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Women in conservation and restoration ecology 2022

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Women in conservation and restoration ecology 2022

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Editorial: Women in conservation and restoration ecology 2022

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Editorial on the Research Topic
Women in conservation and restoration ecology 2022

Women scientists conduct ground-breaking research across the world. Yet, they made up to only 31.7% of all researchers globally in 2021, according to a recent report from the United Nations Educational, Scientific and Cultural Organization (UNESCO, 2024), and only about 4% of Nobel Prize laureates for science and medicine were women as of 2023 (The Nobel Prize, 2024). More broadly, the World Economic Forum (2023) reports that while workforce participation (based on LinkedIn profiles) of women and men is approximately equal in non-STEM fields, in STEM fields women represent only about 29% of workers, and the share of women's participation declines as positions become more senior. This is in part due to the "leaky pipeline" phenomenon, in which numbers of women in STEM fields decline progressively from student and early career roles to senior positions (Resmini, 2016). This leaves fewer women available for senior positions and the opportunities and accolades that come at a later career stage. It is also due to deeply entrenched but hidden biases faced by those who remain – which also contribute to the leaky pipeline in a persistent feedback loop. In short, while there are fewer women at senior levels, it is not because they are less competent or less passionate than men. Even accounting for this, women are still experiencing the consequences of unconscious bias throughout their careers. The academic currency for success is publications (preferably in high impact journals), research funding (preferably national and competitive) and esteem (respect and impact in one's field); there is evidence of gender bias in all of these.

Women get fewer opportunities for high impact publications. Nature recently published an editorial headlined "Nature publishes too few papers from women researchers – that must change" (Nature, 2024). In it, the authors note that only 17% of corresponding authors identify as women. They also note geographic differences, with percentages ranging from 4% (Japan) to 22% (United States), and find that acceptance rates among manuscripts sent for review were lower for woman-authored papers (46%) than for those authored by men (55%).

Women are less likely to apply for competitive national funding (Schmaling and Gallo, 2023). In Canada, for example, according to the most recent funding statistics from the Natural Sciences and Engineering Research Council, only 24% of applicants identify as women, though success rates are similar for women and men (NSERC, 2023). Among early career researchers, women make up 37% of applicants and awardees. These statistics are reflected in other countries, such as Australia (Kingsley et al., 2023), the United States (Rissle et al., 2020), and the United Kingdom (Head et al., 2013; EPSRC, 2022).

In conservation careers, men influence conservation and science decisions more than women (James et al., 2023). The Nature Conservancy (TNC), as one of the world's largest conservation non-profit organizations, provides a case study to better understand how women publish relative to men in conservation science. A review of all papers from Web of Science with at least one Nature Conservancy author (1968–2019) found that women are underrepresented: only 36% of authors were women, 31% of all first authorships were women, and 24% of last authorships were women. Women in the Global South were the least represented group, making up less than 2% of all TNC authorships (James et al., 2022).

At the invitation of Frontiers, we, the Guest Editorial team, assembled a collection of conservation and restoration ecology research conducted by women scientists. This Research Topic celebrates the increasing contribution of women to this research field, and we hope its breadth and depth showcases some of the insightful work done by women and inspires the current and next generation of women scientists. A total of 11 contributions and 69 authors (nine original research articles and two reviews) report significant empirical and theoretical advances in conservation and restoration ecology, including also a study of gaps and gender biases in this field (listed in order of acceptance date):

- Use of runnels to mitigate marsh drowning (Watson et al.);
- Testing phylogenetic conservatism on the performance of seed germinability prediction models (Chen et al.);
- Impacts of fencing and grazing on insect diversity (Wang et al.);
- Pattern-building processes in vegetation recovery (Norris et al.);
- Use of movement data and physiological indicators to identify importance of habitat for migrating shorebirds (Linhart et al.);
- Gender bias in restoration and conservation (James et al.);
- Wetland restoration in tidal rivers (van Proosdij et al.);
- Integration of traditional ecological knowledge into land management (Souther et al.);
- Nutrient dynamics in created tidal marshes (Staver et al.);
- Dynamics of invertebrate communities in salt marsh pools after 50 years of restoration (Noel et al.);
- Global trends in geospatial conservation planning (Cobb et al.).

While the papers in this Research Topic partly reflect the fields of expertise and backgrounds of the guest editors, we hope that this Research Topic will help foster an international network of women researchers working in conservation and restoration. We aim to provide an impetus for future collaborations and discussions. We also hope that this Research Topic of discoveries helps to support and encourage other women wishing to pursue a career in conservation and restoration ecology.

