2002). The timing of the clear-water phase in Alte Donau varied between the 95th (early April) and 145th day (late May) during our investigation, and tends to be observed progressively earlier in recent years due to global warming (Teubner et al., 2018b). Thus, a clear-water phase during the transition from late spring to summer might favor macrophyte growth over phytoplankton summer bloom.

A temporary increase of water clarity by vernal water-level draw-down represents the window of opportunity for sustaining macrophyte development later in the year. It was a cornerstone of macrophyte management during the period of re-establishing macrophytes in Alte Donau, carried out in four successive years, 2002−2005. After the first 2 years, with total submerged plant biomass of 20 t (2002) and 125 t (2003), the annual macrophyte biomass yield strongly increased to more than 350 t afterward of sustained water clarity.

With the re-establishment of underwater vegetation, submerged macrophyte growth takes advantage against phytoplankton growth (Phillips et al., 2016), and thus clear water is stabilized by sustained macrophyte domination (Cristofor et al., 2003; Hilt et al., 2006; Hilt, 2015). The spatial tightness of habitat zonation along the depth is further relevant when considering allelopathic substances which may suppress the growth of certain species within the same assemblage, both within the phytoplankton and the macrophyte community, but can also occur also between species of algae and macrophytes

(Van Donk and Van de Bund, 2002; Gross, 2003; Legrand et al., 2003; Berger and Schagerl, 2004; Hilt and Gross, 2008; Mulderij et al., 2009; Chang et al., 2012). Some of these studies assume that allelopathically active macrophytes contribute to stabilize sustained macrophyte growth and thus clear-water state in shallow lakes.

In our study, the threshold for Secchi disk transparency for sustained macrophyte growth in Alte Donau is at about 3.5 m (annual average) and thus exceeds by far the thresholds of 1.5 m and 2.75 m for bathing aesthetics (Smith et al., 1991, 1995a). The annual Secchi depth transparency of 3.5 m agrees with Secchi depth transparency in June 1987 by Löffler (1988) referring to the mesotrophic state in the 80ties with a dense bottom cover mainly of *Chara* meadows at that time. According to our study, a Secchi disk transparency of 3.5 m seems to satisfy minimum light requirements of macrophytes on the whole lake bottom area and is thus supporting underwater plants if no self-shading of macrophyte stands, nutrient limitation or other environmental stressors suppresses the growth of macrophytes. In addition, although macrophyte growth at dim light is possible (e.g., Nielsen and Borum, 2008), and such minimum light requirements are ecologically relevant for defining the maximum colonization depth, it is clear that optimized macrophyte yield refers to higher ambient light intensities (compare with epilimnetic phytoplankton above, with highest abundances around 12% of surface ambient light within the euphotic zone; see also average requirements of 11% for charophytes and 21% for submerged angiosperms at lowest colonization depth according to Chambers and Kalff, 1985). Assuming that macrophytes meet similar light harvesting requirements as planktonic photosynthetic biota having an optimum at a depth of 12% of surface ambient light (e.g., Teubner et al., 2004), the stratum at 5.5 m (=12% surface-light; 3.5 m Secchi disk transparency) might also be relevant for optimal light harvesting of submerged macrophytes in Alte Donau This optimum depth is exceeding by far the mean lake depth of 2.5 m. The expansion of the epilimnetic layer satisfying an enhanced light requirement of 10−14% surface ambient light discussed above for phytoplankton might be relevant for the macrophytes in two ways: a settlement of near-bottom prospering macrophytes below the mean lake depth and an enhanced light availability in the water column for the spreading tall-growing macrophytes. According to other studies, light requirements of submerged macrophytes range widely from 2 to 25% (mentioned as "typical values" for freshwater species in Middelboe and Markager, 1997) or from 4 to 29% surface light (mentioned as minimum light requirement for marine species in Dennison et al., 1993). Therefore, these results underpin that a Secchi disk transparency of 3.5 m satisfies light requirements of submerged macrophytes yielding in sustained large biomass in mesotrophic Alte Donau.

In 2019, charophytes contributed almost 20% to macrophyte yield. The last step, i.e., to substitute the still abundant *Myriophyllum spicatum* by charophytes in Alte Donau, is thus still ongoing. *M. spicatum* is common in the Danube River Basin and most frequently found in habitats of fine inorganic sediment of steep bank slopes, medium velocity (35−65 cm s^{-1}) connected to main river channels (e.g., Janauer and Exler, 2004). In Alte Donau, dense stands of *M. spicatum* building canopy formations near the water surface were thus nuisance for recreational purposes (e.g., boating or swimming). A shift toward charophytes, which can build up meadows near the lake bottom, would stabilize best of sustained clear water state Van Donk and Van de Bund (2002) and agrees with macrophyte assemblage under mesotrophic conditions described in the 80ies in Löffler (1988). Many charophyte species are superior in nutrient poor clear freshwaters, i.e., oligotrophic state (e.g., Middelboe and Markager, 1997; Melzer, 1999). The advantage of charophyte meadows for sustained restoration effort consists in their capacity to stabilize effectively a clear-water state, as summarized by Hilt et al. (2006). Dense Charophytes stands covering the lake bottom can prevent the re-suspension of sediment particles, thus leading to nutrient-immobilization in the long-term. Further, lakes with *Chara* meadows benefit on their winter-green that may contribute to avoiding oxygen depletion on the sediment surface. Finally, many charophytes are heavily calcified, which ensures that fragments of charophytes sink to bottom instead of floating at the water surface, which is considered beneficial in view of recreational use. When aiming at stabilizing submerged macrophyte stands (Hilt, 2015), in particular in view of sustained growth of charophytes, a critical Secchi disk transparency of 3.5 m or even higher might be the target for further lake management measures in Alte Donau. A Secchi disk transparency of 1.5 m and 2.75 m, which is suggested as critical values for bathing aesthetics according to Smith et al. (1991, 1995a) would be within boundaries of mesotrophic conditions, but would not be satisfactory for sustained macrophyte growth in Alte Donau in the long-term.

Water Clarity for Bridging Ecosystem Health and Ecosystem Services Superimposed by Global Warming

The Pannonian Plain, where Vienna Basin and thus Alte Donau is embedded, is seen as one of the most vulnerable region to global warming in Austria (Zweimüller et al., 2008; Dokulil and Herzig, 2009; Dokulil et al., 2010; Soja et al., 2013) and in Central Europe (Honti and Somlyody, 2009; Olesen et al., 2011; Nistor, 2019), respectively. Accordingly, the year-to-year variation of lake surface water temperature in Alte Donau responded to the climate signal, the North Atlantic Oscillation (NAO) Index. This climate index is commonly used to detect long-term variability and trends from lake physics to lake-biota driven by global warming in the Northern Hemisphere (e.g., Anneville et al., 2002; Straile et al., 2003; Blenckner et al., 2007; Dokulil and Herzig, 2009; Soja et al., 2013; Wrzesiński et al., 2015). Although the climate driven processes are controlled by large scale phenomena throughout the year, climate response to NAO is most pronounced for winter to early spring and is fading later in the year due to ecosystem filters (e.g., Blenckner et al., 2007; Dokulil et al., 2010; Ptak et al., 2018; Teubner et al., 2018a; Schmidt et al., 2019). In accordance, the climate response in Alte Donau to WT was most significant during the cold season, i.e., for the number of days with WT $> 5°C$, $> 6°C$, and $> 7°C$ and the yearly onset (Julian day) for stepwise passing WTs of 6°C, 7°C, and 8°C.

Apart from the direct correspondence with the climate signal, seasonal lake phenology changes could be verified by significant warming trends. The lengthening of periods above a certain value of water temperature, in detail graphically exemplified for length with WT > 14°C, >20°C, and >22°C in our study, were mainly due to a steep and thus significant slope toward an earlier onset passing the WTs than by weak slopes for the delayed offsets. Thus, the lengthening of growing season in Alte Donau relies primarily on an advanced onset in spring than a delayed autumnal cooling, as also described for other phenology studies (Menzel and Fabian, 1999; Chmielewski and Rötzer, 2001; Dokulil and Teubner, 2012; Garonna et al., 2016). According to spring phenology of plant flowering by Roetzer et al. (2000), the Julian day observed for urban sites in Vienna was in all cases in advance (3 to 5 days) to rural sites of the city. Therefore, an interference of suburban climate on surface WT might not be neglected, but such an analysis was beyond the scope of this study. The flowering phenology study, however, should increase the awareness regarding how an urban space can benefit from a natural water body in terms of improving microclimate, and *vice versa* to what extent the urban climate may enhance warming in urban waters.

An increase in bathing visit is associated with a lengthening of the periods that satisfy an intermediate water temperature, in the range of 13 to 16°C, which is relevant for determining the start of recreational use in a year. Secchi disk transparency seems in particular dampened during hot summer periods with a WT from 20°C to 22°C and is not corresponding to an enhanced macrophyte yield.

The impact on water clarity, as controlled by the balance between phytoplankton or macrophytes and the total pool of the main nutrient element, i.e., phosphorus, became evident for certain summer periods during the decadal limnological survey of Alte Donau. With an advanced warming for exceeding WT from 15°C to 21°C, i.e., after the transition from spring to summer when phytoplankton is passing the clear-water phase (Teubner et al., 2018a), sustained macrophyte development at the expense of phytoplankton growth or TP pool size, respectively, takes place. This supports other studies that show how macrophytes benefit from lake phenology in terms of short-term enhancement of water transparency (Van Nes et al., 2002). The same is valid for the lengthening of the warm period. Only extreme high WT above 22°C to 23°C, when also Secchi depth transparency significantly decreases relative to extreme WT increase, do not result in a further increase of macrophyte biomass. The annual biomass yield of submerged plants relative to the pool of nutrient resources (as TP) and to phytoplankton (as Chl-*a*) benefits from elevated but not extreme WT in this water body of the temperate zone. Macrophytes thus seem to benefit from an earlier onset of temperatures between 14°C and 15°C. The year-to-year variation of the day when 19°C or 20°C is reached for the first time seems to correspond best to a maximal biomass yield of macrophyte per year, when related to TP or Chl-*a*. A sustained macrophyte dominance stabilizes the clear-water state as stated before, supports ecosystem health and satisfies recreational use. In principle, many submerged macrophytes may respond with higher yields when just comparing the impact of enhanced water temperature on their growth. *Myriophyllum spicatum* is an angiospermic macrophyte which clearly seems to cope well with climate warming (Aiken, 1981; Patrick et al., 2012). Not in general (Choudhury et al., 2019) but also some common charophytes seem to benefit from a temperature increase (Rojo et al., 2017) as far as ephemeral ponds do not disappear due to climatic drought. To our knowledge, there is no climate response bioassay study for *Myriophyllum spicatum* in comparison with common *Chara* species as found in Alte Donau (Pall, 2018), to answer which macrophyte species would benefit the most from climate warming.

A previous study, however, showed that the prolongation of the warm season in Alte Donau – in addition to a progressively earlier clear-water phase – favors thermophilic zooplankton species in many ways. The most spectacular zooplankton species to mention here is an alien species, the freshwater jellyfish *Craspedacusta sowerbii* (Ciutti et al., 2017; Kozuharov et al., 2017; Trichkova et al., 2017), which builds up its medusa stage more frequently as WT exceeds 21°C more often in Alte Donau (Teubner et al., 2018a). Thus, despite the success of restoration measures, biotic relationships can be superimposed by climate warming and thus finally also interfering ecosystem services and ecosystem health.

CONCLUSION

In conclusion, water transparency can serve as a key indicator of multi-functional socio-ecological values to assess near natural assets of green-blue spaces and ecosystem health as exemplified for the oxbow lake Alte Donau in Vienna. Judgment of water clarity by public perception is of great importance for communicating the success of restoration or urban planning in modern cities life. In ecological terms, water transparency identifies the overall success of lake restoration or ecosystem health status if no other impacts than local nutrient surplus or global risk by climate warming pose potential threats. The critical water transparency forcing alternate nutrient allocation from planktonic algae under nutrient-rich conditions to submerged macrophytes of nutrient-limitation (details in Dokulil et al., 2018), however, exceeds requirements of water transparency that is satisfying people's awareness by littoral "lake bottom view," i.e., judging good water quality by bathing aesthetics. Our results suggest that annual Secchi transparency of 3.5 m or even higher is required to accomplish the still ongoing, last step of sustained lake restoration, i.e., to further the increase of charophytes above 20% macrophyte yield contribution. This step at the expense of tall-growing *Myriophyllum spicatum* aimed at further stabilizing the clear-water state in Alte Donau. In this view, even if water transparency can be indeed judged as reliable socio-ecological indicator, annual surveys of recreational waters should still go further beyond measuring Secchi disk transparency. A knowledge in advance, which goes beyond Secchi depth readings, contributes to mitigating the superimposed response by climate warming and other potential threatening impacts in the accelerated man-made age, which seem to hamper water transparency in general during extreme hot summer seasons and favor long-term thermophilic macrophytes such as *Myriophyllum spicatum* in particular.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

KT mainly conceived the manuscript idea and did data analysis, statistics and preparation of graphs, text, and literature search and writing. IT conducted statistics, advanced data processing concerning underwater light attenuation and climate research in **Tables 2–3**, writing paragraphs in the "Materials and Methods," "Results," "Discussion," and "Concise Abstract". KP contributed by strong expertise in macrophyte biology and management including re-establishing of charophyte-vegetation, providing recent field data about macrophyte yield and success of charophyte plantings in the Alte Donau, co-preparation of graphs, critical review of literature about physiology, and macrophyte management. WK re-assessed measurements of underwater light conducted, refreshed by advanced methodology analyzing critical depths, contribution to text of "Materials and Methods," "Results," and "Discussion". MT contributed most to the main idea of re-emphasizing water transparency, contributed to all analyses and writing about socio-limnological aspects, in particular Secchi depth and its interpretation. TO contributed with data and analysis mostly to **Figure 2** and **Table 1**; discussion and writing about results provided by socio-economic life project at Alte Donau, green-blue spaces in Vienna, in view of city master plan and ongoing macrophyte management. MD contributed in particular to methods of optical properties; restoration perspective Alte Donau, critical contribution at all stages of manuscript preparation concerning analysis, graphical display, text, and literature search. All authors contributed to the article and approved the submitted version.

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Integrating Conflicting Goals of the EC Water Framework Directive and the EC Habitats Directives Into Floodplain Restoration Schemes

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River floodplains are among the most threatened ecosystems of the world and their protection and restoration is of key importance for river managers. In Europe, the Water Framework Directive (WFD) and the Habitats and Birds Directives (HBDs) provide a guideline for decision processes in floodplain restoration projects. While the WFD, however, represents an aggregated, multiple-species approach aiming at the restoration of the natural hydrological dynamics, the single-species focused HBDs regulate the protection of the existing fauna and flora with protection status. Thus, trade-offs between rheophilic and stagnophilic aquatic organisms may hamper the definition of a compromise solution between the ecological objectives of the restoration. We present an assessment scheme for the restoration of a degraded Danube floodplain near Vienna, which equally considers both WFD and HBDs objectives in a transparent, comprehensible, and objective way. In a first step, predictive hydrological and ecological models were generated for different hydrological scenarios considering the aquatic community composition (floodplain index according to WFD) as well as individual protected species of the taxonomic groups fish, amphibians, reptiles, and water birds (HBDs). Based on these models, we developed an assessment scheme which considered potential changes in the available habitats, the current conservation states, and priorities of the species. Thereby, we included experiences from other restoration projects. The results show that both the multiple-species and the single-species approach achieved a similar ranking of the hydrological scenarios, in which the "business-as-usual" alternative without any restoration measure was identified as the worst case. The multiple-species approach of the floodplain index provided a clear ranking of the hydrological scenarios and revealed a low potential of any target measure to restore the pre-regulation state of the floodplain. In contrast, the single-species approach required a much higher degree of decisions by experts, but provided a detailed insight into spatial effects of the measures on different species, thus revealing the potential for local compensation measures. Our study demonstrates that a

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combination of these two approaches can be an effective tool for river managers in the development of sustainable floodplain restoration schemes in accordance with the WFD, the HBDs, and national nature protection laws (in this case, the Nature Conservation Acts of Vienna and Lower Austria).

Keywords: EC water framework directive, EC habitats directive, floodplain index, species distribution models, decision process, nature protection

INTRODUCTION

River floodplains are among the most threatened ecosystems in the world (Tockner et al., 2010). Along the Upper Danube in Germany and Austria, more than 90% of the former dynamic floodplains have been lost due to the construction of flood protection dikes and impoundments for hydropower generation (Hein et al., 2016). During the last decades, an increasing number of restoration projects has focused on the re-integration of these floodplain areas into the hydrological dynamics of the Danube main channel (Schiemer et al., 1999; Baart et al., 2013; Stammel et al., 2016). However, floodplain restoration challenges both, river managers and decision makers, through multiple, often conflicting ecological, economic, and social demands (Buijse et al., 2002; Jungwirth et al., 2002; Preiner et al., 2018). Regarding nature protection, decision makers may additionally have to comply with different regulations in the same area, which sometimes have divergent goals. In specific, conflicts may arise from efforts to restore the former hydrologically dynamic character of the floodplain and the need to protect rare, but stagnophilic species, which have inhabited the area during the phase of disconnection (Moss, 2007; Stammel et al., 2016).

In the European Community (EC), two major directives exist, which set restoration and/or conservation aims for aquatic ecosystems and provide a guideline for decision processes in floodplain restoration projects (Moss, 2007; Gumiero et al., 2013; Hein et al., 2019). The EC Water Framework Directive (WFD) mandates members to restore or maintain the good ecological state of river systems (Council of the European Communities, 2000). The WFD represents a multiple-species approach, based mainly on benthic invertebrates and fish, which is oriented at a near-natural (historical) reference state of the respective aquatic system without human impacts. Although neither floodplains nor specific riparian or floodplain organisms are currently addressed as separate entities in the WFD, the intact structure of riparian zones necessary to support a good ecological state of the river system is mentioned (Meyerhoff and Dehnhardt, 2007; Gumiero et al., 2013). In contrast, nature protection laws are generally single-species approaches, which regulate the protection of endangered species or habitats on a defined spatial scale (e.g., local or national), independent of whether they were originally present in these areas or not. The most important regulations on European Community level are the Habitats and Birds Directives (HBD) which aim at the protection and conservation of aquatic, semi-aquatic, and terrestrial floodplain habitats and protected species within designated Natura 2000 areas as a tool of the EC biodiversity strategy (Council of the European Communities, 1992, 2009; Gumiero et al., 2013). There is an increasing awareness in the EC and the European Environment Agency (EEA) of the need to improve coherence among the different EC directives regulating floodplain management via the development of a consistent method across Europe based on a holistic river basin management perspective (European Environment Agency, 2020). In addition to the HBDs, national nature protection laws may be relevant for the setting of restoration aims for river floodplains. In Austria, nature conservation is regulated in nature conservation laws of nine autonomous federal states (Artmann, 2018).

Due to the high complexity and diversity of river-floodplain systems, conflicts may arise from the different foci of these directives to either restore the original functionality (WFD) or conserve the existing biodiversity (HBDs and nature protection laws) (Acerman et al., 2007; Gumiero et al., 2013; Janauer et al., 2015). Pristine river-floodplain systems are characterized by high lateral hydrological dynamics and alternating erosion-sedimentation processes, where large running waters with shifting lotic and lentic conditions usually dominate (Eupotamon), while stagnant, permanent or temporary water bodies may coexist in margin areas (Para-, Pleisio-, and Paleopotamon) (Amoros et al., 1987; Jungwirth et al., 2002). This creates a diverse mosaic of different terrestrial, semi-aquatic, and aquatic habitats. Disconnection from the main channel reduces this temporal and spatial dynamics severely, thereby stimulating terrestrialisation processes and favoring stagnant conditions (Schindler et al., 2016). This may change the character of the floodplain entirely, leading to the establishment of a more terrestrial, semi-aquatic, and stagnophilic flora and fauna. Nevertheless, such floodplains may harbor rare species and habitats of high nature protection value, which can be threatened by the restoration of the former lateral hydrological connectivity and dynamics of the floodplain. In many cases, a complete re-connection of the artificially disconnected floodplain with the river channel is not feasible due to a multitude of hydrological or socio-economic constraints (Jungwirth et al., 2002). However, the question arises whether and how a partial restoration of the lateral connectivity can stimulate a development toward the original dynamic conditions without threatening the existence of immigrated rare species requiring more stagnant conditions.