Author contributions

IM: Conceptualization, Investigation, Writing – original draft, Writing – review & editing. DH: Conceptualization, Investigation, Writing – original draft, Writing – review & editing. MB: Conceptualization, Investigation, Writing – original draft, Writing – review & editing. CM: Conceptualization, Investigation, Writing – original draft, Writing – review & editing. AC: Conceptualization, Investigation, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Runnels mitigate marsh drowning in microtidal salt marshes

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As a symptom of accelerated sea level rise and historic impacts to tidal hydrology from agricultural and mosquito control activities, coastal marshes in the Northeastern U.S. are experiencing conversion to open water through edge loss, widening and headward erosion of tidal channels, and the formation and expansion of interior ponds. These interior ponds often form in high elevation marsh, confounding the notion applied in predictive modeling that salt marshes convert to open water when elevation falls below a critical surface inundation threshold. The installation of tidal channel extension features, or runnels, is a technique that has been implemented to reduce water levels and permit vegetation reestablishment in drowning coastal marshes, although there are limited data available to recommend its advisability. We report on 5 years of vegetation and hydrologic monitoring of two locations where a total of 600-m of shallow (0.15–0.30-m in diameter and depth) runnels were installed in 2015 and 2016 to enhance drainage, in the Pettaquamscutt River Estuary, in southern Rhode Island, United States. Results from this Before-After Control-Impact (BACI) designed study found that runnel installation successfully promoted plant recolonization, although runnels did not consistently promote increases in high marsh species presence or diversity. Runnels reduced the groundwater table (by 0.07–0.12 m), and at one location, the groundwater table experienced a 2-fold increase in the fraction of the in-channel tidal range that was observed in the marsh water table. We suggest that restoration of tidal hydrology through runnel installation holds promise as a tool to encourage revegetation and extend the lifespan of drowning coastal marshes where interior ponds are expanding. In addition, our study highlights the importance of considering the rising groundwater table as an important factor in marsh drowning due to expanding interior ponds found on the marsh platform.

KEYWORDS

runnel, sea level rise, restoration, salt marsh, climate change, mitigation and adaptation, remote sensing, ditching

1 Introduction

Photogrammetric analysis has shown that coastal salt marsh loss in New York and southern New England (United States) over the past 40 years has occurred at rates of 5% per decade (Smith, 2009; Berry et al., 2015; Watson et al., 2017; Krause et al., 2020). These coastal salt marsh losses have occurred primarily due to symptoms associated with accelerated relative sea level rise (SLR), such as marsh edge loss due to erosion, widening and expansion of the tidal channel network, and the formation and coalescence of interior ponds (Figure 1; Hartig et al., 2002; Mariotti, 2020). Crab herbivory, fungal pathogens, and nutrient pollution have also been implicated as stressors (Deegan et al., 2012; Elmer et al., 2013; Smith and Green, 2015; Raposa et al., 2018). Another important exacerbating factor to the formation of open water areas has been modifications to tidal hydrology, including agricultural embankments and ditching (Burdick et al., 2020; Smith et al., 2021). However, the recognition that marsh loss—as a symptom of climate change—is already occurring has led to a shift in how coastal land managers are approaching restoration and conservation (Watson et al., 2017; Wigand et al., 2017).

Over past decades, the restoration of coastal salt marshes in New York, New Jersey, and New England has focused on reestablishing tidal hydrology to restore ecosystem functions lost when marshes were filled and diked, and to reverse the invasion of *Phragmites australis*. *Phragmites australis* is a cryptic invasive species (Saltonstall, 2002). Its increased abundance over past decades has been associated with negative effects to vegetation and bird diversity (Chambers et al., 1999), and it is one of the most aggressively managed plants in the United States (Rogalski and Skelly, 2012). In addition to *Phragmites*-removal, restoration projects traditionally have focused on the removal of tidal restrictions and dikes to restore or amplify tidal exchange, the removal of fill to reduce elevations, and hydrological alterations to restore water to the landscape, such as plugging the extensive ditches constructed during the Works Progress Administration, or the direct excavation of ponds (Roman et al., 2002; Vincent et al., 2013; Powell et al., 2020). However, support for such approaches is waning because such actions have the potential to compromise the long-term stability of coastal habitats and survival of wildlife given accelerations in SLR. For example, a recent study that focused on the effects of restoration to the saltmarsh sparrow (*Ammodramus caudacutus*), which is a marsh-breeding bird considered globally vulnerable to extinction, found that *Phragmites* removal and tide restoration negatively impacted sparrow reproductive success, as it created habitats unsuitable for