To our knowledge, no approach has been developed so far which tries to balance the different aims of the EC WFD and the EC HBDs and combine them into a single assessment scheme as guidance for floodplain restoration concepts. In this study, we present an approach to compare the different EC directives and integrate the partly conflicting ecological aims. Our case study is a formerly dynamic floodplain of the river Danube east of Vienna, which was cut off from the main channel in the 19th century (Funk et al., 2013; Reckendorfer et al., 2013; Weigelhofer et al., 2015). While the reduced hydrological dynamics has led to the establishment of rare, highly protected species, resulting in the designation as a national park and a Natura 2000 area, it threatens the further existence of the floodplain through severe water supply deficits. Thus, besides other socio-economic demands and hydrological restrictions (described in, e.g., Sanon et al., 2012; Preiner et al., 2018), one of the main tasks of this study was to develop an assessment scheme for potential future scenarios, which equally considers both WFD and HBDs objectives in a transparent, comprehensible, and objective way. The developed approach should identify the compromise solution with the highest potential of restoring the pre-regulation conditions, while keeping losses in the established communities at a minimum. The study was based on the development of predictive hydrological and ecological models for different restoration scenarios, which were supported by long-term monitoring data within the study area as well as by experiences from other restoration projects in the vicinity (Reckendorfer et al., 2006; Hein et al., 2016). Based on these models, we developed an assessment scheme for the WFD and HBDs goals separately in a first step and then integrated these two approaches into an overall weighted evaluation of the different scenarios. In the following sections, the different steps of this approach and the evaluation results are presented for the case study and challenges and solutions for floodplain restoration schemes are discussed.

MATERIALS AND METHODS

Study Area and Scenarios

The floodplain Lower Lobau extends over an area of approximately 1,500 ha on the left bank of the River Danube east of Vienna (48°09′36.8′′N 16°32′15.0′′E). Due to the construction of a flood protection dike in the 19th century, the upstream opening of the main Lobau side arm was cut off from the Danube channel, leaving only a downstream opening for flood water entry (Funk et al., 2013; Reckendorfer et al., 2013; Weigelhofer et al., 2015). The isolation from erosive flood events has led to the transformation of the floodplain water bodies from mainly Eupotamon to Para-, Pleisio-, and Paleopotamon with numerous isolated and seepage or groundwater-fed backwaters harboring a diverse stagnophilic and semi-aquatic fauna and flora (Reckendorfer et al., 2013). The whole floodplain area lies within the jurisdiction of the two Federal states Vienna (upstream part) and Lower Austria (downstream part; **Figure 1**). The Lower Lobau has been assigned as a Natura 2000 area and is part of the National Park Donauauen (Hein et al., 2006).

A range of hydrologically feasible and socially and ecologically acceptable re-connection scenarios were defined to evaluate the restoration potential of the floodplain under different hydrological conditions, to identify trade-offs among the different legal objectives, and to find the best compromise solution. The tested scenarios comprised

1. a controlled water supply of 3 m^3s^{-1} from the Danube to raise the surface and groundwater levels in the floodplain, to increase the connectivity and the surface water exchange through the main side arm, and to establish locally restricted rheophilic conditions (abbreviated as “S3” in the following chapters). This scenario is expected to fully preserve important socio-economic demands in the area such as drinking water supply, recreation or agriculture (Sanon et al., 2012).
2. a partial re-connection with the Danube, discharging 20–80 m^3 s^{-1} into the main side arm (depending on the respective water level of the Danube) to establish permanently flowing conditions there (“S20–80”). This scenario is expected to reflect the highest possible level of reconnection that is still acceptable accounting for socio-economic demands, particularly the potential for drinking water production, as the surface water influence impacts the quality of groundwater (Sanon et al., 2012).
3. a business-as-usual scenario without restoration measures, resulting in a further loss of aquatic areas due to terrestrialisation processes in the floodplain and channel bed incision of the Danube main channel (“S0”).

Due to both, hydrological limitations and socio-economic restrictions, such as, e.g., flood protection or drinking water supply, a full re-connection with the Danube, which would have resulted in a stimulation of rejuvenation and erosion processes at large scale, was not feasible and, thus, not included as restoration scenario.

The hydrological variables for the scenarios (water tables, water depths, flow velocities, and flow directions) were provided by a calibrated 2-D hydrodynamic surface water model (CCHE-2D; Univ. of Mississippi–National Center for Computational Hydroscience and Engineering; Gabriel et al., 2014). The model predicted an increase in total water area by > 25% and > 30% for the S3 and the S20–80 scenarios at mean water level, respectively. The hydrological model was validated by comparing the modeled *status quo* with the actual situation in the floodplain water bodies at different water levels.

The S0-scenario was estimated by extrapolating the aquatic habitat losses between 1938 and 2011 using a regression model based on the evaluation of aerial images (Böttiger, 2011). The models predicted a decrease by almost 20% of the current water body area for the S0 scenario by 2050. The prediction of the historical reference state was based on the distribution of aquatic habitats in 1817 presented in Hohensinner et al. (2004) and hydrological variables were taken from Hohensinner and Jungwirth (2016).

Floodplain Index (FI) According to WFD Principles

To compensate the lack of an official WFD assessment procedure suitable for floodplains, the “floodplain index FI” was developed by Chovanec and Waringer (2001), which assesses the intactness of floodplains via the occurrence of Odonata. This index corresponds to the WFD by using pristine conditions as reference and calculating the ecological state of the floodplain from the presence or absence of species with different habitat preferences (Chovanec et al., 2005). The FI was extended later to other groups, such as caddisflies, mollusks, amphibians, fish, and other

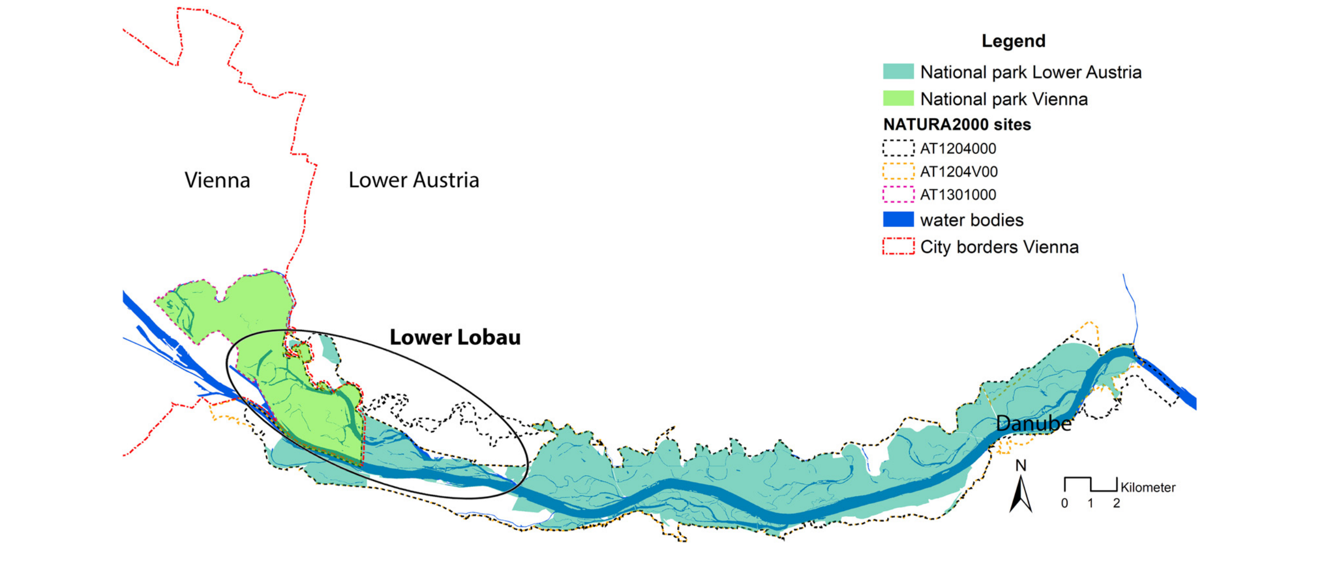

FIGURE 1 | Map of the study area Lower Lobau, showing its location within the two Natura 2000 sites in Vienna (Site code 1301000) and Lower Austria (Site codes 1204000 and 1204V00) and as part of the National park "Danube wetlands" (parts in Vienna and Austria marked in different colors).

invertebrate taxa, to enable a more holistic view of the floodplain's ecological state (Waringer and Graf, 2002; Chovanec et al., 2004; Chovanec et al., 2005; Waringer et al., 2005; Šporka et al., 2009; Funk et al., 2017). In short, 10 valency points are assigned to each target species within a system of five floodplain water body types, Eu- and Parapotamal (types H1, H2 according to Amoros et al., 1987, respectively), isolated permanent water bodies with low to high macrophyte coverage (H3 < 20% and H4 > 20% coverage, respectively) and isolated astatic waterbodies (H5). These valency points represent habitat preferences of species similar to the saprobic index (Brabec et al., 2004), thus, enabling a more accurate assessment of the ecological state of the floodplain water bodies via the community instead of hydro-morphological or chemical parameters. An indicator weight is allocated to each species, ranging from 1 for eurytopic to 5 for stenotopic species, and the floodplain index FI is calculated based on the presence of all species for each water body type. Finally, the ecological state of the floodplain is determined by the current or potential availability of the five floodplain water body types in comparison to natural or near-natural (historical) reference conditions (for details, see Chovanec et al., 2005).

To derive a prediction of the FI for the different scenarios as well as for the historical state, species presences were modeled related to seven environmental parameters (upstream hydrological connectivity, downstream hydrological connectivity, sun exposure, maximal relative water depth at low, mean, and high water levels as well as current velocity at an annual flood event) using Surface Range Envelopes (SRE, Busby, 1991; **Figure 2**). Surface Range Envelope is analogous to Bioclim (Busby, 1991) and uses only occurrence data to define a multi-dimensional environmental space, in which a species can occur, resulting in a multi-dimensional rectilinear envelope, using 5 and 95% percentiles (see also Reckendorfer et al., 2006). This is a fast, simple and intuitive approach which allowed us to model a total of 204 species (33 fish, 7 amphibians, 24 Trichoptera, 38 Odonata, 40 mollusks, and further 62 invertebrate species).

Based on the presence predictions of the different taxonomic groups, the FI was calculated for each scenario and compared to the predictions for the historic reference state (**Figure 2**). The modeling approach was validated by comparing the calculated FI for the *status quo* with field data. The assessment of the ecological state of the floodplain for each scenario followed the protocol provided by Chovanec and Waringer (2001) (**Table 1**). For a more detailed spatial information, the FI was calculated separately for the different basins of the main channel and the individual side-arms (examples shown in **Supplementary Figure S1**).

HBDs and Nature Protection Approach

The EC HBDs aim at the conservation or restoration of a "good conservation status" of each relevant protected species as listed in the standard data form for the respective Natura 2000 area (Gumiero et al., 2013; Hein et al., 2019). Likewise, regional conservation laws in Austria aim for the good status of the protected species. In the case of trade-offs between species, i.e., if a particular conservation measure will support one species, but discriminate against another, it requires the assessment and balancing of potential positive and negative impacts of an envisaged measure via, e.g., smart spatial and temporal planning. For this purpose, 41 aquatic and semiaquatic protected species of the taxonomic groups water birds, fish, amphibians, and reptilians (**Supplementary Table S2**) were divided into habitat guilds based on preferences for flow velocities (e.g., flow guilds according to Schiemer and Spindler, 1989) and water body permanence (i.e., permanent vs. temporary water bodies). For selected species (**Supplementary Table S2**) with sufficient data availability, predictive species distribution models were developed based on a generalized linearized model (GLM) approach (**Figure 2**). From these models, weighted usable areas

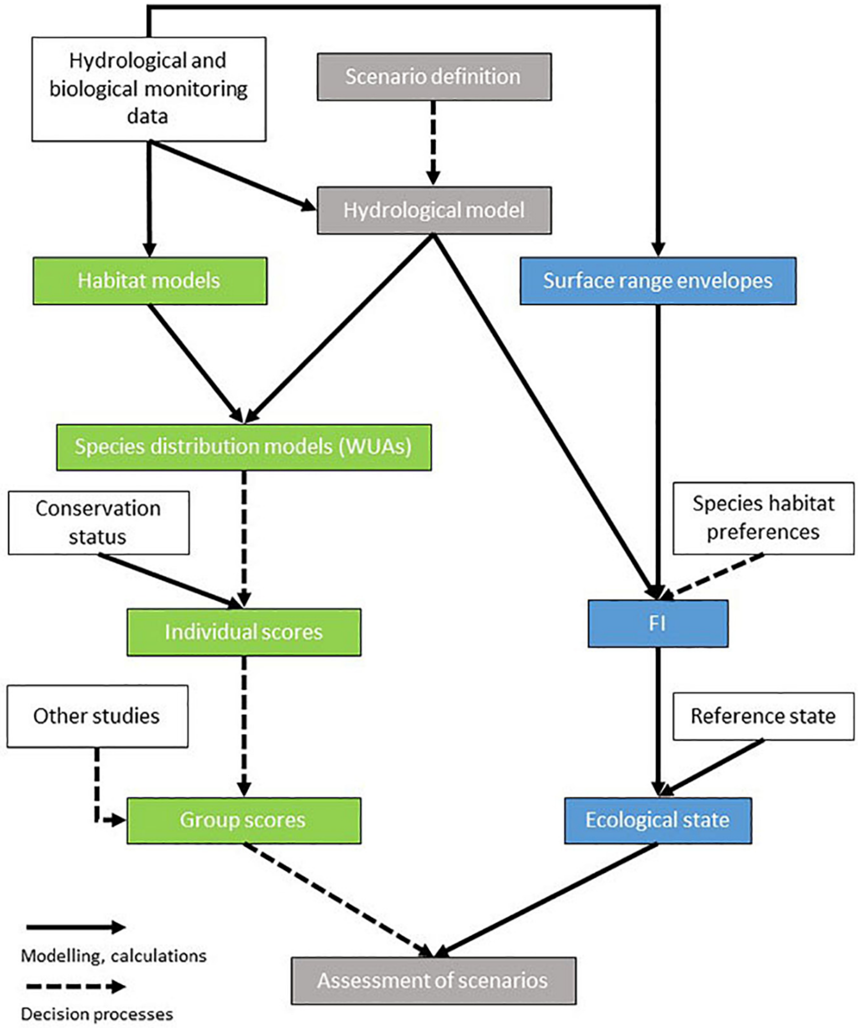

FIGURE 2 | Work flow diagram for the assessment of the restoration scenarios according to the Habitats and Birds Directive and nature protection laws (left, green boxes) and the Floodplain Index (relating to the Water Framework Directive; right, blue boxes). Full lines indicate modeling and calculations, dotted lines decision processes. White boxes indicate data necessary for the modeling and decision processes.

(WUAs) were calculated for each modeled species and each scenario as described in Funk et al. (2013). This approach allowed us to predict quantitative losses or gains of total habitat area in the floodplain for the different species groups and scenarios.

In a second step, the potential change of the conservation status was estimated based on the existing conservation status according to the Natura 2000 assessment (A excellent, B good, and C average or reduced) or regional conservation law (Vienna Nature Conservation Act and Lower Austrian Nature Conservation Act, I excellent, II good, III not satisfying) and the predicted change in WUAs for each species (**Figure 2**). Unfortunately, the assessment had to be performed separately for the upstream part in Vienna and the downstream part in Lower Austria, as these areas are protected under the two different federal laws and are part of two different Natura 2000 sites (**Figure 1**). While the floodplain represents >50% of the Natura 2000 area in Vienna, the Lower Lobau is only a small part of the National Park Donauauen in Lower Austria, covering less than 10% of the Natura 2000 area there. Consequently, species have a different protection and conservation status in the respective Natura 2000 sites. The evaluation was supplemented by local expert knowledge and experiences from other re-connection schemes in adjacent floodplains (Reckendorfer et al., 2006; Hein et al., 2016). Here, our assessments and predictions were checked and – if necessary – slightly adapted for each species by experts of the National Park and the environmental protection agency regarding the actual situation (e.g., potential over- or under-estimation of occurrence) and the potential development (e.g., higher or lower potential due to factors not considered in the model, such as, e.g., predation). We defined the aim of the restoration for each species or habitat by either maintaining the existing good or excellent state or establishing a good state in the case of an existing average or reduced state. Thus, five scores could be achieved for each species and scenario depending on the

TABLE 1 | Definition of the ecological state based on the occurrence of floodplain habitat types according to Chovanec and Waringer (2001) and adaptions for the restoration scheme in the Lower Lobau

Ecological state	Description	Adaptions
I (high)	All habitat types exist, dominance of H1	
II (good)	Small deviation from reference state, all habitat types exist, H1 does not dominate	H1 at least 15% of reference conditions
III (moderate)	Significant deviation from reference state; H1 is missing or two habitat types are missing	
IV and V (bad)	Only 2 habitats types exist; low number of type-specific species	

existing status of the species and the predicted status after the implementation of the measures (**Table 2**).

Significant changes in the conservation status were expected, if (a) the distribution data predicted by the models were consistent with experiences from other restoration projects, (b) the predicted changes in WUAs had a significant influence on the overall distribution of this species in the floodplain, and (c) the floodplain was or may become a distribution hotspot of this species for the whole Natura 2000 area. Consequently, predicted changes with minor consequences did not influence the overall evaluation score. The individual scores were weighted according to the priority and the protection state of the respective species provided by the HBDs (value 4 for all species listed in Annex I or II of the HBDs) and the nature protection law effective in this region (Vienna Nature Conservation Ordinance and Lower Austrian Species Protection Ordinance, value 3, 2, and 1 for priority species, strictly protected, and protected species, respectively; **Figure 2**). The average score for each taxonomic group was calculated via the equation:

$$Average\ score\ per\ group\ =\ \frac{\sum(Ni \times Gi)}{\sum\ Gi}$$

Where Ni is the score and Gi is the weight of each species. For the comparison and evaluation of the different scenarios across all groups, only positive and negative effects were considered. Consequently, three cases were distinguished:

a) the scenario will have only negative effects on one or more groups (worst case scenario)
b) the scenario will have positive and negative effects on different groups
c) the scenario will have only positive effects on one or more groups (best case scenario)

In the case of (b), the magnitude and spatial extend of the potential negative effects as well as potential compensation measures to reduce the negative effects were included in the assessment. To give an example, the increase in water tables in the S3 and S20–80 scenarios were predicted to lead to a loss of isolated shallow water bodies, the dominant habitats for amphibian larvae. However, this negative effect can be easily compensated at low costs as the increase in water tables offers the chance for the creation of new stagnant water bodies in former terrestrial areas, eventually induced by small-scale excavation measures.

Combination of WFD and HBDs Assessments

We used a modification of the evaluation scheme of the HBDs (**Table 2**) to combine the assessments of the two approaches into one recommendation for the water management. Here, scores were assigned to each scenario for both WFD and HBDs, considering whether the overall aim of the Directives could potentially be achieved by the scenario (good ecological state for WFD, average good conservation state for HBDs) and/or a further improvement or deterioration of the *status quo* was likely. For the average scores of the HBDs assessment, taxonomic group scores were weighted (4 for amphibians, reptiles, and fish and 1 for water birds due to their larger areal distribution).

The scores ranged from 1 (aims fully achieved and further improvement) to 5 (aims not achieved and further deterioration) corresponding to the HBDs scores in **Table 2**. For the combination, both assessment schemes had equal importance, thus, no weights were assigned. We only used the assessment of the upstream part of the floodplain located in Vienna in this final step because of the higher proportion of floodplain area represented and the low discriminative power of the assessment in Lower Austria (see scores in **Table 4**).

RESULTS

FI Assessment According to WFD Principles

The results of the modeling based on the taxonomic groups relevant for the FI (Chovanec et al., 2005; Funk et al., 2017) indicated that the scenario S20–80 had the potential to restore the "good ecological status" of the floodplain according to **Table 1**. S20–80 was the only scenario, where a significant proportion of H1 habitats (eupotamon) was predicted (**Figure 3**). However, even this scenario deviated considerably in both quantity and quality of floodplain habitats from the historic reference state. S3 was predicted to achieve a moderate to good ecological state (H1 habitats present, but covering only a very small part of the floodplain), while S0 would still achieve a moderate state (all habitats present except H1). H5 habitats were present in the floodplain, but could not be displayed by the model due to their extremely low areal coverage and their temporary character. The spatial analyses of the different water bodies (see **Supplementary Figure S1** for examples) revealed obvious differences in impact strength on the potential development of habitat types for water bodies of the main floodplain channel connected via surface discharge and isolated water bodies connected only via the groundwater aquifer (**Figure 4**). While directly impacted water bodies showed a clear tendency toward more dynamic conditions in the S20–80 scenario, indicating the potential to foster the rheophilic community, isolated water bodies were predicted to maintain their character and typical stagnotopic

TABLE 2 | Evaluation scheme for the HBDs and nature protection approach for each species based on the respective conservation status and the predicted improvement or deterioration of this status.

Scores	Conservation status	Change of current situation	Examples
1 (best)	The aim of at least a good conservation status is reached	AND the current situation is improved	A species with status A/I gains in WUAs A species with status C/III (or B/II) will reach status B/II (or A/I)
2	The aim of at least a good conservation status is reached	No change	Species with status A/I and B/II maintain their status
3	The aim of at least a good conservation status is NOT reached	BUT the current situation is improved	A species with status C/III will gain more WUAs, but not enough to improve its state to B/II
4	The aim of at least a good conservation status is NOT reached	No change	Species with state C/III maintain their state
5 (worst)	The aim of at least a good conservation status is NOT reached	AND the current situation is deteriorated	Species with state A/I or B/II will be reduced to state C/III

community across all scenarios, corresponding to the results of the HBDs approach.