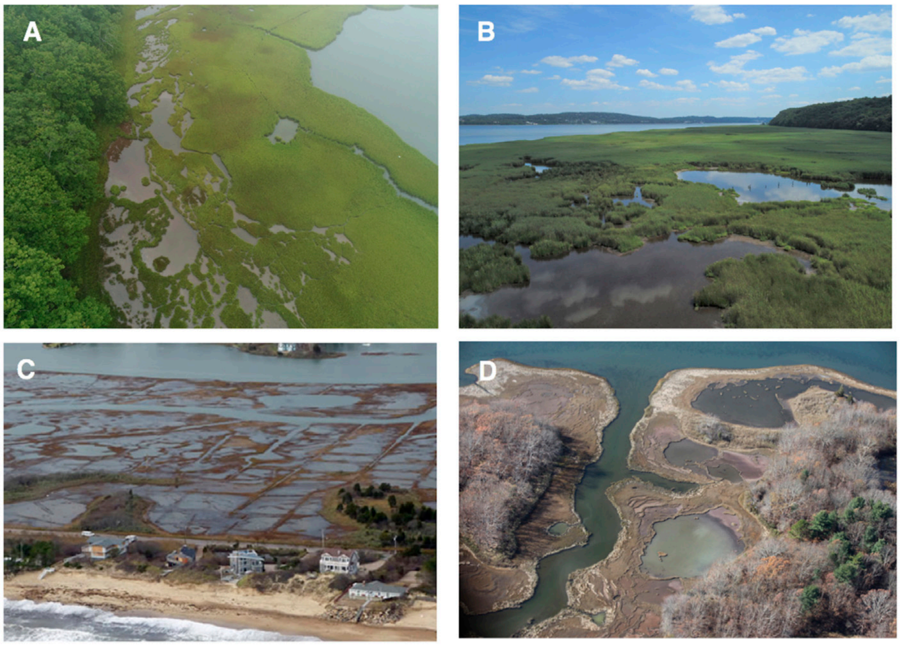

FIGURE 1
Examples of locations where ponding is contributing to coastal marsh habitat loss in New York and New England: **(A)** Bass Creek, Shelter Island, NY where ponds are expanding at the marsh-upland border; **(B)** Piermont Marsh, NY where ponds on the marsh interior are expanding; **(C)** Winnapaug Pond, RI where ponds have formed in grid-ditched marsh islands; and **(D)** the Pettaquamscutt River Estuary, RI, the focus of this study, where the marsh platform is dominated by large shallow ponds. Photographs courtesy of (A/B) Johannes Krause/Florida International University, **(C)** Jonathan Stone/Save The Bay, and **(D)** Greg Thompson/USFWS.

sparrow nesting (Elphick et al., 2015). As such, restoration and conservation of coastal marshes is shifting away from increasing inundation towards extending the lifespan of drowning marshes.

A project that exemplifies this shift in priorities has been the reconstruction of drowning and eroding marsh islands in Jamaica Bay, NYC (Campbell et al., 2017). The Jamaica Bay restoration project used 190,000 m^3 of dredged sediment in combination with planting over 600,000 plant plugs to build the elevation of several disappearing marsh islands, thereby lengthening their lifespan (Messaros et al., 2010). In addition to this work in NYC, which began in 2003, a series of projects were constructed following Superstorm Sandy that focused explicitly on the dual goals of community and coastal marsh ecosystem resilience. Such approaches included the beneficial use of sediment placement to build marsh elevation, shoreline protection through installation of living shorelines, and facilitation of upland migration of marsh habitats (Wigand et al., 2017; VanZomeren et al., 2018; Weis et al., 2021).

One of the newer and less well known techniques that has been piloted over the past decade to extend the lifespan of drowning marshes is the strategic use of runnels, or channel extension features, to drain areas of ponded water found on the marsh platform with the goal of encouraging coastal marsh revegetation (Besterman et al., 2022; Perry et al., 2022). Ponds can be natural marsh features that provide important habitat functions (Adamowicz and Roman, 2005; Smith and Niles, 2016); however, the formation and expansion of shallow depressions filled with standing water that do not drain during daily tidal flow on the marsh platform may also contribute to permanent marsh loss (Mariotti, 2016). This is particularly true when this impounded water is associated with hydrologic modifications, such as agricultural embankments or extensive grid-ditching networks which are often associated with spoils, or where shallow ponds are experiencing runaway expansion caused by wind-wave erosion (Mariotti, 2020) (Figure 1). Also, some impounded water areas are a legacy of altered hydrology and agricultural embankments (Adamowicz et al., 2020).

Ponds form on the marsh landscape where the water table is at or above the marsh surface. Ponds are often described as transitory features, as their formation and capture by the tidal channel network and subsequent drainage has been recognized (Collins et al., 1987; Wilson et al., 2014; Supplementary Figure S1). Cyclic processes of pool formation, enlargement through expansion and mergence, drainage *via* tidal creek incision and recolonization by marsh vegetation has been described for New England, specifically in Maine and Massachusetts (Wilson et al., 2009, 2014), as well as southern New England and the Mid-Atlantic (Smith and Pellew, 2021). Observations of pond drainage resulting from creek incision demonstrate that connecting a pond with the tidal marsh drainage network occurs naturally and results in plant recolonization (Supplementary Figure S1; Smith and Pellew, 2021). The construction of runnels (typically 0.15–0.3 m wide and in depth) is designed to mimic this natural process of pond channel capture that occurs in tidal marshes. However, in microtidal estuaries, this process may take several decades or not occur, as these systems lack robust tidal exchange. Reversing marsh drowning through the installation of runnels can mimic and accelerate the natural process of drainage that occurs following pond capture by the tidal channel network, and can thus be an important tool to counteract marsh drowning (Taylor et al., 2020; Weis et al., 2021; Besterman et al., 2022).

Connecting a marsh pool with a tidal creek can encourage revegetation through promotion of surface drainage (Wilson et al., 2014), but effects on sub-surface drainage are previously unstudied. Generally, ponds occur on the marsh platform due to the high and invariable water table, while the water table adjacent to tidal creeks is more variable (Montalto et al., 2006). Areas adjacent to tidal channels experience high variability in the level of the water table—often decimeters above the marsh surface at high tide and decimeters below the marsh surface at low tide. Adjacent to tidal channels, the low tide water table is typically far below the marsh surface due to the enhanced hydraulic gradient found at the channel edge (Figure 2). Conversely, marsh ponds usually occur on the marsh platform, where the hydraulic gradient is much smaller; and the water table tends to sit close to the marsh surface and vary little diurnally (Montalto et al., 2006). This spatial variability in water table dynamics and through-marsh groundwater flow contributes to the ecological zonation apparent in salt marshes, with larger growth forms of plants found on channel edges where the marsh supports better drained soils, and stunted growth forms in the marsh interior, where the water table is often stagnant and soils are exposed to salinity and sulfide accumulations due to poor drainage (Nuttle, 1988; Wilson et al., 2015). By installing runnels that drain water off the marsh surface, enhanced sub-surface drainage may extend more broadly across the marsh platform.

The purpose of the present study was to ascertain whether the construction of channel extension features (in 2015 and 2016) has contributed to vegetation reestablishment and enhanced drainage at a Rhode Island estuary where pond formation and expansion has contributed to marsh vegetation loss over the past century (Watson et al., 2014; Watson et al., 2017). A Before-After Control-Impact (BACI) study design (Stewart-Oaten et al., 1986) was used to compare vegetation coverage and water table dynamics. Analysis of high-resolution satellite imagery and vegetation surveys were used to establish vegetation trends, and well installation and groundwater monitoring were implemented to establish whether runneling lowered groundwater levels. Results of this study improve our understanding of marsh groundwater dynamics, as well as the advisability of marsh drainage enhancements as a tool to build coastal ecosystem resilience to SLR.

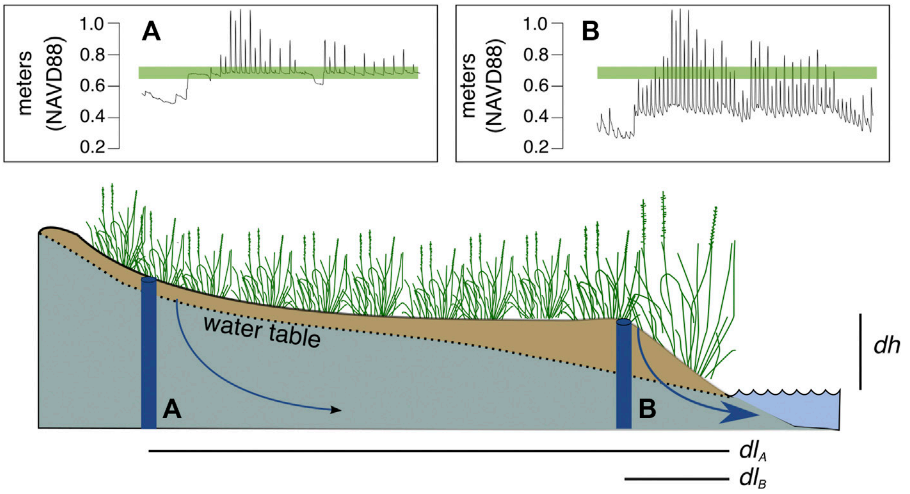

FIGURE 2
In coastal marshes, the water table tends to be close to the marsh surface (indicated by the green line) in the marsh interior, i.e., 30 m+ from the marsh edge, demarcated in this figure as location **(A)**. Along the edge of the marsh where it intercepts the tidal creek, the water table drops to much lower elevations at low tide, demarcated in this figure as location **(B)**. This is because through-marsh drainage is proportional to the product of soil hydraulic conductivity (*K*) and the hydraulic gradient (*dh*/*dl*). Values for the hydrologic gradient are highest adjacent to the tidal channel but decrease proportionally with distance (*l*) from the creek edge. This explains why drainage is reduced at location **(A)** in comparison with location **(B)**. Water table elevations were measured in spring of 2016 at Colt State Park, Bristol, Rhode Island (41.6769°N, 71.2985°W).

2 Materials and methods

2.1 Study site

Research was conducted at the Pettaquamscutt River Estuary (PRE) (also called the Narrow River Estuary), part of the USFWS John H. Chaffee National Wildlife Refuge, Narragansett, Rhode Island (41.4547°N, 71.4533°W). The PRE is a 15 km-long river/estuarine system comprised of a tidal inlet, coastal estuary, and two kettle ponds, spanning the towns of Narragansett, North Kingstown, and South Kingstown, RI, United States (Figure 3). The PRE drains a 35 km^2 watershed, of which 35% is classified as developed, and it supports a variety of diverse estuarine habitats, including eelgrass beds, estuarine channels, tidal mudflats, and salt marsh. Water column salinity ranges from 24 to 27‰ (Greening et al., 2018). Based on this study, we found the average diurnal range of tide to be 0.43 m at our research sites. The two focus areas, Canonchet and Middlebridge (Figure 3), varied somewhat in their inundation patterns. Canonchet has a slightly higher elevation and was found to be inundated 7.1% of the time, while Middlebridge was found to be inundated 14% of the time.