HBDs and Nature Protection Approach

The HBDs and nature protection approach showed distinct trade-offs between the rheophilic community, such as, e.g., rheophilic fish and water birds dependent on erosion/deposition processes, and the stagnophilic community, such as, e.g., amphibians, bird species of stagnant water bodies, the pond turtle, and stagnophilic fish (**Figure 5**).

In general, fish were positively affected by both S3 and S20–80 scenarios due to the creation of new aquatic habitats and the increased connectivity among existing habitats (**Figure 5**). Species, which clearly gained from the enhanced water supply according to the models, were rheophilic species like *Aspius aspius* (asp), *Barbus barbus* (barbel), and *Romanogobio vladykovi* (white-finned gudgeon), which had already shown to benefit from an increased re-connection with the Danube in other restoration projects (Hein et al., 2016). However, comparisons with the estimated historical species distributions revealed that even the S20–80 scenario did not support the creation of conditions necessary for endangered, strongly rheophilic Danube fish. The scenario S0 had mostly negative effects (e.g., on species dependent on large permanent and connected water bodies like *Aspius aspius*) and only positive effects on stagnotopic fish typical for backwaters with high siltation rates (e.g., *Misgurnus fossilis*, weatherfish).

The effects of the different scenarios on the amphibians were diverse. For most species, significant losses of available habitat area were predicted for the S0 scenario due to the increasing terrestrialisation of the floodplain and the drying-out of small temporary ponds (**Figure 5**). The S3 and S20–80 scenarios were expected to initiate flowing conditions in some of the current amphibian habitats and to increase the connectivity with the main side arm colonized by fish, thereby increasing the predation pressure on tadpoles. However, these scenarios showed the potential to create new, isolated and temporary water bodies in margin areas of the floodplain due to the improved water supply. Besides, compensation measures were expected to reduce potential habitat losses through the construction of new isolated habitats. Thus, most amphibian species were positively affected by S3 and S20–80 depending on their respective sensitivity to water current and predator pressure as well as on their actual occurrence.

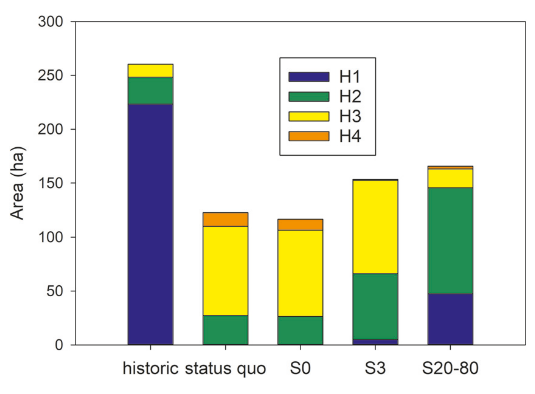

FIGURE 3 | Quantitative representation (area in ha) of the four different habitat types (H1–H4) defined under the FI according to Chovanec et al. (2005) for the four different scenarios as well as the historic state. H5 habitats were present, but could not be displayed by the model due to their low areal coverage.

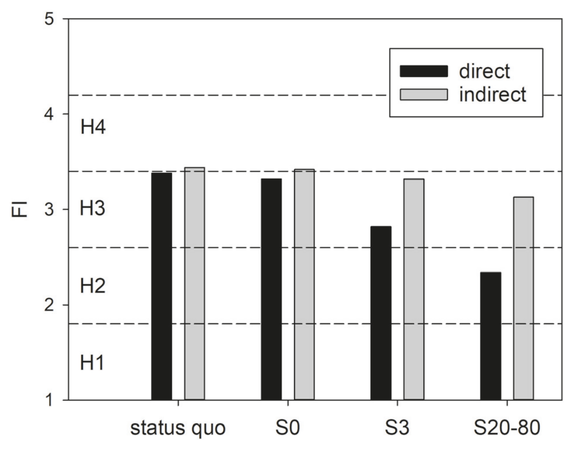

FIGURE 4 | Mean predicted value of the FI (habitat types H1-H5 according to Chovanec et al., 2005 are marked in the graph) in water bodies directly impacted by the respective restoration measure via surface discharge (direct) and indirectly due to increase in groundwater levels (indirect).

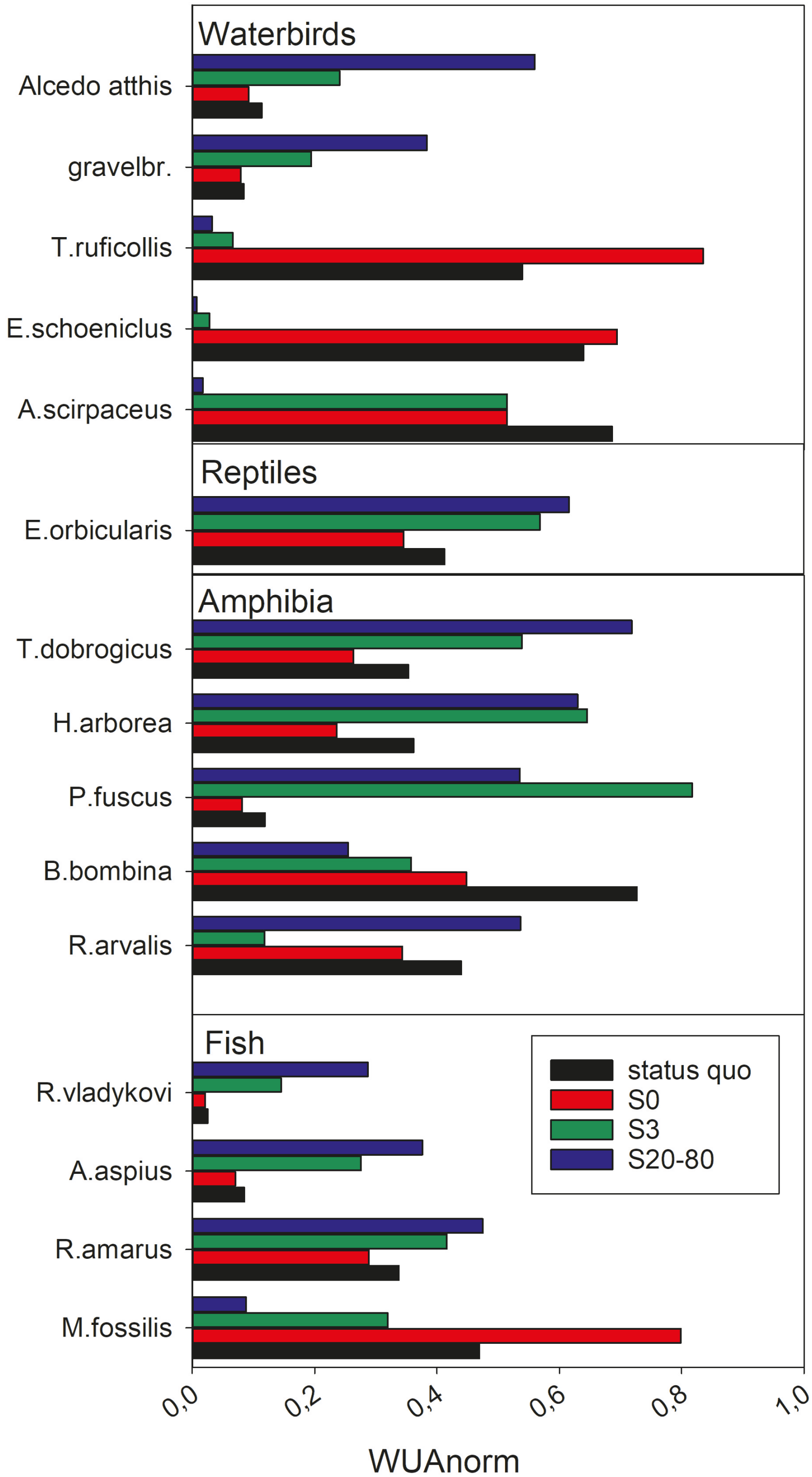

FIGURE 5 | Summarized normalized WUA values for selected species protected by the HBDs for the three scenarios and the modeled *status quo*. *Alcedo atthis* (kingfisher), gravelbr.: gravelbreeding water bird species (common sandpiper, *Actitis hypoleucos* and little ringed plover, *Charadrius dubius*), *Tachybaptus ruficollis* (little grebe), *Emberiza schoeniclus* (reed bunting), *Acrocephalus scirpaceus* (reed-warbler), *Emys orbicularis* (European pond turtle), *Triturus dobrogicus* (Danube crested newt), *Hyla arborea* (European tree frog), *Pelobates fuscus* (common Eurasian spadefoot toad), *Bombina bombina* (fire bellied toad), *Rana arvalis* (moor frog), *Romanogobio vlaycovi* (white-finned gudgeon), *Aspius aspius* (asp), *Rhodeus amarus* (European bitterling), *Misgurnus fossilis* (weatherfish). Only species protected under HBDs are displayed.

The S0 model revealed declining water tables in habitats for *Emys orbicularis* (pond turtle), which already had a low conservation status in the floodplain (**Figure 5**). Thus, the S0 scenario was predicted to decrease the habitat suitability further, while S3 and S20–80 showed a high potential of improving the situation due to the increased water supply and stabilization of water levels.

Regarding the water birds, a strong trade-off between species typical for isolated, macrophyte-rich water bodies dominated by siltation (Palaeopotamon) and species typical for dynamic water bodies (dependent on erosion patterns) was visible (**Figure 5**). An increase of habitat area in the S0 scenario was predicted especially for species which nest in emergent vegetation like extensive old reed belts (e.g., *Ixobrychus minutus*). In contrast, species breeding in young and dynamic reed zones benefited more from the increased water velocities in S20–80 (e.g., *Acrocephalus arundinaceus*). The S20–80 scenario showed positive effects due to the creation of local erosion zones, such as, e.g., gravel bars and erosion banks (*Actitis hypoleucos* and *Alcedo atthis*).

The grading of the scenarios for each species did not only consider the gains or losses in WUAs relative to the actual distribution (i.e., if losses occurred in key distribution areas or not), but also the chance for immigration from the surroundings (e.g., from other floodplains in the National Park in Lower Austria), the possibility of compensation measures (e.g.,excavations or constructions of dams to create/protect isolated water bodies) as well as experiences from other restoration projects within this area (Hein et al., 2016). Furthermore, the division into two different Natura 2000 sites with different areal extensions of the floodplain resulted in quite different scores for the two floodplain parts (**Table 3**). In Vienna, the Lower Lobau covers not only more than 50% of the Natura 2000 area there, it also represents the most valuable part, as the rest of the Natura 2000 site is surrounded by dense settlements and, thus, is heavily degraded. In contrast, the downstream section of the Lower Lobau situated in Lower Austria is only a small part of the much larger and less degraded national park and Natura 2000 area "Danube wetlands," which will buffer most of the predicted restoration effects (**Figure 1**). Consequently, only the grading for the Viennese part yielded differences among the scenarios (**Table 3**). Overall, the differences between the restoration scenarios S3 and S20–80 were usually small, because gaining and losing species partly outweighed each other. While S20–80 achieved better scores for fish and water birds due to the increase in water area and connectivity, the S3 scenario ranked higher for amphibians. The S0 scenario was identified as the worst-case scenario for all groups due to the continued drying-out of the floodplain and the low potential of compensating these water supply deficits.

Combined Assessment of the Scenarios

Considering the low predicted occurrence of H1 habitats and the still high deviation from the historic reference state even in the S20–80 scenario, we decided for the combined assessment that S20–80 only partly accomplished the WFD aim to establish a good ecological state in the floodplain, while S3 and S0 failed (**Table 4**). This was done to avoid over-estimating the subtle positive effects of an increased water supply or a partial re-connection by the WFD assessment compared to the much stricter HBDs assessment.

TABLE 3 | Overall scores per group for the different scenarios, based on both HBDs species and species protected by nature conservation laws and divided between the upstream part in Vienna and the downstream part in Lower Austria.

	Vienna			Lower Austria		
	S0	S3	S20–80	S0	S3	S20–80
Fish	2.8	2.5	1.8	2.9	2.9	2.3
Reptiles	5.0	1.0	1.0	2.0	2.0	2.0
Amphibians	5.0	2.0	2.3	2.4	2.4	2.4
Water birds	2.6	2.2	1.8	1.2	1.2	1.2

Overall, the S0 scenario scored worst in both assessment schemes, whereby the affects were assumed to be less severe in the WFD assessment as the FI did not predict huge changes in the current distribution of habitat types (**Table 4**). Regarding the other two scenarios, the WFD assessment showed a clear preference for S20–80. This scenario also scored slightly better in the HBDs assessment, which is why S20–80 was identified as the best ecological scenario for the floodplain.

DISCUSSION

Comparison of the Two Assessment Approaches

The FI approach corresponding to the WFD principles represents a relatively fast whole-system aggregated multi-species approach for riverine species, which provides a target vision for restoration aims and, thus, facilitates an effective evaluation and clear ranking of the scenarios (Jungwirth et al., 2002). It helps to identify deficits in comparison to a defined reference state and reveals the potential of different management scenarios to reverse the current development and restore the original floodplain conditions similar to the WFD assessment (Janauer et al., 2015). However, one major drawback of the FI approach is the rather generous definition of the good ecological state as suggested by Chovanec et al. (2005). This allows to assign the good ecological state for the floodplain, if H1 habitats (eupotamon) are just present, but not dominating, without providing a threshold for a "significant deviation" from the reference state. Here, we suggest the definition of a maximum deviation from the reference state in H1 habitat occurrence (e.g., at least 15% of the original coverage of H1 habitats reached; **Table 1**) as target for the good ecological state, as it is also often done for other WFD indicators (Birk et al., 2013). Furthermore, the FI approach does currently neither include the aquatic vegetation nor terrestrial species, which are at least temporarily associated with water bodies, such as e.g., water birds, and could provide a more holistic representation of the ecological status. Including those groups would strengthen the explanatory power of the assessment further and also improve the comparability of the FI with the HBDs approach (Janauer et al., 2015). The calculation of the FI is based on a multitude of

TABLE 4 | Combined evaluation of the different scenarios for the floodplain Lobau based on the WFD and HBDs assessments of the floodplain area located in Vienna.

Scenario	Assessment	Aim reached	Probable development	Score
S0	WFD	No	No change/slight deterioration: further loss of aquatic areas highly probable, but distribution of habitat types not affected	4(−5)
	HBD	No	No change/slight deterioration: Loss of habitats for reptiles and amphibians, but no changes for fish and water birds	4.1
S3	WFD	No	No change/slight improvement: increase in water supply will maintain existing habitats; short flowing sections (H1) may support colonization by rheophilic macrozoobenthos	3(−4)
	HBD	Partly	Improvement for existing species: increase in water levels will create new habitats for amphibians and reptiles and support eurytopic fish and water birds	1.9
S20–80	WFD	Partly	Improvement: Establishment of H1 habitats for rheophilic species, but not for strongly rheophilic Danube fish; H1 still underrepresented compared to historic reference state	2
	HBD	Partly	Improvement for existing species: Fish and water birds supported, creation of new amphibian habitats	1.7

Aims were defined as the establishment or maintenance of the good ecological state for the WFD (based on the Floodplain Index FI) and the establishment or maintenance of an average good conservation state for fish, amphibians, reptiles, and water birds according to the HBDs. Colors mark the best (green) and worst (red) compromise solution.

species showing the full spectrum of habitat preferences and does not originally allow any omissions as, otherwise, the assessment would become strongly biased. However, if information is not available for all species of the FI, we suggest to use a balanced mixture of rheophilic and limnophilic species, such as, e.g., only the macroinvertebrate community or a combination of fish and amphibian species. Finally, the definition of a reference state may present a problem in heavily modified floodplains in urbanized areas, where the reversibility toward pristine conditions has been long-lost (Jungwirth et al., 2002).

In contrast to the FI/WFD assessment, the HBDs represent a single-species approach, which does not aim at one desirable scenario for the entire floodplain, but focuses on the conservation status of individual species (Janauer et al., 2015). Consequently, this approach does not yield a clear ranking of scenarios, but rather reveals losers and winners for each individual scenario. It requires more individual decisions about the priority and weighing of species than the FI approach, but also provides more information on species level with a higher spatial resolution, including even terrestrial species. This facilitates the definition of compensation measures in the case of habitat losses under a certain scenario. In our case study, amphibian-rich side-arms were predicted to suffer a severe deterioration in the S20–80 scenario due to migration of eurytopic predatory fish, without offering habitat for other threatened species (e.g., rheophilic fish). Thus, for these water bodies, the construction of dams was planned, which facilitated the entry of seepage water, but prevented the migration of predators. One major drawback of the HBDs approach is the tendency to prefer already existing species over those, which originally inhabited the floodplain, but were significantly reduced or lost during the floodplain degradation, as those are often not listed in the standard data forms of the respective sites. This may lead stakeholders to protect existing values rather than try to restore pre-regulation conditions (Moss, 2007). Another drawback is that the HBDs only aim at species and habitats listed in the directives, but ignore others, which contribute to the biodiversity and ecosystem functioning of the floodplain. For example, macro-invertebrates are currently under-represented by the HBDs, despite their key role in floodplain food webs and matter cycling (Gladden and Smock, 1990). Finally, the different spatial scope of application of the directives may challenge the formulation of a compromise solution. While the holistic WFD-related FI approach (Chovanec et al., 2005) treats the river-floodplain system as an entity, the species-centered HBDs consider the regional context of the respective Natura 2000 area, which may not necessarily coincide with the floodplain area. This different spatial focus may not only result in divergent assessments between the directives, but it may also create problems, if the planned measures and the assessment do not cover the same area.

Despite the differences mentioned above, both approaches clearly ranked S0 as the worst-case scenario in our study. This was due to the predicted general loss of aquatic habitats in the future without any obvious gains for the aquatic flora and fauna and also due to the restricted options for compensation measures. Furthermore, both approaches revealed the low potential of restoring near-natural conditions in the floodplain even with the larger discharge of Danube water in the S20–80 scenario. Regarding the best-case scenario, the FI approach clearly ranked the scenario S20–80 best, while the HBDs approach showed almost similar values for S3 and S20–80. However, the differences between the two scenarios were subtle.

Decision Support Tools

A high proportion of floodplain areas along large European rivers are protected by the HBDs (Funk et al., 2019) and all are included in the WFD objectives. These floodplains are widely threatened by diverse human pressures, including hydromorphological alterations, and restoration and conservation measures are, thus, gaining in importance. In such human altered river-floodplain systems, the achievement of the targets of the WFD and the HBDs requires a detailed planning of different, ecologically, commercially, and socially acceptable compromise solutions (Rouquette et al., 2011). In our case study, for example, an ecologically significant full re-connection with the Danube was not considered as potential scenario due to economic and social restrictions (e.g., threatening the drinking water supply and nearby settlements due to increased groundwater levels and flooding events). Thus, the decision process has to focus on realistic and hydrologically feasible options.

Although both WFD and HBDs offer some flexibility of action to find an environmentally sound compromise solution in individual cases, there is currently no general regulation about how to deal with conflicts between the different directives (Janauer et al., 2015). This study presents an approach to consider the partly conflicting goals of the WFD and the HBDs as objectively and as transparently as possible by (a) basing the species-specific assessments on a combination of long-term monitoring data, spatial modeling, and expert judgment (**Figure 2** and **Supplementary Figure S1**) and (b) developing a comprehensible scoring scheme for the scenarios applicable throughout all species, groups, and floodplain levels (**Tables 1–4** and **Supplementary Table S2**). However, we are aware that our approach depends on the quality of the available hydrological and biological data and the long-term expertise on the floodplain's state and development, including information about the historic reference state. Thus, depending on the respective situation, adaptions may be necessary for both the definition of the desired future state of the floodplain as well as for the assessment of the current ecological state and deviations from this desired state. Besides, the applicability of a classification scheme via species-based habitat distributions has to be tested and alternative classifications schemes may have to be developed for other river-floodplain systems.

The trade-offs between the stagnotopic and rheotopic community protected under the HBDs (Sanon et al., 2012; Funk et al., 2013) as well as potential trade-offs between targets of the WFD and the HBDs have already been described in detail for different floodplain systems (Janauer et al., 2015). In this context, Species Distribution Models (SDMs) are gaining in importance for the evaluation of potential restoration measures related to both the WFD (e.g., Bennetsen et al., 2016; Zucchetta et al., 2016) and the HBDs (e.g., Funk et al., 2013). Using SDM predictions for a variety of species differing in their habitat requirements can help to predict winners and losers of different restoration and conservation scenarios and, thus, help to find solid compromise solutions (e.g., Funk et al., 2013; Heuner et al., 2016; Remm et al., 2019). However, as our case study shows, predictive models do not necessarily provide a clear result in relation to preference ranking of the scenarios, as the gain of habitats for certain species may be associated with habitat losses for others. Assigning a specific weight to individual species in the analysis is therefore an important step forward in the decision process, especially if the assessment shows both winners and losers. In this case, high weights for winners and low weights for losers would show a clear preference for the respective management measure, while the reverse would entail rejection. Another important item is the consideration of the status of the individual species according to the respective legislation on European and national level (De Nooij et al., 2005). We have developed a transparent decision tree based on the actual and the predicted distribution and conservation status of the relevant species according to the HBDs and regional nature protection laws to assess the significance of potential habitat changes for the state of the different species in the future. Within our approach, we are able to account for the importance of the species in the system, the likeliness that the status is deteriorated or improved due to different restoration measures, and the potential for compensation measures.