Runnels were constructed as part of resilience restoration actions occurring during 2015–2018, which included installation of living shorelines, dredging and sediment deposition to raise marsh elevation, and runneling to restore marsh hydrology in parts of the PRE (Wigand et al., 2017; Perry et al., 2022). This study focuses only on effects of runnels at Canonchet and Middlebridge; sediment addition and living shoreline installation were undertaken outside our area of study. Installation of these channel extensions was chosen as a restoration action because a substantial amount of habitat at the PRE was considered degraded due to a lack of drainage, and marsh elevation change data suggested that marsh accretion was not keeping pace with rates of SLR (Watson et al., 2014; Raposa et al., 2017). Improving drainage was a specific concern due to the focus on restoring high marsh vegetation to support marsh breeding birds (Berry et al., 2015), and because an analysis of vegetation distribution patterns suggested high marsh vegetation was controlled by drainage rather than by elevation (Watson et al., 2014). Runnels were constructed in two separate areas: an area south of the tidal inlet which we refer to as “Canonchet” due to its proximity to Canonchet Farm, and a northerly site we refer to as ‘Middlebridge’ due to its location north of Middlebridge Road (Figure 3). A total of 605 m of runnels (476 m at the Canonchet site; 129 m at the Middlebridge site) were constructed in spring of 2015 and 2016 by hand and using a low ground pressure excavator, connecting ponded areas with existing ditches or tidal channels (Figure 3). The runnels were 0.15–0.30 m in diameter and in depth. The peat excavated was retained on the marsh platform, but outside of the footprint of the vegetation transects. Although needed permits vary by jurisdiction, to complete this work, permits were obtained from the Coastal Resources Management Council (a State Agency), and the US Army Corps of Engineers.

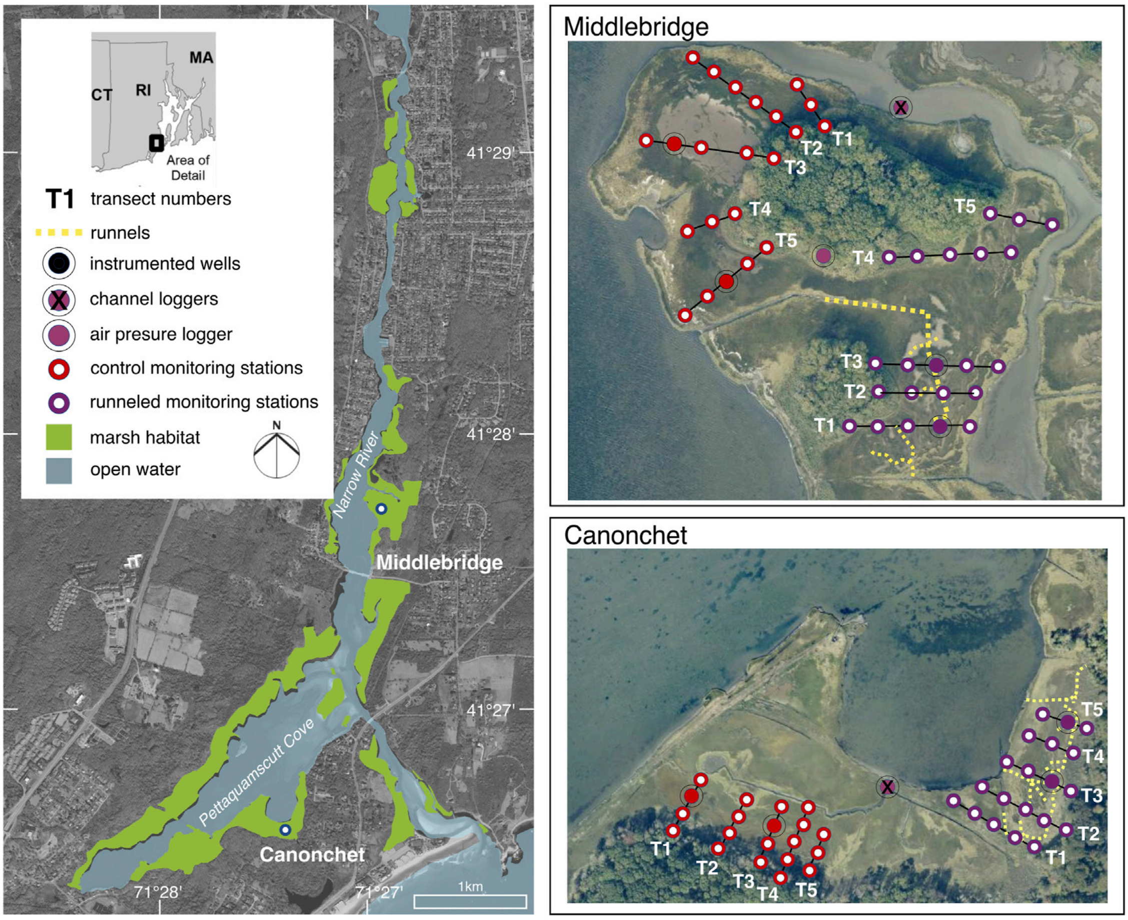

FIGURE 3
Location map showing the Narrow River Estuary, including runneled and control areas at Middlebridge and Canonchet. Vegetation monitoring transects are depicted as T1–T5. Red areas are control areas, purple are runneled areas. Groundwater wells monitored (focal wells) are depicted by a circle with a solid fill.