An SDM approach can also give river managers a first insight into which measures are feasible to achieve an improved ecological status as required by the WFD (Bennetsen et al., 2016). In our case study, we used SDMs to predict the potential impact of proposed restoration measures on the ecological status of the floodplain using the FI developed by Chovanec et al. (2005). The FI includes a direct comparison with the reference state and clearly ranks the scenarios according to their potential to reach the good ecological state. However, the WFD does not refer to single floodplain sections. Instead, a water body is defined as a whole "discrete and significant" section of a river. In our case, this refers to the whole remaining free flowing stretch of the Danube between Vienna and the national border to Slovakia, which constitutes the National park Donau-Auen (**Supplementary Figure S2**). Our study shows that the inclusion of this area into the analyses, as it was done for Lower Austria, buffered the impact of the different scenarios (compared to the Viennese part) and offered the opportunity for spatial compromises. Thus, habitat losses as well as gains in the Lower Lobau were mostly neglectable when considering the entire National Park. A more detailed spatial resolution of the FI based on SDMs, may help to identify local impacts better. Water bodies, which were located within the main water course and were dominated by a eurytopic community, for example, were expected to gain from a reconnection with the Danube due to the improved water supply and the increased range of flow conditions. In contrast, our spatial models revealed that valuable lentic and temporary water bodies outside the main water course should not be included in the reconnection scheme, but rather kept isolated from inflowing Danube water by local compensation measures, such as, e.g., protection dikes, to protect the stagnotopic community from increased predation (Schmidt-Mumm and Janauer, 2016; see **Supplementary Figure S1**). This would keep losses of valuable amphibian habitats small, without affecting the eurytopic community. Thereby, seemingly negative impacts on the large-scale can be relativized. Consequently, the combination of a large-scale re-connection scheme and local protection measures may improve the ecological status of the floodplain as well as increase the overall biodiversity, thereby meeting the aims of both EC WFD and EC HBDs in a well-balanced approach.

CONCLUSION

The combination of multiple-species and single-species approaches provides a solid basis for decision processes in floodplain restoration in accordance with the EC WFD, the EC HBDs, and local legislation. Further, we could show that the "business-as-usual" alternative (i.e., no implementation of any restoration measure) is the worst scenario and that restoration actions are required to preserve at least the existing aquatic and semi-aquatic habitats in such systems. Our case study demonstrates that a detailed spatial resolution of the effects of management measures offers the opportunity to protect isolated water bodies and restore lotic conditions at the same time in the case of trade-offs between stagnophilic and rheophilic species. Therefore, detailed spatial planning is an important next step in floodplain restoration to find the optimal combination of spatially distinct large- and small-scale measures to increase the habitat availability for all relevant species as well as the overall biodiversity (e.g., Maire et al., 2015; Heuner et al., 2016; Remm et al., 2019).

Apart from the ecological challenges addressed in this paper, the management and restoration of riverine floodplains usually concerns a variety of other economic and social demands, such as, e.g., food production, tourism, or flood protection. The development and application of a Decision Support System to equally consider all demands in a transparent and reproducible way has been widely acknowledged in river floodplain management, but requires both the assessment and the weighing of the individual demands in the most objective way (e.g., Rouquette et al., 2011; Sanon et al., 2012; Stepniewska and Sobczak, 2017; Richards et al., 2018; Stammel et al., 2020). Our study provides such an approach for the aims of the WFD and HBDs, based on objective criteria and decision trees, which can be integrated into such a Decision Support System to help finding the best-compromise solution for a more holistic and, thus, sustainable management of these highly complex river-floodplain systems.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

GW and AF were responsible for the manuscript outline, the graphs, and the writing. EF, EP, and DT contributed to the data analyses, the interpretation, and the collection of background information about nature protection states. TH contributed with revisions and comments. All authors have read and approved the submitted version.

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SUPPLEMENTARY MATERIAL

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Incorporating Established Conservation Networks into Freshwater Conservation Planning Results in More Workable Prioritizations

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Resources for addressing stream fish conservation issues are often limited and the stressors impacting fish continue to increase, so decision makers often rely on tools to prioritize locations for conservation actions. Because conservation networks already exist in many areas, incorporating these into the planning process can increase the ability of decision makers to carry out management actions. In this study we aim to identify priority areas within established networks to provide an approach which allows managers to focus efforts on the most valuable areas they control, while identifying areas outside of the network, which support species with minimal representation within the network, for acquisition or conservation partnerships. The goal of this approach is to prioritize sites to achieve high levels of species representation while also developing workable solutions. We applied a methodology incorporating established networks into a systematic conservation planning process for fish in temperate wadeable streams located in Missouri, USA. We compared how well species were represented in our approach with two commonly used alternatives: A blank slate approach which used the same systematic conservation planning technique but did not incorporate established networks, and a habitat integrity approach based solely on anthropogenic threat data. Relative to the blank slate approach, our approach required 210% more segments for representation of all species, and contained an average of 0.5 additional occurrences for the least well-represented species. Although the blank slate solution was more efficient in achieving species representation, 77% of segments in this solution were not already protected. This would likely pose a challenge for implementing conservation actions. Relative to habitat integrity-based priorities, our approach required only 38% of the number of stream segments to achieve representation of all species and contained an average of 5 additional occurrences of the least represented species, representing a substantial gain in representation. Incorporating established networks may allow managers to focus resources on areas with the greatest conservation value within established networks and to identify the most valuable areas complementary to the established networks, resulting in priorities which may be more actionable and effective than those developed by alternative approaches.

Keywords: fish, protected areas, conservation, stream, representation, freshwater, conservation planning

INTRODUCTION

Conservation networks are important for the protection of increasingly imperiled stream fish communities (Saunders et al., 2002; Abell et al., 2007; Nel et al., 2009b; Arthington et al., 2016; Hermoso et al., 2016; Thieme et al., 2016). Habitat degradation, invasive species, flow alteration and climate change are expected to contribute to future declines of stream fish (Dudgeon et al., 2006). Conservation plans are important for the protection of biodiversity from these threats and have been developed to protect the current suite of species or communities, often through reserves or protected areas (Saunders et al., 2002; Abell et al., 2007; Nel et al., 2011b; Arthington et al., 2016; Jones et al., 2016; Bicknell et al., 2017). Resources for the establishment and management of reserves and protected areas are often limited; therefore, it is important to make scientifically informed decisions to achieve the greatest conservation outcomes for aquatic biodiversity (Thieme et al., 2012; Hermoso et al., 2016; Maire et al., 2016).

Effective conservation planning depends on the consideration of both biodiversity and the amount of resources available for protection, management, and research to meet goals (Linke et al., 2011). Historically, many conservation efforts have been aimed at protecting sites with minimal levels of anthropogenic impacts either locally or in their watersheds (Pressey et al., 1993; Margules and Pressey, 2000). Conservation plans for freshwater ecosystems have more recently centered on the development of spatial networks supporting a targeted set of species or features. Because resources for conservation are often limited, these plans also try to minimize cost by focusing on the complementarity (combined ability of set of sites to represent a suite of biodiversity features) of selected sites (Nel et al., 2009b). A variety of strategies and tools have been developed for creating conservation plans that emphasize complementarity and have been applied to a range of conservation planning efforts (Moilanen et al., 2009; Linke et al., 2011).

In freshwater stream systems, systematic conservation planning tools often have been used to design conservation networks or develop sets of priorities without consideration of any established conservation networks (i.e., Blank slate approach; Sowa et al., 2007; Leathwick et al., 2010; Strecker et al., 2011; Stewart et al., 2017; VanCompernolle et al., 2019). However, conservation networks may already have been established (e.g., state and federal wildlife management areas, refuges, and parks), and decision makers sometimes lack the flexibility or resources to start with a blank slate to create new conservation networks or priority areas. The implementation of conservation plans can present substantial challenges to practitioners as the majority of published conservation assessments do not result in conservation actions (Knight et al., 2008). Incorporating established conservation networks into the conservation planning process is gaining popularity in freshwater systems (Nel et al., 2009a; Esselman and Allan, 2011; Esselman et al., 2012; Hermoso et al., 2015a; Grantham et al., 2016; Howard et al., 2018; Linke et al., 2019; Jézéquel et al., 2020), however comparisons of these approaches to other frameworks are limited. This study expands on previous efforts by evaluating how the results derived from a prioritization which accounts for established conservation networks compares to two alternative approaches, one which does not incorporate established conservation networks (Blank slate approach) and another which relies on habitat integrity rather than species representation (Human threat index approach). In areas where conservation networks have already been established, evaluation and prioritization techniques which account for already established conservation networks may constitute a more feasible approach, and increase the likelihood that the results will be put to use by decision-makers by allowing them to work within the constraints of existing infrastructure (Esselman and Allan, 2011).

Management of established conservation networks can benefit from the prioritization of sites both within and complementary to the network. Due to the large size of many networks, and the frequent presence of competing uses, many conservation networks cannot be entirely managed for the purpose of freshwater conservation. Identifying the most critical areas within the network can facilitate conservation by prioritizing the allocation of limited resources to the areas most likely to have the greatest returns for conservation (Iojaa et al., 2010; Watson et al., 2014; Maire et al., 2016). Prioritizing areas outside of the network is also important, particularly since species sometimes lack representation within established networks (Rodrigues et al., 2004; Nel et al., 2007; Hermoso et al., 2015b; Jenkins et al., 2015; Raghavan et al., 2016; Cooper et al., 2019). Conservation networks are sometimes expanded (Jenkins and Joppa, 2009), and targeting locations for expansion which complement already protected lands is a valuable way for rare and underrepresented species to gain protection (Nel et al., 2009a).

The primary aim of this study was to evaluate the performance of a freshwater conservation plan which incorporated established conservation networks into the planning process relative to two alternative approaches to conservation planning (Blank slate; Habitat integrity). The results of these comparisons can be used to aid decision-makers in selecting what may be the most appropriate approach to take in a given situation.

MATERIALS AND METHODS

Study Area and Data Sources

Wadeable stream segments (confluence to confluence sections), classified as 2nd−5th order and perennial, throughout Missouri, USA (Abbitt et al., 2004) were the focus of this research. The state of Missouri is comprised of three ecologically unique aquatic subregions: Central Plains, Ozarks, and Mississippi Alluvial Basin (MAB) (Sowa et al., 2007). The Central Plains is primarily composed of open grassland and agricultural land use (78% percent of landuse, Blodgett and Lea, 2005) with low gradient streams with high turbidity and fine silt and sand substrates. The Ozarks are primarily forested (51.4% percent of landuse, Blodgett and Lea, 2005), with high relief and rugged terrain resulting in streams with higher gradients with gravel, cobble, or bedrock as dominant channel substrates. The MAB is dominated by agriculture (83% percent of landuse, Blodgett and Lea, 2005) with low relief and streams are predominately low gradient, highly channelized, and have fine silt substrates. These aquatic subregions are subdivided into watersheds with shared physiographic characteristics, and are presumed to correspond to distinct fish communities (ecological drainage units, EDU; Sowa et al., 2007). The drainage unit boundaries were used to summarize species occurrences.

Prioritization was conducted with consideration of a network of traditional protected areas (TPA) in Missouri, USA. The TPA network was comprised of both public lands (e.g., state conservation areas, U.S. Fish and Wildlife Service Refuges, U.S. Forest Service Lands, and others), and private lands (e.g., Wetlands Reserve Program, The Nature Conservancy Preserves, Ozark Regional Land Trust, and others), which are managed with a primary purpose of wildlife conservation (Hoskins, 2005; Missouri Department of Conservation, 2005). In Missouri, there are 3,943 TPA units encompassing 13,183 km^2 (∼7% of the state's area) and 2,590 km (∼6.5%) of wadeable stream length (Abbitt et al., 2004; Figg, 2011).

Fish community data were provided by Missouri Department of Conservation and included data collected from wadeable streams from 1990 to 2011 having at least 0.5 h of sampling effort using seines and electrofishing. All 769 samples from 1990 to 1999 represented community sampling efforts by Missouri Department of Conservation; while all 1,107 from 2000 to 2011 were sampled using standard procedures (electrofishing and seining within a reach bounded by block nets) as part of the Resource Assessment and Monitoring (RAM) program (Fischer and Combes, 2003; Sievert et al., 2019; Paukert et al., 2020). Sites were selected for RAM sampling based on a stratified random approach, in which sites were randomly sampled within select drainages each year and the drainages being sampled were rotated on an annual basis (Fischer and Combes, 2003; Paukert et al., 2020). Additional occurrence locations of state listed species were included from the Missouri Natural Heritage Program database (651 records), which were collected between 1990 and 2011 from wadeable streams, were used as supplementary data for rare species (Sievert et al., 2019).

Twenty-seven environmental variables were used to predict the probability of species presence in each wadeable stream segment in Missouri. These included variables related to biogeography, stream features, local landscape, upstream landscape, and anthropogenic impacts to each confluence to confluence stream segment acquired from the Missouri Resource Assessment Partnership (Appendix 1 in **Supplementary Material**; Abbitt et al., 2004). These variables were selected based on known linkages to fish species distributions in Missouri and elsewhere (Sowa et al., 2007; Strecker et al., 2011). Multicollinearity was largely avoided in variable selection by only including variables with correlation coefficients <0.75 except in specific cases where collinear variables were both identified as being ecologically relevant to the species being modeled (Appendix 2 in **Supplementary Material**). These variables included forested, agricultural, and grassland watershed landuse, and local riparian intact percentage in the Plains; forested, and grassland watershed land use, and local intact riparian percentage in the Ozarks (Snyder et al., 2003; Allan, 2004; Nislow, 2005; Diana et al., 2006; Stewart et al., 2007; Marshall et al., 2008; Lange et al., 2014).

Quantifying Species Representation

Species distribution models were developed to determine species representation in each permanent, wadeable stream segment in Missouri. We developed four separate component models for each species with a minimum of 40 occurrences using commonly used distribution modeling approaches including multivariate adaptive regression splines [MARS], generalized additive models [GAM], boosted regression trees [BRT], and random forest models [RFM]. There were not enough stream segments sampled (36) to generate distribution models for species in the MAB subregion. Because of both temporal variability in species abundance and the differences in habitat volume between small and large streams we conservatively used presence absence rather than abundance or other population metrics as our response variable for species distribution modeling. A suite of 27 environmental variables commonly used in freshwater fish distribution modeling were used as predictors (Appendix 1 in **Supplementary Material**). Distribution models were developed using R statistical software with the "earth" package (MARS; Milborrow, 2014), "gam" package (GAM; Hastie, 2014), "gbm" package (BRT; Ridgeway, 2013), and "randomForest" package (RFM; Liaw and Wiener, 2002). Models were developed using randomly selected subsets of 70% of the species occurrence data for training with the remaining 30% used for model evaluation. Each component model was evaluated using three metrics; area under the receiver operator characteristic (AUC), calculated using the "ROCR" package (Sing et al., 2013), model bias (Difference between predicted and observed occurrences expressed as a percentage), and model fit (Mean absolute error (MAE) of a calibration curve with 10% probability of occurrence bins). We created our final distribution models using an ensemble model based on the average predicted probability of species occurrence of all component models which met our predetermined minimum evaluation standards: AUC $\geq$ 0.6, bias of $\pm$ 25%, and MAE of $\leq$ 0.125.

Species representation within and complementary to Missouri's TPA network was assessed by determining the number of stream segments a species was predicted to occupy within each conservation network. Species occupancy was accounted for in two ways. For species with models meeting the modeling requirements listed above, the predicted probabilities of occurrence were used. Because rare and vulnerable species are often some of the most important targets of conservation action it was important that known occurrence locations and watersheds they are known to inhabit be included for the development of conservation priorities. This approach gives high priority to sites with known occurrences of rare species. Although this approach likely elevates the prioritization values for known sites above unknown sites, in an applied study this is an approach which may appeal to managers who wish to invest resources in conserving rare species in areas where they are known to occur. For species without acceptable models, an occurrence probability of 1 was assigned to stream segments where the species had been collected, while the proportion of sites a species occurred at within each ecological drainage unit was assigned to all other stream segments (Sievert et al., 2019). This allowed known occurrences of species to be included in the planning process for species which could not be modeled and allowed a low level of potential representation to be included in watersheds they were known to inhabit. The predicted number of occupied stream segments within Missouri's TPA network was calculated for each species by summing the probabilities of occurrence for all stream segments within the network (e.g., Species A has probabilities of occurrence at four sites of 0.75, 0, 0.75, and 0.25; summing these probabilities of occurrence predicts two occurrences for this species across the four sites).

Determining Conservation Value

Stream segments were prioritized based on a measure of relative conservation value using the conservation planning software, Zonation, version 3.1, following an approach which will be referred to as Freshwater Conservation Network Prioritization (FCNP; **Figure 1**). Conservation value rankings were based on species representation, weighted by species vulnerability, while accounting for upstream watershed integrity, and stratifying removal based on established conservation network (more details on each of these components in following paragraphs). Conservation values were calculated via core-area Zonation which iteratively removes stream segments while minimizing marginal loss to conservation value of the remaining network until all segments have been removed (Moilanen et al., 2012).

Representation was weighted by species vulnerability to emphasize the selection of areas important for species in need of conservation. By implementing the weighting functionality of Zonation more vulnerable species gain additional representation at high priority levels proportional to their weight (a species with a weight of 2 will have occurrences retained at approximately twice the rate as would be retained if they had a weight of 1). Vulnerability weights ranged from 1 (lowest vulnerability score) to 2 (highest vulnerability score) based on scaled vulnerability scores {Weight = 1+(Species Vulnerability Score-Minimum Vulnerability Score)/(Maximum Vulnerability Score-Minimum Vulnerability Score)} from Sievert et al. (2016). These scores were taken from an assessment of a species vulnerability to habitat degradation, warming stream temperatures, and alterations to the flow regime while also considering a species dispersal ability, range size, rarity, and range-wide fragmentation (Sievert et al., 2016). By incorporating species weights based on their vulnerability, Zonation software emphasized the prioritization of sites with occurrences of highly weighted species retaining a proportionally larger percentage of those species' distributions at a given priority level.

The ability of species to persist was accounted for both through the predictions of distribution models of suitable habitat and by encouraging the protection of upstream watersheds in the prioritization process. To emphasize the protection of the upstream watershed for sensitive species we utilized a function of Zonation, the Neighborhood Quality Penalty, which penalizes the removal of upstream areas from a prioritization for species who are sensitive to upstream habitat degradation (Moilanen et al., 2008; Figure 2). Species-specific penalty curves were developed to account for the potential effect of habitat degradation of upstream segments on the local stream fish community. Penalty curves were created to represent the loss of value to downstream segments when an upstream segment was removed from the solution, potentially allowing the upstream watershed to become degraded. These penalty curves are based on observed decreases in species occurrence rates as levels of anthropogenic land use increase, where a sensitive species experiences a decrease in occurrence rates in areas with high levels of anthropogenic land use and tolerant species have stable occurrence rates across a range of anthropogenic land use. First each site was classified into one of three bins covering equal ranges of anthropogenic land use (Agricultural and Urban) in the watershed (Low 0–33%; Medium >33–66%; and High >66%; **Figure 2**). Next the occurrence rate for each species (with a minimum of 10 occurrences) was calculated for each habitat class within a species range by dividing the number of sites a species occurred at by the total number of sampled sites within that species range (**Figure 2**). For those rare species having <10 occurrences no penalty curves could be created, so no penalties were applied. Species ranges were defined as all sites within ecological drainage units where a species had at least one occurrence (Sowa et al., 2007). The relative biological value of each class, for each species, was determined by dividing the occurrence rate of each class by the occurrence rate of the low degradation class which served as a baseline (**Figure 2**). This identified the species that experienced declines in occurrence rates in the presence of anthropogenic habitat use. In order to create discrete penalty curves these values were rounded to the nearest value of 1 (no change in relative biological value), 0.66 (loss of 1/3 relative biological value), or 0.33 (loss of 2/3 relative biological value; **Figure 2**). The biological value cutoffs were determined by expert knowledge as suggested by Moilanen et al. (2008). Biological value was never allowed to be rounded below 0.33 in order to maintain some level of local value no matter how much of a segments upstream watershed was given a lower prioritization. The relative biological value for each species was calculated at each of the three habitat classes and plotted against

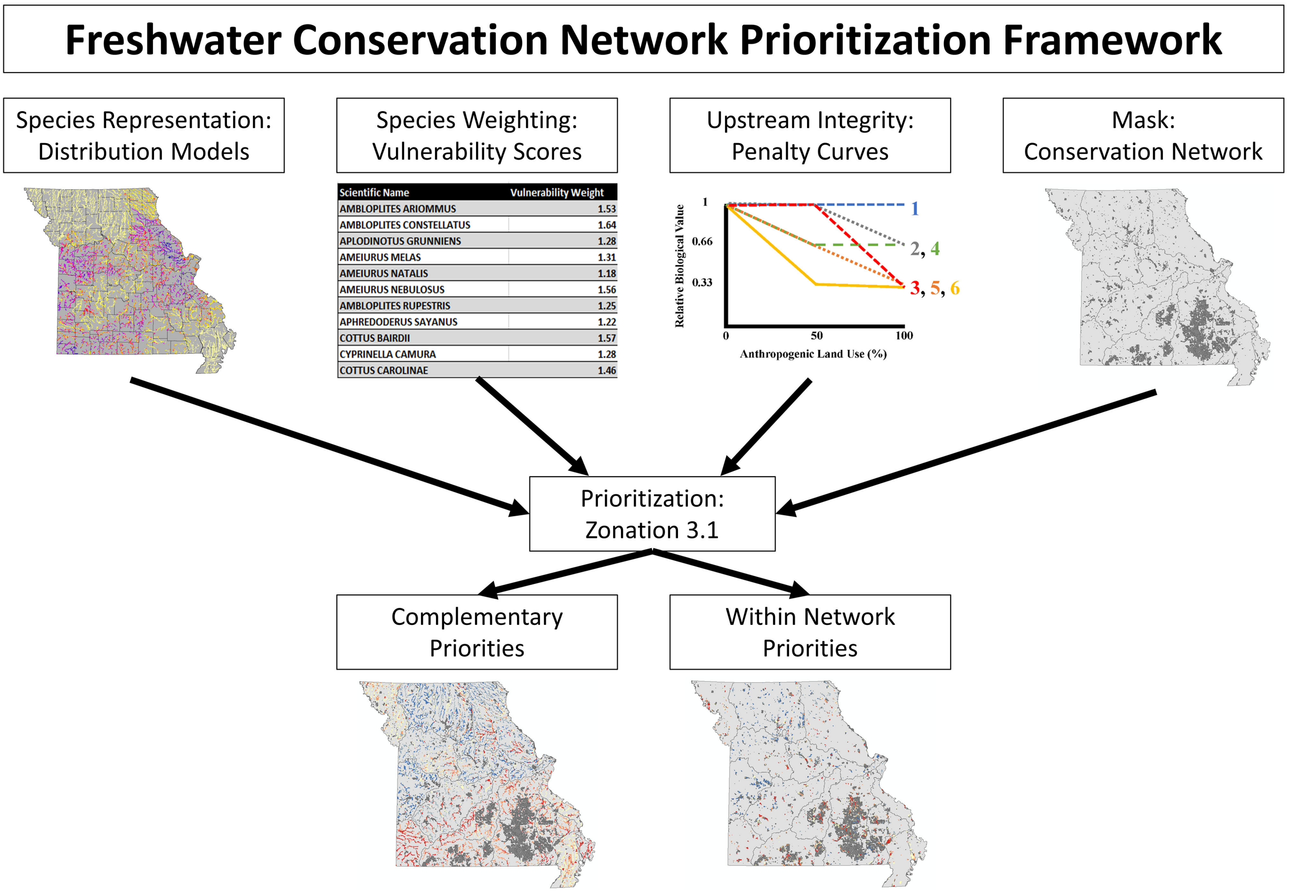

FIGURE 1 | Schematic illustrating the Freshwater Conservation Network Prioritization framework. The top row illustrates the inputs which are fed into the conservation planning software, while the bottom row displays the results which are obtained.

anthropogenic land use percent. Following the calculations above each species values correspond directly with one of the 6 discrete penalty curves (**Figure 2** [procedure], Appendix 3 in **Supplementary Material** [penalty curve assignments]). The relative biological value of the high anthropogenic habitat class was not allowed to exceed that of the medium anthropogenic class, when this occurred the value of the medium class was retained for the high class for purposes of assigning the correct penalty curve. These curves quantify species potential sensitivity to upstream habitat degradation by representing the relative change in the biological value of a stream segment based on the remaining proportion of its upstream watershed.

The established conservation network was used to stratify prioritization based on whether a segment is within or outside (complementary) of the protected area network. This was accomplished with the use of the removal mask feature of Zonation which constrained the initial removal to segments outside of the conservation network, once all complementary segments (segments outside of the network) were prioritized (removed); prioritization was allowed to proceed within the network. This creates a set of priorities in which the streams outside the network are ranked based on how well they complement what is represented within the network, while the streams within the network highlight the most and least valuable opportunities for conservation within protected areas.

Comparing Alternative Prioritization Methods

In addition to prioritization with the FCNP, we also conducted prioritizations using a blank slate approach which did not incorporate conservation networks into the planning process and used a set of priorities based on habitat integrity rather than species representation. The blank slate approach used all of the same inputs and settings as the FCNP except it did not use the masking feature which stratifies prioritization based on conservation network status. This created a prioritization where all stream segments are given equal consideration (no differentiation based on conservation network status) in prioritization. We also developed a third set of priorities based on human threat index (HTI) scores, which quantify stream health based on a suite of landscape level and local stressors where low values represent relatively low risk of degradation

Step 1: Habitat Classes

All sites are classified based on percent anthropogenic land use in watershed.

Low (0-33%)	Medium (>33-66%)	High (>66%)

Step 2: Occurrence Rates

The occurrence rate for each species is calculated, within each species range, for each of the habitat classes.

Low Occ. Rate (Baseline)	Medium Occ. Rate	High Occ. Rate

Step 3: Relative Biological Value

Relative biological value is calculated for each class, for each species, by dividing each occurrence rate by the low occurrence rate (Baseline). Round to nearest of 1, 0.66, or 0.33.

Low /Baseline	Medium/Baseline	High/Baseline

Step 4: Penalty Curves

Assign each species to the penalty curve which corresponds to the correct relative biological values for each class.

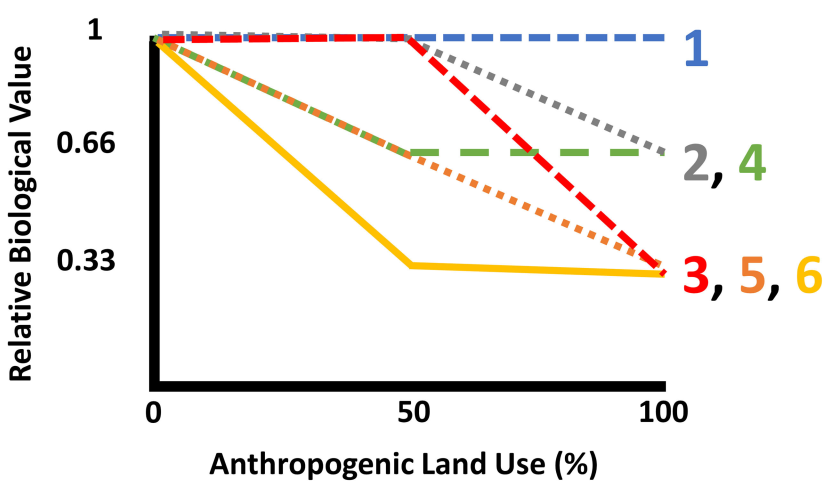

FIGURE 2 | Framework used for developing upstream habitat integrity penalty curves. The penalty curve associated with each species can be found in Appendix 3 in **Supplementary Material**.

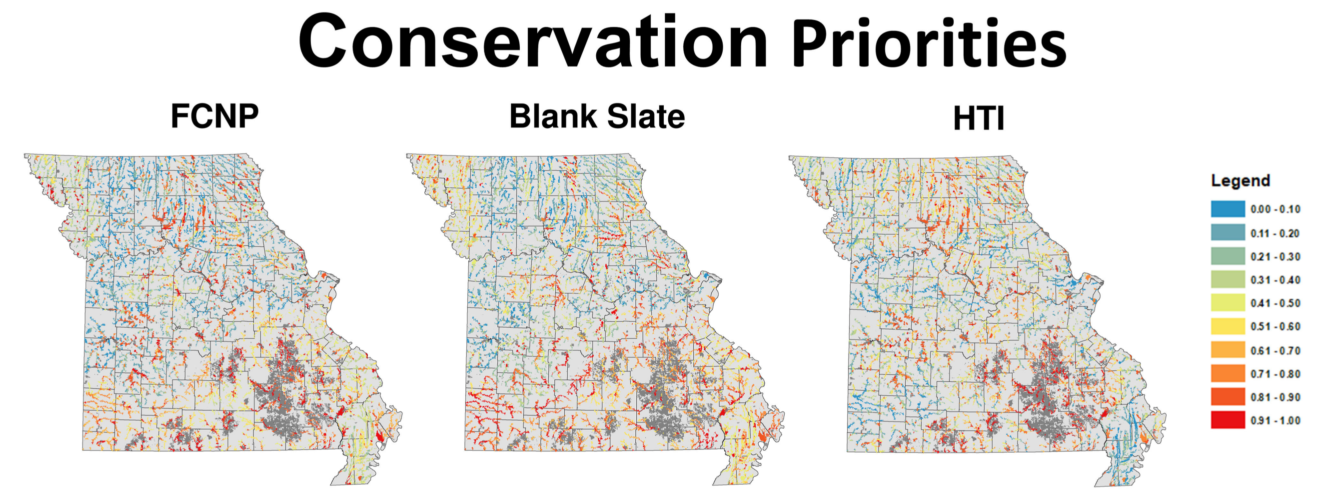

FIGURE 3 | Conservation priority scores for all wadeable streams in Missouri USA for each of the three approaches used in this research. Scores range from 0 (least valuable) to 1 (most valuable). FCNP, Freshwater Conservation Network Prioritization, HTI, Human Threat Index.

and high values represent high risk of habitat degradation (Sowa et al., 2007). To create our HTI prioritization, segments were ranked both within and complementary to the conservation network from lowest to highest HTI score. HTI priorities were developed with consideration of the established network by ranking from lowest HTI (highest conservation value) to highest HTI (lowest conservation value) within and complementary to the established network. The efficiency, or difference in representation of species, achieved by the alternative approaches was compared to the FCNP results to determine how well the framework performed. Additional metrics including the number of unrepresented species, the minimum species representation, and the average level of species representation were calculated based on the sum or average of the predicted occurrences for all segments at or above each priority level for each prioritization set (FCNP, HTI, and Blank slate). The proportion of species having greater representation based on the FCNP framework vs. the HTI and the blank slate approaches was calculated at two levels; high priority within the network (top 10% of segments) and high priority complementary areas (entire conservation network and top 10% of complementary segments). For the blank slate approach, we also calculated the number of unprotected stream segments to be added to create a new network of the same size as the established network. This allowed us to note the potential additional resources necessary to implement priorities with a blank slate approach.

RESULTS

Quantifying Species Representation

Species distribution models were developed for 40 species in the Plains subregion, and 68 in the Ozarks subregion (Appendices 1, 3, 4 in **Supplementary Material**). All species with >40 occurrences, except Black Bullhead (*Ameiurus melas)* and Green Sunfish (*Lepomis cyanellus)* (both Plains models), had at least one of the four ensemble models meet minimum evaluation standards and were therefore represented via a species distribution model (Appendix 4 in **Supplementary Material**). All remaining species representations (44, 64, and 50 species for the Plains, Ozarks, and MAB respectively) had <40 occurrences within a subregion and were therefore classified based on occurrence locations and frequency of occurrence. More detailed information regarding the species distribution models can be found in Appendices 1 and 2 in **Supplementary Material** and in Sievert et al. (2019). All species were predicted to occur in at least 1 stream segment within the TPA network with seven species expected to be found in <10 stream segments (out of 4,010 segments). Ninety species were predicted to occupy >100 stream segments in the TPA network.

Determining Conservation Value

Statewide priorities developed using the FCNP framework for the TPA network revealed that high priority segments were distributed across the state but were most commonly found in areas with unique and diverse fish assemblages (Sievert et al., 2017, Appendix 5 in **Supplementary Material**). The greatest concentration of high-value complementary areas tends to be in the southwestern portion of the state, which has several unique species assemblages and a smaller proportion of the landscape within the TPA network. High priority areas within the TPA network tended to occur throughout the Ozarks where there are relatively unique assemblages among catchments, and also in species-rich basins in the Plains. The blank slate priorities mirrored the general patterns of the FCNP framework priorities with high-value areas concentrated in the Ozarks and scattered pockets of high-value areas in the Plains (**Figure 3**). High priority areas identified based on habitat alone (i.e., HTI) were concentrated in the central Ozarks similar to FCNP priorities, however the southwestern portion of the state had low values based on habitat integrity and high values based on FCNP,

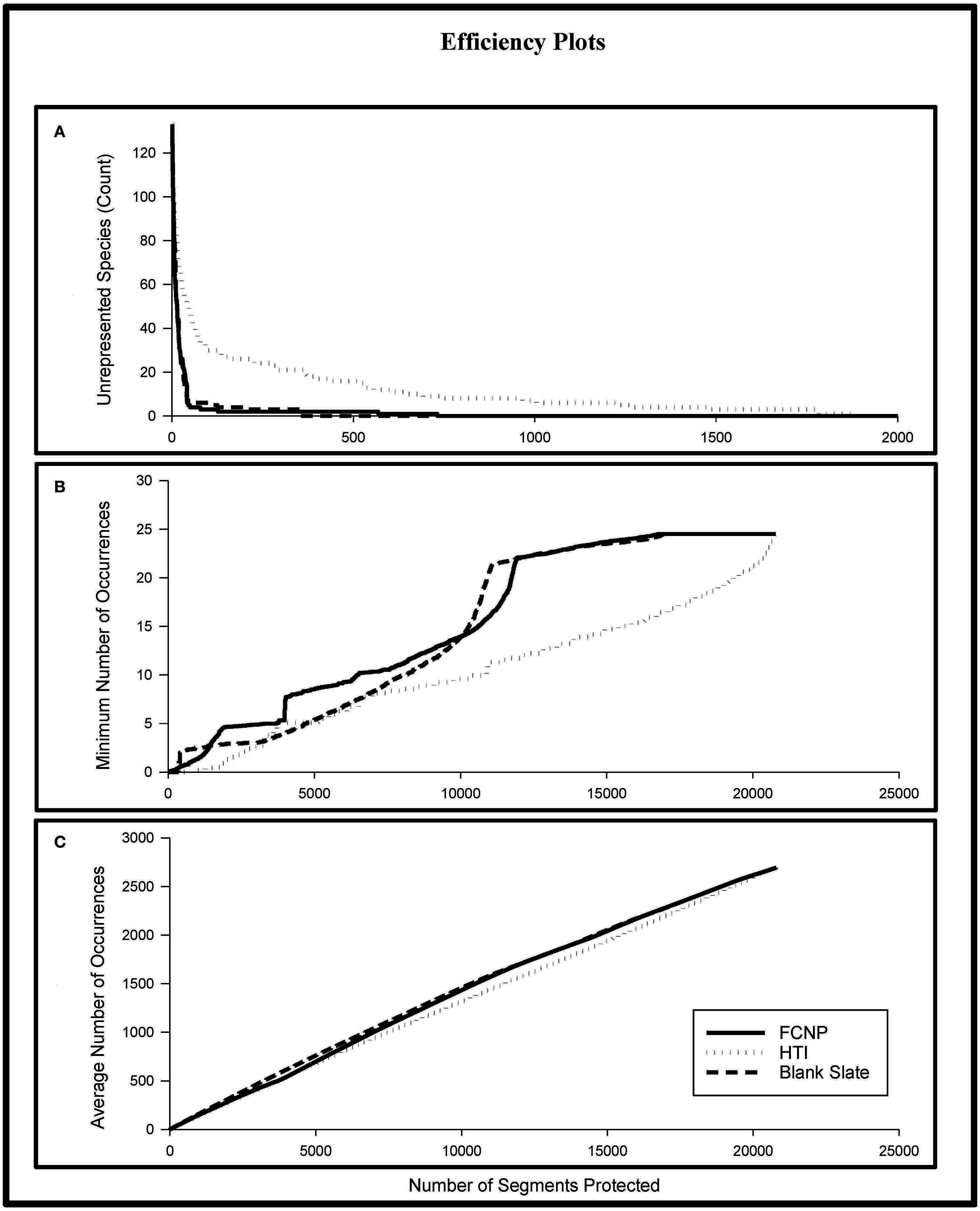

FIGURE 4 | Differences in species representation for the FCNP, HTI, and Blank Slate prioritization approaches. Moving from left to right across the x-axis represents increasing levels of cumulative protection from only the highest priority stream segment (leftmost) to all stream segments (rightmost). **(A)** shows the number of species unrepresented; **(B)** shows the minimum level of representation; **(C)** shows the average level of representation. The steep increase in the minimum number of occurrences in **(B)** for the FCNP is due to the inclusion of high value complementary areas outside of the established network once all segments within the network have been included in the solution. FCNP, Freshwater Conservation Network Prioritization; HTI, Human Threat Index.

the MAB had very low values based on habitat integrity and intermediate to high values based on FCNP, and values in the Plains tended to be slightly higher according to HTI than FCNP (**Figure 3**).

Comparing Alternative Prioritization Methods

Efficiency analysis revealed substantial gaps in species representation between FCNP priorities and the HTI alternative prioritization. The number of segments to achieve representation of all species was ∼2.6 times greater using the HTI approach compared to the FCNP approach (**Figure 4A**). The FCNP approach yielded a maximum of 51 more species represented at the same priority level as the HTI approach (**Figure 4A**; 133 species included in analysis). Across all priorities, the FCNP approach averaged five more occurrences for the species with the lowest level of representation (**Figure 4B**). The average number of additional occurrences, based on priorities established using the FCNP framework, for all species across all priorities, was 67 (**Figure 4C**). The majority of species (71%) achieved higher levels of representation based on FCNP priorities for the top 10% of segments within the conservation network and the entire network plus the top 10% of complementary segments.

The blank slate approach will always represent the maximum efficiency in species representation (based on the inputs to the prioritization) because of the lack of constraint over the areas selected for inclusion in the solution, however that lack of constraint may lead to the selection of areas unavailable for conservation (i.e., private lands with landowners uninterested in engaging in conservation). On the other hand, the FCNP approach will necessarily achieve lower efficiency in representation than the blank slate approach due to the constraints on the inclusion of certain areas, but will create a solution that is compatible with established networks. Our analysis attempted to quantify the differences in both efficiency in representation and feasibility of carrying out the plan. The comparison of FCNP priorities to blank slate priorities revealed that creating a new network (of equal size to the TPA network) would require the addition of many currently unprotected segments for a relatively small gain in species representation. A blank slate network with the same number of segments as the established network would only have 23% of its segments within currently protected areas and would require the addition of 2,894 currently unprotected segments to duplicate the number of segments of the established network. There were relatively small differences in the efficiency of species representation between stream segments prioritized using the FCNP framework compared to the priorities established using a blank slate approach. The losses in the efficiency of species representation for the FCNP was relatively minor compared to the blank slate approach. The blank slate approach required 2.1 times fewer stream segments to achieve representation of all species, however both approaches had all but two species represented within the top 1% of sites (**Figure 4A**). The average number of unrepresented species across priorities established with the blank slate approach was nearly identical to the FCNP approach (average difference of 0.002 unrepresented species; **Figure 4A**). Across all priorities, the average of the minimum level of representation was slightly higher (0.5 occurrences) for the FCNP approach (**Figure 4B**). However, the blank slate approach achieved slightly higher average levels of species representation (21 occurrences; **Figure 4C**). The majority of species had higher levels of representation for the top 10% of segments within each network (62%) and the entire network plus the top 10% of complementary areas (71%) when priorities were established using the blank slate approach.

DISCUSSION

This study examined the potential benefits and draw-backs of utilizing a prioritization approach which incorporates established conservation networks into the planning process (FCNP) with commonly used alternatives (Blank slate, HTI). Our results suggest that the FCNP approach provides actionable priorities for stream fish conservation over a broad spatial scale (State/Region, several hundreds of thousands of square kilometers). Incorporating established conservation areas resulted in more workable solutions, and incorporating species data rather than only anthropogenic threats resulted in better species representation,. Freshwater conservation planning often focuses on the development of priority areas through the use of a blank slate approach (Sowa et al., 2007; Strecker et al., 2011; Stewart et al., 2017; VanCompernolle et al., 2019), however recent work which incorporates established networks in conservation planning efforts represents a step forward in providing information to aid practitioners in converting planning into action (Nel et al., 2009a; Esselman and Allan, 2011; Esselman et al., 2012; Hermoso et al., 2015a; Grantham et al., 2016; Raghavan et al., 2016; Howard et al., 2018; Jézéquel et al., 2020). Our study provides a comparison between an approach which incorporates established networks into the planning process and two approaches which do not. This comparison represents a step forward by allowing researchers to evaluate some of the potential effects of selecting one approach over the other. Our results suggested that the implementation of a blank slate prioritization in Missouri would require the majority of conservation actions to occur on stream segments not currently protected (77% of a network of the same size as the current TPA are not protected), which is unlikely to be a workable solution for management agencies operating with limited resources (Naughton-Treves et al., 2005; Iojaa et al., 2010; Thieme et al., 2012). It is likely that in other states, ecoregions, or countries blank slate solutions would have limited overlap with established networks and the implementation of those prioritizations would be limited due to financial and logistical constraints. An approach which allows prioritization to account for areas already being protected and identify priority areas within and complementary to established networks, potentially allows for a more cost-effective, workable solution, than might be achieved with a blank slate approach, with a relatively small sacrifice in the efficiency of species representation (Esselman and Allan, 2011).