TABLE 1 Dates of vegetation monitoring and satellite image collection used for vegetation change analysis. Tide level is from the Newport, RI, tide station. All satellite images were 4-band, pansharpened imagery with 0.5 m spatial resolution.

Vegetation monitoring	Satellite imagery date	Satellite	Tide level (m)
18 September 2014	5 July 2014	World View-2	0.76
5 August 2015	2 August 2015	World View-2	−0.09
7 August 2016	29 August 2016	World View-2	0.76
12 September 2017	12 June 2017	World View-3	0.09
21 August 2018	23 March 2018	World View-3	0.30
16 September 2019	4 April 2019	World View-2	0.15

2.2 Restoration monitoring

A Before-After Control-Impact (BACI) study design was used to study the effects of runnel excavation (Stewart-Oaten et al., 1986), with pre-construction plant surveys conducted in 2014. A series of transects were established in summer of 2014, with vegetation monitoring stations established every 12–20 m and groundwater monitoring stations installed every 25 m across the transects (Figure 3).

2.2.1 Vegetation

Vegetation monitoring was conducted in 2014–2019 and coincided with peak biomass (mid-August through mid-September) (Table 1). Plant species composition and abundance along transects were measured along five transects per site randomly situated in each experimental unit traversing the marsh from creek or open water to the upland edge (Roman et al., 2001). Vegetation was sampled in 1-m^2 plots located along transects, yielding a total of 20 plots each along the five transects. Using the point-intercept method (Roman et al., 2001) vegetation at 50 points in the plot was recorded. These data were used to calculate percent cover for each species; values may sum to excess of 100% where dowels touched multiple plants.

Changes in vegetation cover from 2014 to 2019 were also monitored using image classification and spectral indices calculated from georeferenced satellite imagery (Table 1). Imagery of the study sites was collected from spring and summer months. Habitat classification of annual satellite imagery was performed using a maximum likelihood classification algorithm using ENVI version 5.4 (Exelis Visual Information Solutions, Boulder, Colorado, United States) and ArcMap version 10.2.2 (Environmental Systems Research Institute, Redlands, CA, United States) (Otukei and Blaschke, 2010). Classification categories included fully vegetated, patchy vegetation, and open water. Annual satellite imagery was further examined using the normalized difference water index (NDWI) and a modified bare soil index (BSI) (Gao, 1996; Azizi et al., 2014). These band indices were calculated as:

$$NDWI = \frac{green - NIR}{green + NIR} \tag{1}$$

$$BSI = \frac{[red + blue] - green}{[red + blue] + green} \tag{2}$$

where $NDWI$ refers to the normalized reflectance difference between the green and near-infra red [NIR] spectral bands (510–581 nm and 780–920 nm, respectively), and the BSI refers to the ratio of the difference between the sum of the red (655–690 nm) and blue (450–510 nm) spectral reflectance and the green (510–581 nm) reflectance to the sum of the red, blue, and green reflectances. $NDWI$ was used to estimate the amount of open water habitat, while BSI was used to determine the area of bare soil.

2.2.2 Water table and porewater salinity

The water table was monitored during the years 2014 through 2018 using shallow (0.70-m depth; 10 cm diameter; screened across the full 0.7-m length) wells installed along transects (Figure 3). At Canonchet and Middlebridge, two wells each were instrumented and monitored in control and runneled areas, as well as in the tidal channel (10 total; 4 runneled, 4 control, 2 channel). Wells were instrumented with pressure transducers during fall of each year (Table 2), with water levels measured at a 15-min interval, with reference water levels measured upon deployment and removal. Hydraulic conductivity of the marsh sediments was measured in spring and fall of 2020 from bail down tests performed in the four focal wells at each site (Figure 3) where the water was removed from the well using a pump and the rate at which the water rose was recorded (Hvorslev, 1951).

TABLE 2 Dates when wells were instrumented with water level loggers. Four wells and two channels were instrumented, and an air pressure logger was deployed at Middlebridge in a shaded upland area. Figure 3 depicts the location of instrumented wells and loggers.

Dates	Loggers	Purpose
18 September–30 October 2014	Solinst levelogger 5	Well monitoring
9 October–18 November 2015	Hobo U20L	Well monitoring
22 October–14 December 2016	Hobo U20L	Well monitoring
22 September–27 November 2017	Hobo U20L	Well monitoring
2 October–26 November 2018	Hobo U20L	Well monitoring
14 September 2020	Hobo U20L	Bail down test
7 October 2020	Hobo U20L	Bail down test

Porewater salinity monitoring was conducted biweekly at low tide during the growing season following the protocol developed by Roman et al. (2002). Porewater was taken from 15 cm below the marsh surface using a stainless-steel probe, near the PVC wells mentioned above. The salinity of the porewater was measured with a refractometer. If water was not able to be collected at 15 cm depth, the probe was inserted to 30 cm, then 45 cm if necessary. If porewater was not able to be collected in this manner, water was taken directly from the well.

2.2.3 Data analysis

2.2.3.1 Vegetation comparisons between treatments

Comparison of vegetation cover (bare and dominant plant species), species richness, and the Shannon Diversity Index (SDI) were carried out using a repeated measures, multi-factor ANOVA, with transect nested within the treatment variable. The effects of time (before, 2014; during, 2015–2016; after, 2017–2019) and treatment (runneled vs. control) were examined for each site (Canonchet and Middlebridge). Evaluations of treatment significance were performed using transect variability as the associated error term, and evaluations of the time by treatment interaction significance and individual pairwise comparisons within the context of that interaction were done using transect by time variability as the associated error term. The model was fit using means of normal score-transformed values for each transect.

2.2.3.2 Groundwater elevation comparisons

Daily mean, minimum, and maximum tide levels were extracted from water level data sets using package

VulnToolkit (Hill and Anisfeld, 2021) in R version 3.5.2 (R Core Team, 2018). Where tidal variations were not detected in marsh groundwater records using VulnToolkit, the timing of low and high tides in the channels was used to identify corresponding high and low tides from the groundwater levels. Mean amplitude ratios (A_r) were calculated for each well as the ratio of the amplitude of the water fluctuation in the marsh well (A_x) to the amplitude of the water fluctuation in the tidal channel (A_s) (Jiao and Post, 2019).

$$A_r = \frac{A_x}{A_s} \tag{3}$$

Hydraulic conductivity was measured twice for focal wells using a bail down test, and saturated hydraulic conductivity was calculated according to Hvorslev's Method (Hvorslev, 1951) for an unconfined groundwater aquifer:

$$K = \frac{r^2 \ln \frac{L_e}{r}}{2L_e} \frac{\ln \frac{h_1}{h_2}}{t_2 - t_1} \tag{4}$$

where K = hydraulic conductivity in cm s^{-1}, r = radius of well; L_e = the length of the well or piezometer that is screened; t_1, t_2 = time points during refilling; h_1, h_2 = head height during refilling.

Daily mean, minimum, and maximum groundwater elevations at sites were examined to compare effects of treatment (runneled vs. control) and time (pre- vs. post-runneling) effects using two-factor ANOVAs. Year and treatment were factors, and a year by treatment interaction term was produced. We specified an autoregressive error correlation structure to help account for the non-independence of measurements. Following the BACI design, we first evaluated the interaction term. If the interaction term was significant, control vs. runneled differences would be year-specific and year differences would be treatment-specific. If the interaction was not significant, evaluation would depend on whether the main effect for the given factor was significant. For example, if year was determined to be a significant main effect but the interaction was not, then this would indicate that year differences were consistent regardless of whether the data were from a control or an runneled location and were presented that way. Pairwise differences were evaluated using Bonferroni's adjustment.

2.2.3.3 Salinity comparison between treatments

Salinity was examined along selected transects at each runneled and control area. The effect of year (pre- vs. post-runneling) on salinity was examined using a multi-factor ANOVA with treatment (control vs. runneled) and time as factors, and transect as a nested random effect within treatment. Pairwise comparisons performed with interaction combinations were carried out using Bonferroni adjustment.

3 Results

3.1 Vegetation transect data

At Canonchet, the area of bare ground coverage was greater prior to runnel construction than it was post-runneling (2017–2019) for runneled locations, while at the control locations there was no significant difference between pre- and post-runneling bare ground coverage (Figure 4, Supplementary Figure S2; Supplementary Table S1). Before runneling, there was no difference between control and runneled locations, but after runneling, control areas had greater bare ground cover (10.5% in control areas vs. 0.94% in runneled areas in 2019). Similar to Canonchet, at Middlebridge there was a significant ($p < 0.001$) treatment by time interaction. The pre-runneling bare ground coverage (13.5%) was significantly greater ($p < 0.001$) than the post-runneling bare ground (3.5%) in runneled lobations vs. post-runneling control bare ground (9.0%).

3.1.1 *Spartina alterniflora* coverage

The coverage of *S. alterniflora* significantly increased over time at the runneled locations at Canonchet ($p = 0.044$) (Figure 4, Supplementary Figure S2). While there was no difference in coverage of *S. alterniflora* between the control and runneled locations prior to runnel installation, the coverage of *S. alterniflora* was significantly greater at the runneled locations post-runneling at Canonchet (28.4% at runneled vs. 24.2% at control) ($p = 0.026$). Prior to runneling, the coverage of *S. alterniflora* at the Middlebridge site was significantly greater at the control locations compared to the runneled locations (12.2% at runneled areas vs. 29.4% at control areas) ($p < 0.001$), but coverage was significantly greater at the runneled locations post-runneling (33.5% at runneled areas vs. 25.7% at control areas) ($p < 0.001$) (Supplementary Table S1).