In many areas around the globe stream fishes are lacking representation within protected areas (Cooper et al., 2019). All 133 stream fish species found in wadeable streams in Missouri were predicted to be represented within the TPA network. However, protecting multiple areas to allow for redundancy in case of catastrophic declines and habitat changes due to climate change, invasive species, or anthropogenic disturbances may be needed to ensure species persistence (Stein et al., 2000). A lack of redundant coverage within protected areas suggests that long-term protection may be precarious for seven species predicted to occur within <10 protected stream segments. When possibilities for network expansion arise, targeting the complementary areas identified using FCNP approach may increase protection for underrepresented species and may improve the long-term outlook for those species, while bolstering the comprehensiveness of the established network.

Prioritization using the FCNP approach resulted in higher levels of efficiency (lower numbers of unrepresented species, higher minimum numbers of occurrence, and higher average numbers of occurrence across priority levels) in achieving species representation compared to an approach based on habitat integrity alone (HTI, Sowa et al., 2007). This suggests that using the FCNP approach for prioritizing conservation may result in substantial gains in the comprehensive protection of stream fish communities over a habitat only based approach. The use of the FCNP approach resulted in lower numbers of unrepresented species (and less stream segments needed to protect all species), higher minimum levels of representation, higher average levels of representation, and a majority of species with higher levels of representation at both high priority segments within the network and high priority complementary segments. Watershed level threat data are commonly used for identifying priority areas (Mattson and Angermeier, 2007; Sowa et al., 2007; Paukert et al., 2011; Terrado et al., 2016). These areas are often selected because they are pristine or have minimal anthropogenic impacts, or opportunistically because of lack of competing uses due to areas being rugged, isolated, or have limited economic value (Pressey et al., 1993; Margules and Pressey, 2000). Although these factors are important to consider, species with distributions in marginal habitats or close to anthropogenic development may be left out of high priority areas based on this approach. Landscape and habitat surrogates are both a useful alternative to representation based planning when sufficient data on species representation are not available (Trakhtenbrot and Kadmon, 2005) and a valuable piece of complementary information to better inform management. Ideally, representation-based and habitat or threat-based planning would both be used to capture both streams which would best protect a broad suite of species while also selecting areas with high quality habitat. Consideration of habitat integrity is often linked to selecting areas where species are likely to persist, however if these measures are not linked to the species being considered, their ability to inform management may be limited. Oftentimes species can persist and even thrive in degraded habitats if a species is not sensitive to the conditions resulting from the degradation (Morrow and Fischenich, 2000). If the primary objective is to ensure the adequate representation of all species, a systematic conservation planning approach which accounts for both species representation and likelihood of species persistence, through habitat models or protecting upstream watersheds, may be best suited to ensure adequate, long-term, species representation within high priority areas (Margules and Pressey, 2000; Linke et al., 2011).

While the blank slate approach provides the optimal solution in terms of the representation of species with consideration of the other constraints placed on the prioritization (vulnerability weighting, upstream integrity, etc.), it also creates a solution that may have limited utility given potential difficulties in protecting or managing lands which are not owned by the management agency or partner groups. In making this comparison, we aimed to assess the trade-off between loss of efficiency in species representation but gains in feasibility of implementation of the plan due to not requiring large-scale land acquisition or development of partnerships. The blank slate approach identified a set of priorities requiring the addition of many currently unprotected segments but achieved similar levels of efficiency of species representation. Implementing conservation plans based on blank slate approaches may be difficult due to limited resources to acquire land (Naughton-Treves et al., 2005; Iojaa et al., 2010; Thieme et al., 2012; Maire et al., 2016). Our results indicate that in Missouri over 75% of segments within blank slate priorities of equal size to the TPA network are currently outside of the established network, requiring acquisition of large amounts of land if a blank slate approach was to be implemented. The FCNP approach yielded similar numbers of unrepresented species across all priority levels (with more segments required to achieve representation of all species), slightly higher minimum levels of representation, slightly lower average levels of representation, and a minority of species with higher levels of representation at both the top 10% of segments within the conservation network and the entire network plus top 10% of complementary areas. This suggests that the gains in representation efficiency achieved through a blank slate approach may not be enough to offset the potential reductions in workability and cost, due to the additional resources required for acquisition or forming partnerships for the conservation of currently unprotected lands. The use of a blank slate approach is likely warranted where (1) robust conservation networks do not exist (Jenkins and Joppa, 2009), (2) conservation networks that do exist fail to achieve comprehensive species representation (Rodrigues et al., 2004; Hermoso et al., 2015b; Jenkins et al., 2015), or (3) large amounts of resources are available for the establishment of new networks. However, when robust networks exist (e.g., DellaSala et al., 2001; Commission of the European Communities, 2002; Pugh and Hall, 2006), building from the existing infrastructure using an approach incorporating established conservation networks may be a more effective method for developing actionable priorities.

Our approach is useful when existing conservation networks are established, but our methods have several limitations. Much of the literature employing species distribution modeling for stream fish does not account for spatial autocorrelation, and some studies have found that it may have limited impacts on results (Huang and Frimpong, 2016), however researchers may want to account for spatial autocorrelation to improve future species distribution models (Record et al., 2013). Relying on presence and frequency of occurrence data for rare species when species distribution models cannot be generated biases prioritizations toward selecting known sites and may cause sites with unknown populations to be given lower priority. Finding ways to better account for potential unknown occurrence locations for rare species would certainly benefit conservation planning efforts. Additionally, a variety of other methods of developing species distribution models exist and researchers should evaluate which techniques are most suitable for their dataset and objectives (Shabani et al., 2016). Our models were based on species presence/absence however recent work has shown that using other biological metrics such as species abundance can provide benefits for predictive accuracy (Yu et al., 2020). Zonation is a flexible conservation planning tool that works well for this purpose, however researchers should critically evaluate which specific tools and features may be most useful to achieve their desired results (Moilanen et al., 2009; Sievert et al., 2019), or whether and alternative conservation program such as Marxan (Watts et al., 2009) may be a better fit for their data and objectives.

Using an approach incorporating established conservation networks into the conservation prioritization process may aid aquatic biodiversity conservation efforts at regional, national, and international scales. Although some regions do not currently have sufficient biological or environmental data to tackle these types of analyses, there are examples from North and South America, Africa, Asia, and Europe where sufficient data exists (Lassalle and Rochard, 2009; Iojaa et al., 2010; Esselman and Allan, 2011; Nel et al., 2011b; Strecker et al., 2011; Thieme et al., 2012; Hermoso et al., 2015a; Maire et al., 2016; Raghavan et al., 2016; Bicknell et al., 2017; Jézéquel et al., 2020). Protected and priority areas, such as South Africa's National Freshwater Ecosystem Priority Areas (Nel et al., 2011a), Europe's Natura 2000 (Commission of the European Communities, 2002), and areas identified in State Wildlife Action Plans in the United States (Pugh and Hall, 2006), among many others, are examples of established networks upon which prioritization incorporating established conservation networks has been or could be beneficial. The ability to consider established conservation networks during the prioritization process increases the feasibility of taking action based on the results of systematic conservation planning. In regions where sufficient data exist to estimate the distributions of aquatic biodiversity, this framework may be utilized to inform management decisions within established networks, and can guide land acquisition and partnerships in selecting areas which best complement what is already being protected, and help prioritize restoration and management both within and complementary to established conservation networks.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because, this study was based entirely on existing data, no surveys or samples were conducted for this study on living creatures.

AUTHOR CONTRIBUTIONS

NS, CP, and JW contributed to the conception and design of this study. NS developed the species distribution models and zonation prioritizations and ran the analyses. CP and JW provided feedback on analysis. NS wrote the first draft of the manuscript. CP and JW provided revisions and editing of the manuscript. All authors read and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2020.515081/full#supplementary-material

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Tissue Hydrogen Peroxide Concentration Can Explain the Invasiveness of Aquatic Macrophytes: A Modeling Perspective

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In recent years, an invasive macrophyte, *Egeria densa*, has overwhelmingly colonized some midstream reaches of Japanese rivers. This study was designed to determine how *E. densa* has been able to colonize these areas and to assess the environmental conditions that limit or even prevent colonization. Invasive species (*E. densa* and *Elodea nuttallii*), and Japanese native species (*Myriophyllum spicatum*, *Ceratophyllum demersum*, and *Potamogeton crispuss*) were kept in experimental tanks and a flume with different environmental conditions. Tissue hydrogen peroxide (H_2O_2) concentrations were measured responding to either individual or multiple environmental factors of light intensity, water temperature, and water flow velocity. In addition, plants were sampled in rivers across Japan, and environmental conditions were measured. The H_2O_2 concentration increased in parallel to the increment of unpreferable levels of each abiotic factor, and the trend was independent of other factors. The total H_2O_2 concentration is provided by the sum of contribution of each factor. Under increased total H_2O_2 concentration, plants first started to decrease in chlorophyll concentration, then reduce their growth rate, and subsequently reduce their biomass. The H_2O_2 concentration threshold, beyond which degradation is initiated, was between 15 and 20 µmol/gFW regardless of the environmental factors. These results highlight the potential efficacy of total H_2O_2 concentration as a proxy for the overall environmental condition. In Japanese rivers, major environmental factors limiting macrophyte colonization were identified as water temperature, high solar radiation, and flow velocity. The relationship between the unpreferable levels of these factors and H_2O_2 concentration was empirically obtained for these species. Then a mathematical model was developed to predict the colonization area of these species with environmental conditions. The tissue H_2O_2 concentration decreases with increasing temperature for *E. densa* and increases for other species, including native species. Therefore, native species grow intensively in spring; however, they often deteriorate in summer. For *E. densa*, on the other hand, H_2O_2 concentration decreases with high water temperature in summer, allowing intensive growth. High solar radiation increases the H_2O_2 concentration, deteriorating the plant. Although the H_2O_2 concentration of *E. densa* increases with low water temperature in winter, it can survive in deep water with low H_2O_2 concentration due to diffused solar

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radiation. Currently, river rehabilitation has created a deep zone in the channel, which supports the growth and spreading of *E. densa*.

Keywords: alien macrophytes, hydrogen peroxide, reactive oxygen species, stress indicator, vegetation management

INTRODUCTION

Macrophyte responses to environmental conditions are species specific, and invasive plants tend to exhibit more tolerance than native species (Zerebecki and Sorte, 2011; Bates et al., 2013). Therefore, invasive species are able to dominate or distribute in areas where native species fail to survive. Among different invasive aquatic macrophytes, *Egeria densa* is a well-known worldwide species that causes significant ecological issues in freshwater ecosystems. In Japan, *E. densa* was used as an ornamental aquarium plant in the early 19th century. However, it has escaped into natural freshwater bodies and became naturalized in the 1940s. Although *E. densa* mainly invaded lakes during the initial spreading stage in the 1970s (Kadono, 2004), this species has been recorded increasingly in many western Japanese rivers over the last two decades (MLIT, 2019). These rivers were originally nearly free of macrophytes and consisted of gravel beds and hyporheic flow (Tanida, 1984; Hauer et al., 2016). Though native species (e.g., *Myriophyllum spicatum*, *Potamogeton crispuss*, and *Ceratophyllum demersum*) were colonized patchily, no large colonies were found in major rivers (Kunii, 1982; Kadono, 2004). Another alien species, *Elodea nuttallii*, also invaded at nearly the same time in 1961. However, it did not produce large colonies except for lakes and small streams. In contrast, *E. densa* spread to cover the entire river channel of major rivers. The widespread colonization of *E. densa* has led to extreme changes in these river ecosystems. After establishment, *E. densa* behaved as ecological engineers, changing the environment to their benefit (Schoelynck et al., 2012; Schoelynck et al., 2014). They reduced water flow velocity and attenuated wave energy, leading to particle settlement and, consequently, hyporheic flow capacity reduction (Madsen et al., 2001; Boano et al., 2014). It has also caused economic losses. For example, the presence of macrophytes substantially decreases the yield of Ayu (*Plecoglossus altivelis altivelis*), a grazer of benthic algae (Kawanabe, 1970). Casual monitoring between present-day abiotic conditions and plant traits, such as growth rate and biomass, is the method commonly used to evaluate the preferable habitat for macrophyte species (Barko et al., 1991; Riis et al., 2012; O'Hare et al., 2018). However, environmental conditions frequently change, and there are various types of effective factors in the natural rives. Thus, it is difficult to apply the monitoring system in the field, particularly to derive the most influential factor.

Aquatic macrophytes growing in their natural environment often face an array of unpreferable environmental conditions, for example, too low or too high water temperatures, high flow velocity (Atapaththu and Asaeda, 2015), pollution, or substrate alteration (Asaeda et al., 2013). They can survive and propagate if the conditions remain within the plants' tolerance levels. When the environmental conditions exceed the tolerance thresholds for a considerable period of time, macrophytes become stressed, lose their colonization capacity, and ultimately decay. However, following a short-term exposure to such conditions, they can recover, depending on the extent of the damage caused and the characteristics of the species (Weerakoon et al., 2018). Thus, the presence of a specific macrophyte species in an area depends on whether environmental factors are within their tolerance levels as well as on the duration of the exposure. When plants are subjected to unpreferable environmental conditions, reactive oxygen species (ROS) are generated in different organelles (Zaman and Asaeda, 2013; Das and Roychoudhury, 2014; Asaeda et al., 2017; Choudhury et al., 2017; Helaly et al., 2017; Parveen et al., 2017; Asaeda et al., 2018; Elsheery et al., 2020a; Elsheery et al., 2020b), which damages the plant body by the oxidative stress. Some ROS are scavenged relatively quickly by antioxidants (Omar et al., 2012), and the homogeneity of ROS in tissues is maintained by balancing the ROS and antioxidants. The balance flips over when oxidative stress surpasses the scavenging capacity of the antioxidants (Naser et al., 2016; El-Sheery, 2017; Dumont and Rivoal, 2019). Among ROS, hydrogen peroxide (H_2O_2) is widely generated (Asada, 2006; Sharma et al., 2012), relatively stable, and can be easily measured (Satterfield and Bonnell, 1955; Zhou et al., 2006; Asaeda et al., 2020). The concentration of H_2O_2 in plant tissues does not depend on a particular stress but is subjected to sum magnitude of unpreferable environmental conditions (Suzuki et al., 2014; Asaeda et al., 2020). Thus, H_2O_2 concentration in the plant tissue can be used as an indicator of the physiological status of a particular macrophyte species (Smirnoff and Arnaud, 2019). The system has been used for *E. densa*, which has successfully identified the channel slope that it can colonize (Asaeda et al., 2020).

The trend of H_2O_2 concentration is likely as a result of a long history of acclimatization to the natural condition of a particular area; thus, it may vary widely between native and invasive species. To apply tissue H_2O_2 concentration as an indicator to elucidate the intensive growth of invasive species, it is necessary to determine the relationship between H_2O_2 concentration and environmental factors both for native and invasive species. The main objective of the present study is to 1) empirically determine the H_2O_2 concentration generated by unpreferable conditions of abiotic environmental factors for both native and invasive species, 2) develop the model to predict the environment where these species can colonize, and 3) elucidate the reason for the overwhelming growth of *E. densa* in rivers of particular areas.

METHODOLOGY

Experimental Methodology

In the experiment, invasive macrophyte species (*E. densa* and *E. nuttallii*) and major Japanese species (*C. demersum*, *P. crispuss*, and *M. spicatum*) were tested (MLIT, 2019). They were exposed to different types of physical conditions, temperature, irradiance, and water flow velocity, following the range of the rivers where these species were colonized from ~8°C in winter to 30°C in summer for water temperature, 0–1,200 μmol/m^2/s for the irradiance in water, and 0–50 cm/s for flow velocity (MLIT, 2019). For the laboratory experiments, healthy macrophyte stocks were collected from the Saba River (*E. densa*) and the Moto-Arakawa River near Tokyo (*E. nuttallii*, *C. demersum*, *P. crispuss*, and *M. spicatum*). Collected plants were cleaned with water to remove debris, and any attached macro-algae were carefully separated with tweezers. The plants were then cultured in a glass tank at 25 ± 2°C under a 12/12 h photoperiod with photosynthetically active radiation (PAR) (~125 μmol/m^2/s using fluorescent lamps) for over 2 months. Commercial sand (D_{50} < 0.1 mm) was used as a substrate, and 5% Hoagland solution was provided as the nutrient medium (Atapaththu and Asaeda, 2015). Algae were removed weekly, and algae-free plants were used in the experiments. Three types of experiments (triplicate) were conducted in total, each focusing on different combinations of environmental factors.

Experiment 1: Water Temperature and Irradiance

A number of studies have reported that water temperature can significantly affect the abundance of different aquatic plant species (Pip, 1989; Barko et al., 1991; Lougheed et al., 2001; Pandit, 2002). An experiment was conducted to identify the increment of H_2O_2 concentration of the plant tissue under different water temperatures and irradiance levels, and, thereby, to make empirical relations between these factors. Several light levels (0–1,300 μmol/m^2/s of PAR) were tested in small aquaria (dimensions: 50.0 cm × 35.0 cm × 35.0 cm). Temperature level was maintained at 10 ± 2 (*E. densa*), 15 ± 2 (*E. densa*), 20 ± 2, 25 ± 2 (*E. densa*), and 30 ± 2, 35 ± 2°C using a temperature controlling system (Aquarium cooler ZC-100α, Zensui Corporation, Tokyo, Japan). PAR intensity was irradiated under natural solar radiation or using LED lights (Model LT-NLD85L-HN, OHM Electric Inc., Japan) with a 12 h light:12 h dark photoperiod for 3 weeks.

Experiment 2 and 3: Flow Velocity and Irradiance

This experiment was designed to test the effect of water flow velocity on the H_2O_2 concentration of the plant tissues and the interaction with irradiance (Atapaththu and Asaeda, 2015; Asaeda et al., 2017). Two sets of experiments were conducted. In the first experiment, experimental plants (*E. nuttallii*, *P. crispus*, *C. demersum*) were exposed to two water flow levels (16 and 25 cm/s) using custom-made recirculating flumes (dimensions: 240 cm long × 25 cm width × 28 cm depth) exposed to artificial light intensity by the LED lights, or dark conditions. Pre-aerated tap water was circulated by centrifugal electric motor pumps. Pre-acclimatized potted plants were allocated to a section in the flume where water was introduced though a gradually shrinking entrance section to reduce turbulence. Plants were continuously exposed to low or high mean flow velocities for up to 4 days. During the experiment, mean water flow velocity was detected using an ultrasonic velocimeter (Tokyo Keisoku Co. Ltd., Japan) directly above the plant leaf surface and recorded daily to minimize flow variation. Temperature level was maintained at 15 ± 2°C using an aquarium water temperature controlling system (Aquarium cooler ZC-100α, Zensui Corporation, Tokyo, Japan). Stress assays by means of H_2O_2 measurements were performed every 3 h from 6:00 to 18:00 after 4 days' exposure, and each treatment contained three replicate flumes. For another experiment, a flume channel 2.4 m long, 25 cm wide and 22 cm depth was constructed outdoors. Eighteen flat pots with more than three *E. densa* plants were carefully and randomly installed. Water temperature was kept at 25 ± 2°C throughout the experiment. Flow velocities from stagnant to 40 cm/s were employed under different solar radiation, and after 3 h, three plants were sampled at each time and a stress assay was conducted immediately. PAR intensity in the water was measured with a portable quantum flux meter (Apogee, MQ-200, United States).

Field Observations

Several rivers that are highly colonized by *E. densa* were selected from the species distribution database in Japan (MLIT, 2019). The selected rivers were assessed to obtain detailed location information pertaining to the colonization of *E. densa*. Sampling was conducted in the Eno River and its tributary Tajibi River (April, May, and September 2016; April and June 2017); in the Saba River and its tributary Shimaji River (May, June, and September 2016; April and June 2017; August 2018), and in the Hii River (October 2016). At each sampling point, water flow velocity was measured with an ultrasonic velocimeter (Tokyo Keisoku Co. Ltd., Japan) at 20% (reference velocity) and 80% (depth of the colony) of the total water depth (Chow, 2009). PAR intensity in the water was measured with a portable quantum flux meter (Apogee, MQ-200, United States) at 10 cm depth intervals. *M. spicatum* was sampled in the Moto-Arakawa River near Tokyo in April 2015. The river was approximately 5 m wide and 40 cm deep, and the channel slope was approximately 1/1,000. The bottom surface was patchily covered with *M. spicatum*, *E. nuttallii*, *C. demersum*, and *Sparganium* spp. PAR, and velocity distributions were measured with a portable quantum flux meter (Apogee, MQ-200, United States) and an ultra-sonic velocimeter, respectively. *E. nuttallii* was sampled in July and September 2018 from the same river. Sampling was conducted approximately every 3 h in the light-exposed and dark-adapted conditions to remove the effect of solar radiation. The dark treatment involved placing a black plastic sheet (3 m × 3 m) floating over part of the plant colony for 30 min. The 30 min pre-dark period was determined by laboratory experiments, which were specifically conducted to determine the optimum pre-darkness duration (data not shown). In August 2017, a sampling of *M. spicatum* was conducted in the Sakuradabori of the Imperial Palace Moat, at the center of Tokyo, where *M. spicatum* made a mono-specific stand. The depth of the sampling site was 0.3 m–2.5 m. Both solar-exposed and dark-adapted samples were taken. Plant biomass was sampled from 50 cm × 50 cm quadrats in all sampling sites. The plant samples were placed in plastic bags and immediately stored in a cooling box containing dry ice for transfer to the laboratory where it was stored at −80°C until an H_2O_2 assay and chlorophyll estimation were conducted.

Determination of Shoot Growth Rate, H_2O_2 and Chl-a Concentrations

The length of the plants grown in the experimental units was measured using a millimeter scale at 5–7 day intervals. The shoot growth rate (SGR) was calculated as the difference in shoot length between two observations divided by the duration, and it was expressed in cm/day. At the end of each experiment, fresh plant shoots were extracted (~500 mg) in an ice-cold phosphate buffer (50 mM, pH 6.0) that contained polyvinylpyrrolidone (PVP), and the extractions were centrifuged at 5,000 × *g* for 20 min at 4°C. This extraction was used to analyze the H_2O_2 content spectrophotometrically following the $TiSO_4$ method (Satterfield and Bonnell, 1955) with modifications. The reaction mixture contained 750 μl of enzyme extract and 2.5 ml of 1% $TiSO_4$ in 20% H_2SO_4 (v/v), which was centrifuged at 5,000 × *g* for 15 min at 20°C. The optical absorption of the developed yellow color was measured spectrophotometrically at a wavelength of 410 nm. The H_2O_2 concentration in samples was determined using the prepared standard curve for known concentration series and was expressed in μmol per gram fresh weight (μmol/gFW).

Chlorophyll *a* (Chl-a) concentrations of experimental plants were determined spectrophotometrically (UV Mini 1210, Shimadzu, Japan) by extracting pigments with N,N-dimethylformamide after keeping them in darkness for 24 h, and they were expressed in terms of fresh weight (FW) (Wellburn, 1994).

Statistical Analysis

Data were tested for normality with the Shapiro–Wilk test before statistical analyses. All results were presented as the mean ± SD of more than three replicates. Data were subjected to a one-way analysis of variance (ANOVA) with Tukey's *post-hoc* test for mean separation. The *t*-test was performed where necessary. Bivariate analysis was used and followed by Pearson's correlation to evaluate the relationship among parameters. Statistical analyses were performed in IBM SPSS V25.

Development of the Species-Specific Model to Identify the Colonization Zones

Asaeda et al. (2020) proposed the total H_2O_2 concentration formed in plant tissues for a particular temperature (*Temp*) by the sum of H_2O_2 generated by metabolism ($H_2O_{2\mathrm{met}}$), flow velocity ($H_2O_{2\mathrm{vel}}$), and solar radiation ($H_2O_{2\mathrm{rad}}$). If the value is between 15 and 20 μmol/gFW, then *E. densa* growth deteriorates.

$$H_2O_{2tot}\,(Temp) = H_2O_{2rad}\,(Temp) + H_2O_{2vel}\,(Temp) + H_2O_{2met}\,(Temp) < H_2O_{2cr}\,(= 15-20\ \ \mu\text{mol/gFW}\ \text{ for }\ E.\ densa) \tag{1}$$

For other species, empirical formulas obtained by experiments and field observation were introduced to H_2O_2 concentrations generated by each environmental component, solar radiation, H_2O_{2rad} (*Temp*), temperature inclement, $H_2O_{2rad}(Temp)$, the basal level of the metabolism, the H_2O_{2met} (*Temp*) (Apel and Hirt, 2004), and the threshold level to deteriorate, H_2O_{2cr}.

In rivers flowing with moderate velocity, water is fully mixed. Therefore, the light attenuation coefficient is nearly uniform at all depths, and the light intensity is given by $I_0\exp(-kz)$, where I_0 is the light intensity just below the water surface, k(=0.083 cm^{-1}) is the attenuation constant of light in water, and z is the canopy depth. The intensity of solar radiation, I_0 (μmol/m^2/s), and water temperature (°C) at the Eno and Saba rivers are empirically given as a function of month, *month*:

$$I_0 = 0.93month^4 - 22.3month^3 + 134.5month^2 - 2.22month + 868 \tag{2}$$

$$Temp = 0.022month^4 - 0.66month^3 + 6.16month^2 - 17.5month + 20.4 \tag{3}$$

Flow velocity in a river channel "*Vel*" (cm/s) is estimated by the Manning's equation, assuming the channel is sufficiently wide compared to the depth and is longitudinally uniform, such that:

$$Vel = \frac{4.63}{n} R^{2/3} S^{1/2} \tag{4}$$

where R is the hydraulic radius, approximately given by the depth H (cm), S is the channel bed slope, and n is the Manning's roughness coefficient, where n is ~0.090 in the river zones considered in the present study (personal information).

RESULTS

Empirical Relationships of H_2O_2 Concentration With Abiotic Factors

Combined effects of temperature and light intensity on H_2O_2 formation in macrophyte tissues showed a species-specific response (**Figure 1**). The basal H_2O_2 concentrations were 4.6 μmol/gFW at 20°C for *E. densa* and *E. nuttallii*, and 3.0 μmol/gFW at 20°C for other species, respectively, after being exposed to dark conditions. The increment of H_2O_2 driven by the temperature change were −0.32 μmol/gFW/°C for *E. densa* ($r = -0.985$, $p < 0.01$), 0.39 μmol/gFW/°C for *M. spicatum* ($r = 0.800$, $p < 0.05$), 0.41 μmol/gFW/°C for *C. demersum* ($r = 0.900$, $p < 0.01$), 0.60 μmol/gFW/°C for *P. crispuss* ($r = 0.974$, $p < 0.01$), and 0.48 μmol/gFW/°C for *E. nuttallii* ($r = 0.956$, $p < 0.01$), respectively. H_2O_2 concentrations of different light intensity groups were plotted nearly in parallel, higher with higher light intensity groups ($p < 0.05$).

Water flow velocity and light intensity had significant impacts on the H_2O_2 metabolism in macrophytes. The tissue H_2O_2 concentration linearly increased responding to increasing water flow velocity for all these species (**Figure 2**). The increasing rate of H_2O_2 concentration with respect to flow velocity showed no significant difference among species with

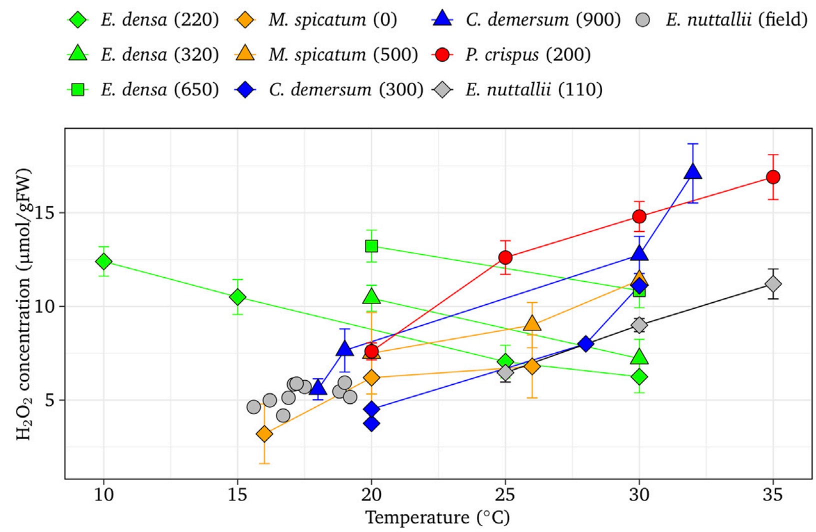

FIGURE 1 | Effect of temperature on H_2O_2 concentration at different light intensities in native aquatic macrophytes (*M. spicatum*, *C. demersum*, and *P. crispuss*) and invasive species (*E. densa* and *E. nuttallii*). Vertical bars indicate the standard deviation. The values in parentheses are light intensities (μmol/m^2/s).

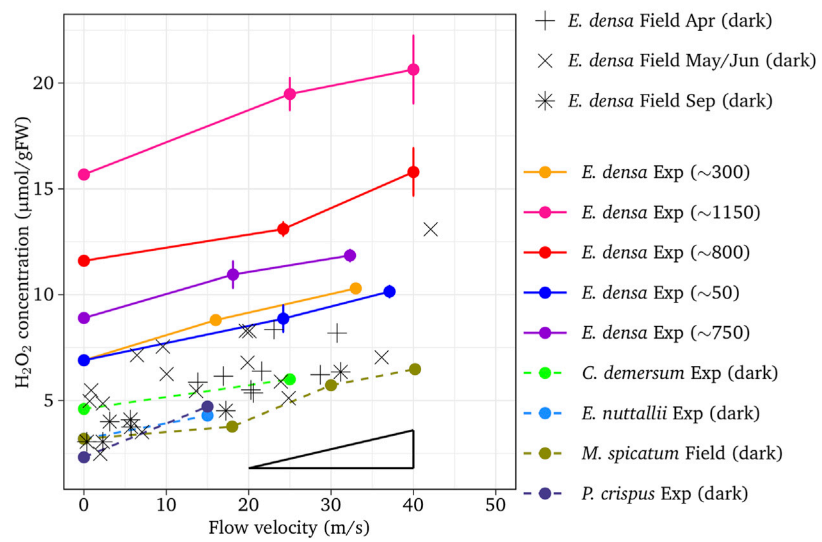

FIGURE 2 | Effect of flow velocity on H_2O_2 concentration with different light intensities or different sampling time. Vertical bars indicate standard deviation. The triangle shows the average gradient. The values in the parentheses are light intensities (μmol/m^2/s)

the gradient due to the velocity of 0.09 H_2O_2/velocity (μmol/gFW/cm/s) ($r = 0.921$, $p < 0.01$ for *E. densa*, 0.878, $p < 0.01$ for *E. nuttallii*, $r = 0.875$, $p < 0.01$ for *P. crispuss*, $r = 0.700$, $p < 0.01$ for *C. demersum* and $r = 0.957$, $p < 0.01$ for *M. spicatum*). It was similar to the results of field samples, 0.072 H_2O_2/velocity (μmol/gFW/cm/s) as shown in the figure. No significant difference was obtained among the sampling seasons. For *E. densa*, H_2O_2 concentrations for different light intensity groups were plotted nearly in parallel, higher with higher light intensity groups ($p <$ 0.01). The increments of H_2O_2 concentrations for the light-exposed samples with respect to the dark-adapted ones are shown in **Figure 3**. Experimental samples of *E. densa* had a similar increasing trend with field observation in H_2O_2 concentration.

From the field data, Asaeda et al. (2020) derived the following relationship for *E. densa*:

$$H_2O_{2\,rad}\left(Temp\right) = \frac{\left[I_0 e^{(-kz)} - 40\right]^{\frac{2}{3}}}{10} \quad \text{for } I_0 e^{(-kz)} \geq 40 \ \ \mu\text{mol/m}^2/\text{s}$$
$$\text{for } I_0 e^{(-kz)} < 40 \ \ \mu\text{mol/m}^2/\text{s} \tag{5}$$

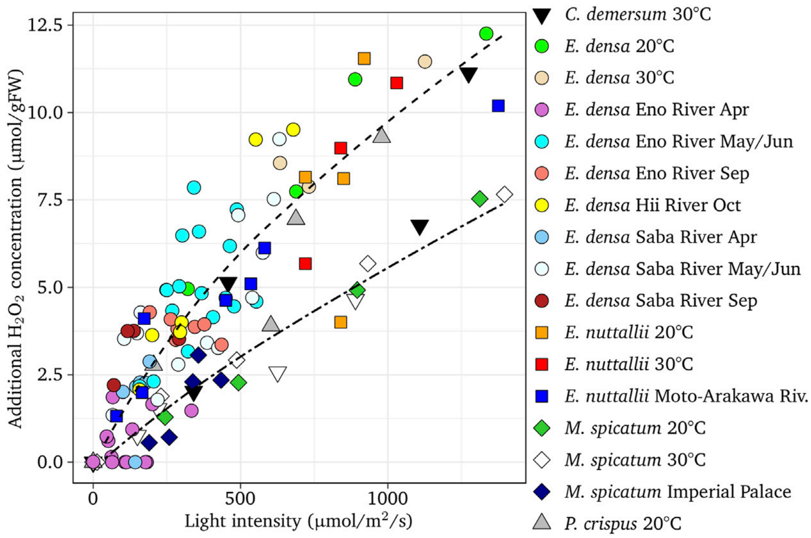

FIGURE 3 | Additional H_2O_2 concentration of light-exposed tissues with respect to dark-adapted ones of different rivers and experiments as a function of the light intensity for different species. The regression curves, H_2O_2 = [light intensity−40]$^{2/3}$/10 (upper dotted curve) and H_2O_2 = [light intensity−40]$^{5/6}$/55 (lower dotted curve) are presented. Field samples of *E. densa* (Asaeda et al., 2020) are shown for comparison.

Figure 3 indicates that a similar relationship is available for *E. nuttallii* and *P. crispuss* without a large error ($r = 0.97$, $p < 0.01$ for *E. nuttallii* and $r = 0.99$, $p < 0.01$, respectively). For *M. spicatum* and *C. demersum*, the increasing rate of H_2O_2 with respect to solar radiation was slightly lower, decreasing the effect of the solar radiation. Therefore, a different equation was derived for *M. spicatum*, and *C. demersum* ($r = 0.98$, $p < 0.01$ for *M. spicatum*, and $r = 0.89$, $p < 0.01$ for *C. demersum*, respectively).

$$
\begin{aligned}
H_2O_{2\,rad}(Temp) &= \frac{\left[I_0 e^{(-kz)} - 40\right]^{\frac{5}{6}}}{55} \quad \text{for } I_0 e^{(-kz)} \geq 40 \ \ \mu\text{mol/m}^2/\text{s} \\
H_2O_{2\,rad}(Temp) &= 0 \qquad\qquad\qquad \text{for } I_0 e^{(-kz)} < 40 \ \ \mu\text{mol/m}^2/\text{s}
\end{aligned} \tag{6}
$$

The Threshold H_2O_2 Concentration for Growth Deterioration

Chl-a concentrations and SGR as functions of H_2O_2 concentrations at different flow velocities, water temperatures, and light intensities of *E. densa* are shown in **Figure 4A**. Regardless of environmental factors, both Chl-a concentrations and SGR decreased with increasing H_2O_2 concentrations (flow velocity $r = -0.944$, $p < 0.01$ for Chl-a and $r = -0.964$, $p < 0.01$ for SGR; temperature $r = -0.945$, $p < 0.01$ for Chl-a and $r = -0.980$, $p < 0.01$ for SGR; light $r = -0.924$, $p < 0.01$ for Chl-a and $r = -0.965$, $p < 0.01$ for SGR). **Figure 4B** presents the relationships of H_2O_2 and Chl-a concentrations for *M. spicatum*, *C. demersum*, *E. nuttallii*, and *P. crispuss*. Chl-a concentration decreased with the H_2O_2 concentration ($r = -0.896$, $p < 0.01$ for *M. spicatum*, $r = -0.752$, $p < 0.01$ for *C. demersum*, $r = -0.497$, $p < 0.01$ for *E. nuttallii*, and $r = -0.963$, $p < 0.01$ for *P. crispuss*), and was eliminated at approximately 16–20 μmol/gFW. In the field observation, tissue deterioration occurred when similar H_2O_2 concentrations continued for a few days.

Simulated Results

The Comparison With the Observed Data

Figure 5 shows the comparison between the observed H_2O_2 concentration and simulated H_2O_2 concentration for experimental and observed results. Satisfactory agreement between the simulated and observed values were found in the simulation ($r = 0.798$, $p < 0.01$ for *E. densa*, $r = 0.700$, $r < 0.05$ for *E. nuttallii*, $r = 0.919$, $p < 0.01$ for *M. spicatum*, $r = 0.976$, $p < 0.01$ for *C. demersum*, and $r = 0.974$, $p < 0.05$ *P. spicatum*).

The Depth-Wise Distribution of H_2O_2 Concentration of Different Species

The H_2O_2 concentration of *E. densa* was simulated for channel slopes of 1/300 at 10, 20, and 30°C, which were close to the condition of the observed reaches of the Eno and the Saba rivers in March, May/June, and October as well as August to September, respectively. **Figure 6** shows the simulated results with respect to the depth, observed H_2O_2, and macrophyte biomass. The threshold H_2O_2 concentration was assumed as 16 μmol/gFW. The H_2O_2 concentration was high at the water surface and gradually decreased. With deeper depth, increasing velocity increases the H_2O_2 concentration. The decreasing or increasing trend with respect to depth depends on the combination of these two factors. The H_2O_2 concentration of the stagnant water is lower than the sloped channel, as H_2O_2 generated by the velocity is zero. In the case of *E. densa*, the H_2O_2 concentration is higher with lower temperature, and

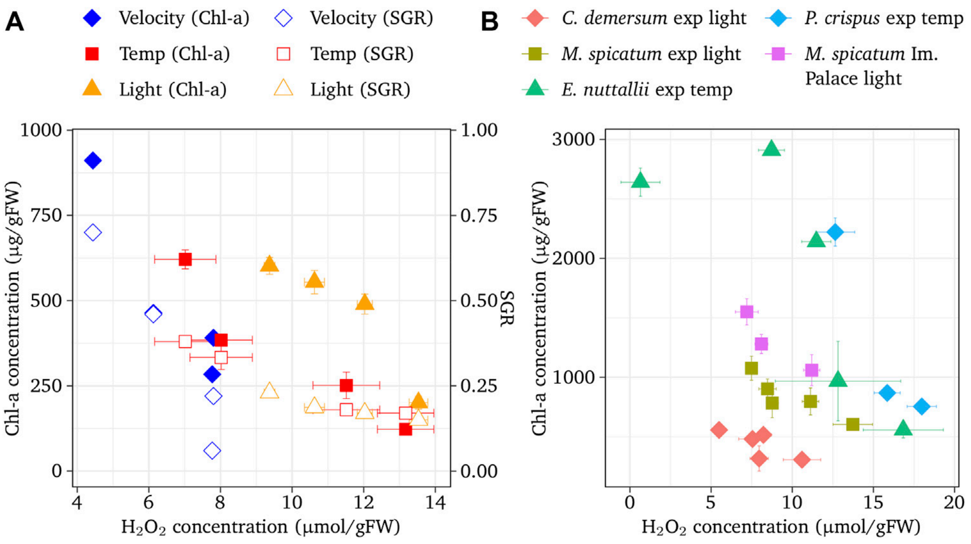

FIGURE 4 | (A) Chlorophyll a concentration and shoot growth rate (SGR) of *E. geriadensa* with respect to H_2O_2 concentration. Velocity (Ellawala et al., 2011), others: the present experiment. Vertical bars indicate standard deviation. **(B)** Chlorophyll is a concentration of *M. spicatum*, *C. demersum*, *E. nuttallii*, and *P. crispuss* with respect to H_2O_2 concentration. Vertical bars indicate standard deviation.

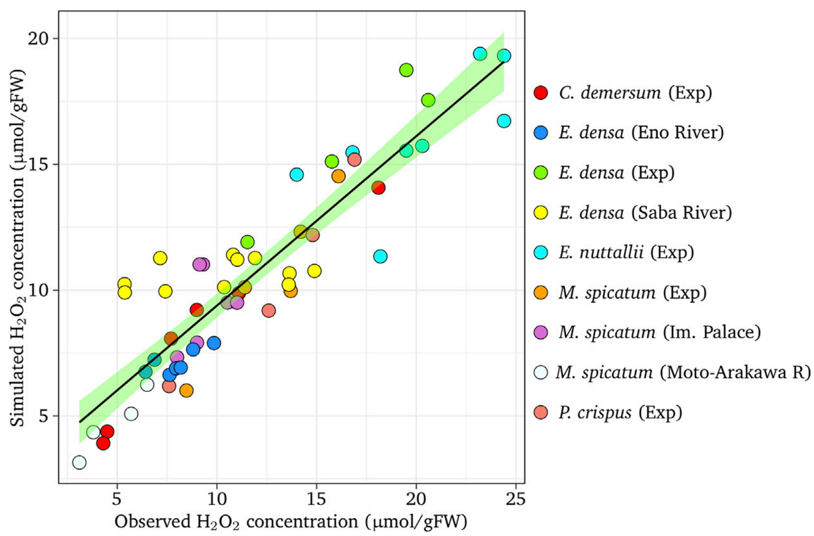

FIGURE 5 | The comparison of simulated H_2O_2 concentration with observed H_2O_2 concentration. The dashed line indicates the perfect agreement. The shaded band (green) represents the 95% confidence interval on the fitted values.

mostly above the threshold value at 10°C, indicating the colonization is limited. The observed H_2O_2 concentrations were plotted within 2 µmol/gFW from the simulated corresponding temperature line. All the biomass data were plotted in the depth where the H_2O_2 line of the corresponding temperature was below the threshold value. The simulated results agreed with the field sampling. The H_2O_2 concentration was simulated for *M. spicatum*; *C. demersum*, *P. crispus*, and *E. nuttallii* were compared to the observed H_2O_2 values and biomass in the field (**Figures 7–9**). Both the H_2O_2 concentration and the existing biomass range agreed well with observed data (H_2O_2 concentration: within 2.5 µmol/gFW, all positive biomass range was in the range where the H_2O_2 values were below the threshold). The H_2O_2 concentration of these species increases with increasing temperature. The H_2O_2 concentration is higher at the shallow zone; thus, the total H_2O_2 concentration exceeds the threshold value.

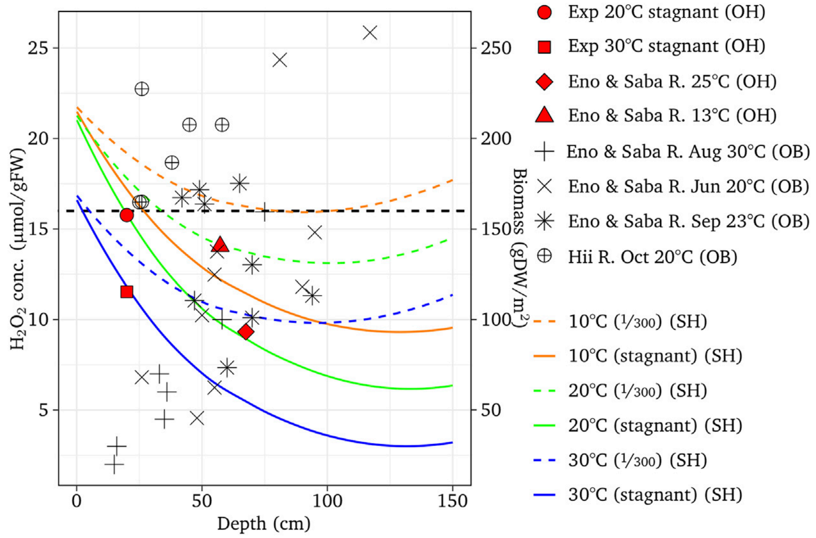

FIGURE 6 | Simulated H_2O_2 concentration with respect to the river depth for the channel slopes of 1/300 or stagnant water condition, and different temperature, compared with the H_2O_2 concentration and biomass of experiments at the Eno and Saba rivers. 'OH', 'OB' and 'SH' designate observed H_2O_2, observed biomass, and simulated H_2O_2, respectively.

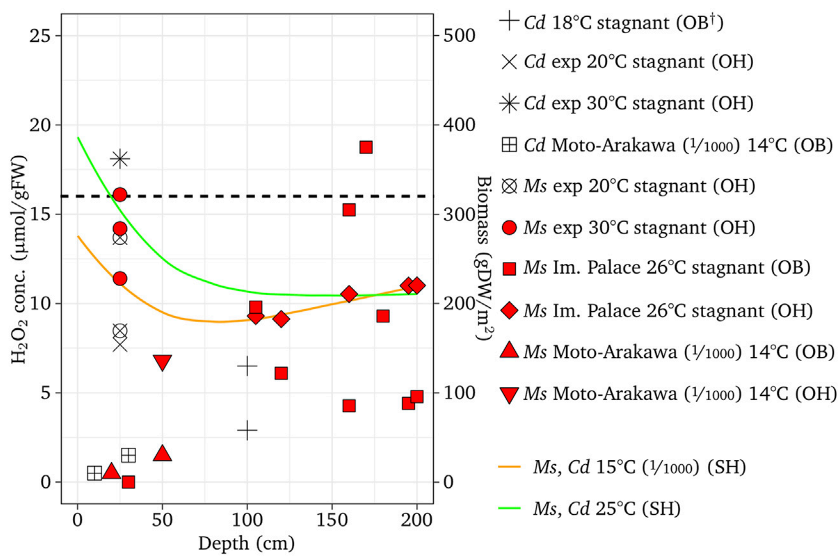

FIGURE 7 | Simulated H_2O_2 concentrations with different temperatures compared with the observed results for *M. spicatum* (Ms in the legend) and *C. demersum* (Cd in the legend) compared with observed data. † Represents Fukuhara et al. (1997); 'OB', 'SH' and 'SH' designate observed biomass, observed H_2O_2 and simulated H_2O_2, respectively. The fractions in the parentheses are channel slopes.

The Composition of the H_2O_2 Component for Different Types of Rivers

Figure 10 presents the simulated results of H_2O_2 fractions generated by environmental conditions: temperature-dependent metabolism ($H_2O_{2met}(Temp)$), solar radiation (H_2O_{2rad}), velocity, H_2O_{2vel}, fora 0.4 m deep (*E. densa* and *M. spicatum*), and colonized and non-colonized rivers. A 5 year average of monthly temperatures was used for the Eno and the Saba rivers, where *E. densa* are colonized, and for the Arakawa River and the Tone River in the Tokyo metropolitan area, where no *E. densa* colonies were recorded while *M. spicatum* was colonized (MLIT, 2019). The former groups are slightly warmer than the latter. The total H_2O_2 concentration without a velocity component is available to estimate for stagnant water. At >1 m depth, the H_2O_2 fraction for the solar radiation was almost nil. The increment of H_2O_2 concentration due to increasing temperatures after spring has opposite trends between *E. densa* and *M. spicatum*; the H_2O_2 concentration decreased with *E. densa* and increased with

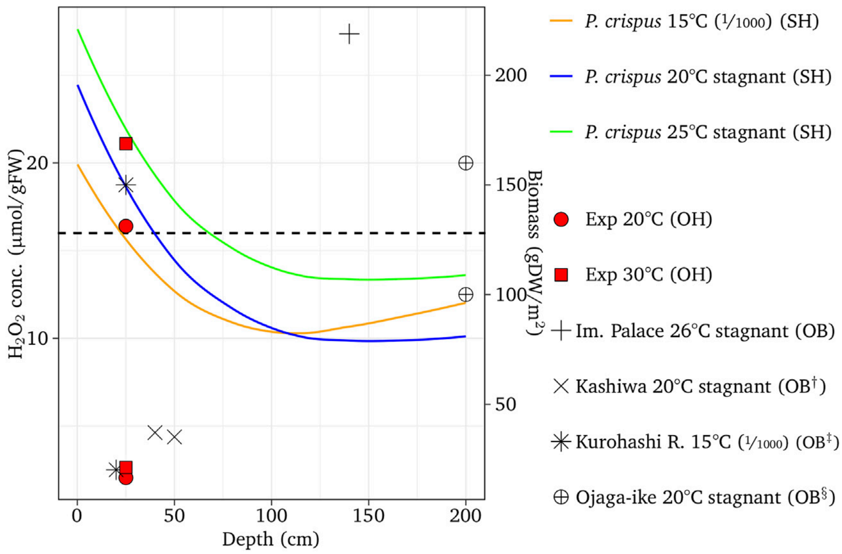

FIGURE 8 | Simulated H_2O_2 concentrations with different temperatures compared with the observed results for *P. crispus* compared with observed data. 'OH', 'SH' and 'OB' designate observed H_2O_2, simulated H_2O_2, and observed biomass, respectively. †, ‡ and § designate Shinohara et al. (2014), Takahashi and Asaeda (2014), and Kunii (1984), respectively. The fractions in the parentheses are channel slopes.

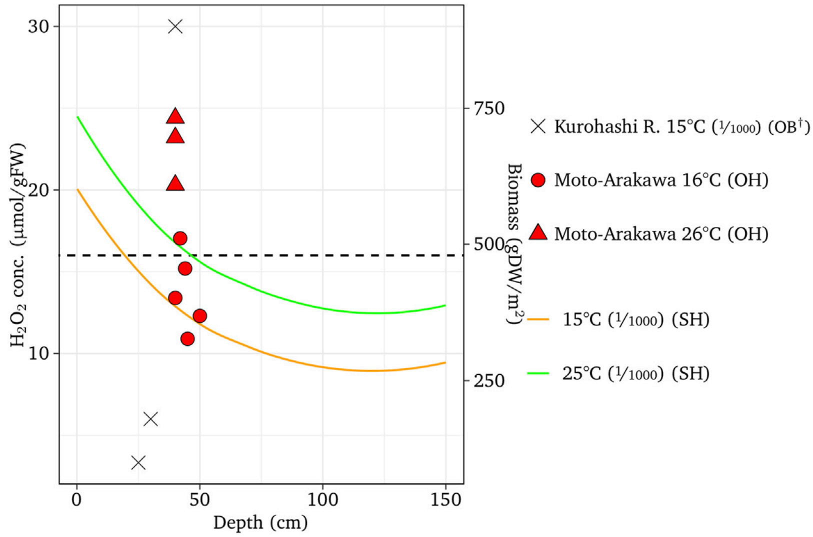

FIGURE 9 | Simulated H_2O_2 concentrations with different temperatures compared with the observed results for *E. nuttallii* compared with observed data. † = Takahashi et al. (2014); 'OH' and 'SH' designate observed and simulated H_2O_2, respectively. The fractions in the parentheses are channel slopes.

M. spicatum. Temperature was the most effective component to differentiate the annual patterns of the total H_2O_2 concentration. The fraction of H_2O_2 due to solar radiation was higher for *E. densa* than for *M. spicatum*; thus, *E. densa* colonization was highly affected by solar radiation. For *E. densa*, the H_2O_2 concentration maintained higher than the threshold value until June in the colder group of rivers, but it becomes lower than the threshold from April/May in the warmer group. For *M. spicatum*, on the other hand, the total H_2O_2 concentration exceeded the threshold value from April in the warmer group while only in August in the colder group. In the stagnant water, the total H_2O_2 concentration of *M. spicatum* exceeded the threshold value in summer.

DISCUSSION

Tissue H_2O_2 Concentration as Affected by Environmental Conditions

Previous studies have shown that H_2O_2 concentration of the plant tissues increases in unpreferable environmental conditions

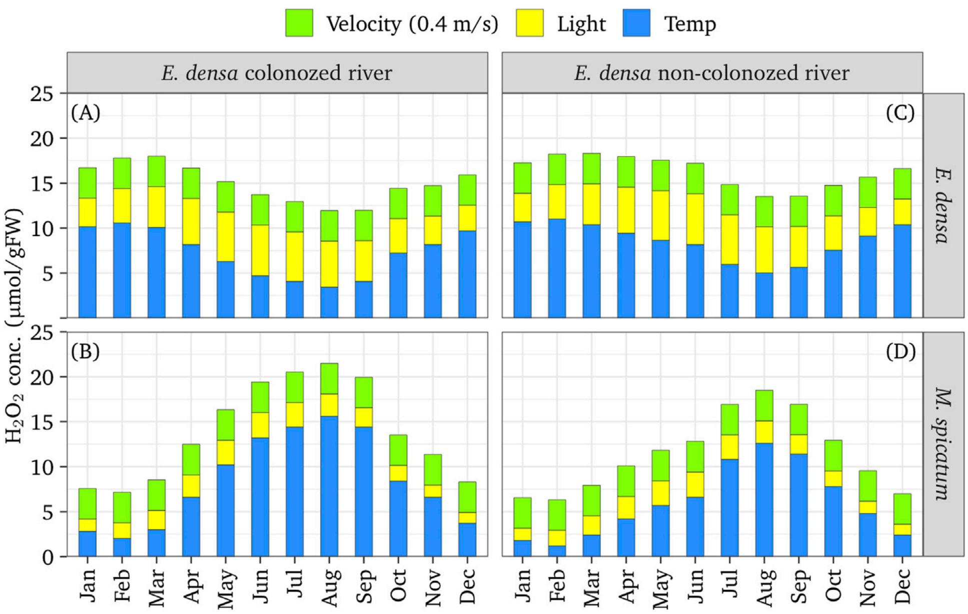

FIGURE 10 | Simulated annual H_2O_2 component generated by each environmental component of a 0.4 m deep colonized [**(A,C)** for *E. densa* and *M. spicatum*] or non-colonized [**(B,D)** for *E. densa* and *M. spicatum*] rivers.

(Asaeda et al., 2020; Elsheery et al., 2020a; Elsheery et al., 2020b), and it is highly correlated with the intensity of a single environmental factor (Asaeda et al., 2017; Asaeda and Sanjaya, 2017; El-Sheery, 2017; Parveen et al., 2017; Chalanika De Silva and Asaeda, 2018). The present study elucidates that under a combination of different environmental factors, the total H_2O_2 concentration is provided as the sum of H_2O_2 generated by individual factors and the amount generated by metabolism (Apel and Hirt, 2004). In addition, the relationship between H_2O_2 concentration and the intensity of each environmental factor does not vary much between seasons and phenological stages of the plant (Asaeda et al., 2020). Therefore, the H_2O_2 concentration is considered an indicator of the degree of the unpreferable condition. The Chl-a concentration and the growth parameter decreased with increasing intensity of the total H_2O_2 concentration (Coleman et al., 1989; French and Moore, 2003; Boustany et al., 2010). Interestingly, when the tissue H_2O_2 concentration exceeded 16–20 μmol/gFW, the plants became brownish and deteriorated. Therefore, the environmental conditions reflected by H_2O_2 concentrations below this threshold allows macrophytes to form a large and healthy colony. This system can be applied to elucidate the growth area of macrophyte species, by formulating the H_2O_2 concentrations and abiotic conditions in the environment.

Environmental Conditions Influencing Macrophyte Colonization in Japanese Rivers

In Japanese rivers, the water quality is relatively good and there is no salinity in the midstream (Luo et al., 2011). Organic matter accumulates on the bottom in stagnant zones, which creates an anoxic zone in the sediment layer. There are such areas in the lowland zones; however, anoxia of the bottom sediment contributed only ~3 μmol/gFW of H_2O_2 (Parveen et al., 2017). Chalanika De Silva and Asaeda (2018) showed that the H_2O_2 concentration differs between mono- and mixed-cultures of species in stagnant water, indicating the effect of species competition. However, the difference was only ~2 μmol/gFW. In field sampling, Japanese native species, *P. crispuss* and *C. demersum,* were often found in thick *E. densa* colonies due to the reduction of flow velocity inside the colony (20 cm/s inside compared to 50 cm/s outside, according to our own observation). This indicates that the increment of H_2O_2 concentration due to competition is less than the reduction of velocity-induced H_2O_2 (~3 μmol/gFW). In this study, the H_2O_2 concentrations attributed to water temperature, high solar radiation, and high flow velocities of natural conditions are ~10, ~10, and ~5 μmol/gFW, respectively. Therefore, water temperature, solar radiation and flow velocity are the major dominant environmental factors determining the colonization patterns of macrophytes in the midstream of Japanese rivers.

Species-Specific Trait of H_2O_2 Concentration in Response to Environmental Conditions

Laboratory and field experiments showed a typical species-specific relationship between H_2O_2 concentration and the environmental factors of temperature, flow velocity, and solar radiation. With increasing flow velocity, the similar increasing trend of H_2O_2 concentration was obtained for all tested species. Although flow velocity generates a large amount of H_2O_2, it does not affect the dominance of a particular species. High solar radiation intensively generates H_2O_2 (Asada, 2006). Specifically, the H_2O_2 concentrations of *E. densa* and *E. nuttallii* were ~10 μmol/gFW under the daily highest solar radiation, which were much higher than those of Japanese native species, *M. spicatum* and *C. demersum*, which were ~6 μmol/gFW. This impacts the ability of *E. densa* to colonize in the shallow zone, where the solar radiation is high; thus, *E. densa* was found to colonize in relatively deep zones (<30 cm deep). Japanese native species were, on the other hand, often found at shoreline or close to the water surface. There was an opposite trend in H_2O_2 concentrations for water temperature between *E. densa* and other species. With *E. densa,* H_2O_2 concentration decreased with increasing temperature, while major Japanese native species, *M. spicatum*, *C. demersum*, and *P. spicatum* as well as another invasive species, *E. nuttallii*, showed an increasing trend of H_2O_2 concentration with temperature. The different trends between Japanese native species and *E. densa* are reflected to their phenology and colonization area.

Possible Reason for the Overproduction of *E. densa* in Japanese Rivers

Low water temperature increases *E. densa* H_2O_2 concentration. In rivers where *E. densa* colonized overwhelmingly, water temperature decreases below 8°C in winter. However, even at that time, H_2O_2 concentration remains below the threshold value at around 1 m deep in stagnant water. Small patchy colonies were found in the upstream of weirs. With increasing temperatures in spring, they started to grow and form a large summer colony, expanding to a shallow zone in the downstream. The channels were originally covered with gravel bed; the bed morphology easily changed under high flow and pools disappeared. However, river rehabilitation for the flood control has been intensively conducted in the last five decades. The shallow zone of the channels was excavated to deepen the channel, and *E. densa* can now colonize with low H_2O_2 concentration. Weirs were constructed frequently, which created deep stagnant water in the upstream. Thus, the H_2O_2 concentration of *E. densa* due to velocity and solar radiation may decrease. Gravel mining was conducted, substantially reducing the amount of gravel in the river channel, and there is no longer any sediment transport even at flood time (Asaeda and Sanjaya, 2017). Thus, the modified river morphology does not change even during floods. The artificially created deep zone became a trigger for the overproduction of *E. densa* in the river channel. In the last three decades, river water temperature has significantly increased due to global warming at approximately 0.1°C/year, often reaching 30°C, particularly in western Japanese rivers (Ministry of Environment, 2013). It seems difficult for Japanese native species and *E. nuttallii* to grow in these rivers. Particularly, *E. densa* and *E. nuttallii* are closely related species and came to Japan at nearly the same time. However, the overwhelming colonization of *E. densa* and the limitations of *E. nuttallii* seem to be attributed to the different temperature traits of these species. Local people emphasize the recent reduction of flow rate (personal communication). During the day, in addition to high solar radiation, water temperature is approximately 2°C higher than at night, particularly under a low summer flow rate. Thus, during this time, both solar radiation and temperature increases the H_2O_2 concentration for Japanese native species. However, their effects are reciprocal and do not affect *E. densa* very much. It is likely another reason for the overwhelming presence of *E. densa*.

CONCLUSION

Under unpreferable environmental conditions, H_2O_2 concentrations increase in plant tissues and reflect the macrophyte condition fairly accurately. Potentially, this could be a good indicator of submerged macrophyte colonization. This approach will save time by not requiring casual observations and biomass monitoring of macrophytes in ecosystem monitoring. The experimental and field observations indicated a clear positive relationship between the level of unpreferable conditions and H_2O_2 concentrations, regardless of abiotic factors. The total H_2O_2 concentration is provided by the sum of H_2O_2 generated by each environmental factor, and <16–20 μmol/gFW is required for colonization. The relationships of H_2O_2 concentrations and the contribution of each abiotic factor were obtained for invasive species (*E. densa* and *E. nuttallii*) and three major Japanese native species (*M. spicatum*, *C. demersum*, and *P. crispuss*). The system was applied to develop a mathematical model to simulate the colonization area of these species. The tissue H_2O_2 concentration decreases with increasing temperature for *E. densa* and increases for other species, including native species. Therefore, native species grow intensively in spring; however, they often deteriorate in summer. For *E. densa*, on the other hand, H_2O_2 concentration decreases with high water temperatures in summer, allowing intensive growth. High solar radiation increases the H_2O_2 concentration, deteriorating the plant. Although the H_2O_2 concentration of *E. densa* increases with low water temperatures in winter, it can survive in deep water with low H_2O_2 concentration due to solar radiation. Currently, river rehabilitation has created a deep zone in the channel, which has supported the growth and spread of *E. densa*.

DATA AVAILABILITY STATEMENT

The datasets generated for this study are available on request to the corresponding author.

AUTHOR CONTRIBUTIONS

TA: contributed the conceptualization and field work, and wrote the manuscript together with other members; MR: contributed to field sampling, laboratory and data analyses, and helped write the manuscript; JS: reviewed and commented on the manuscript.

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