3.1.2 *Spartina patens* coverage

Prior to runneling there was no significant difference in the coverage of *S. patens* between the runneled and control locations at the Canonchet site (11.3%), but post-runneling, the coverage of *S. patens* was significantly greater at the runneled locations compared with the control locations (14.9% at runneled areas vs. 8.1% at control areas) ($p = 0.001$) (Figure 4, Supplementary Figure S2; Supplementary Table S1). In contrast, the coverage of *S. patens* at the Middlebridge site was significantly greater ($p = 0.008$) at the control locations (12.2%) compared with the runneled locations (7.6%) post-runneling, and there were no significant differences in coverage pre-runneling (10.6%), although there was a trend towards greater *S. patens* coverage in the control area (Supplementary Table S1).

3.1.3 Plant diversity

At Canonchet, species richness increased at runneled but not control areas ($p < 0.001$; post-runneling > pre-runneling). The treatment by time interaction for species richness was significant

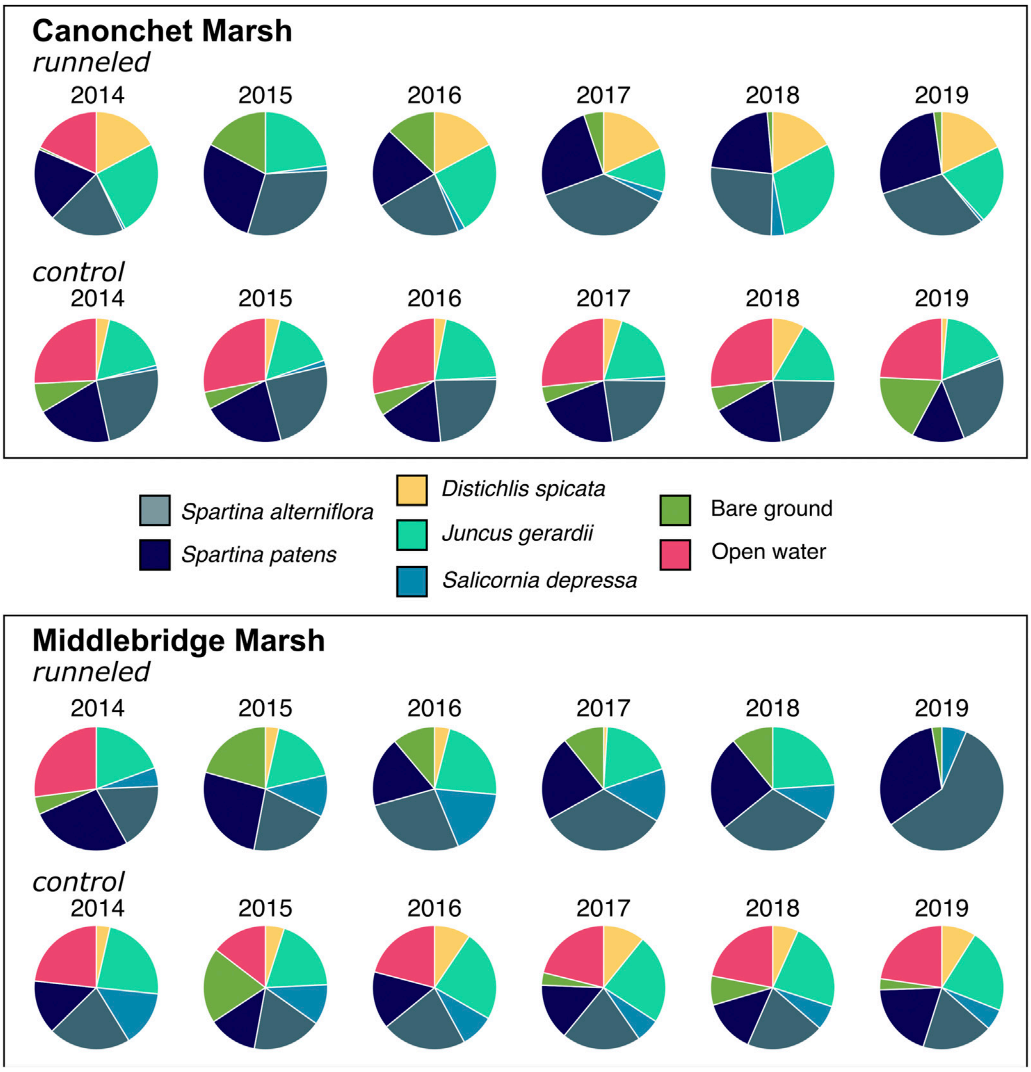

FIGURE 4
Relative abundance of *S. alterniflora*, *S. patens*, *D. spicata*, *J. gerardii*, *S. depressa*, and area of open water and bare ground along runneled and control transects at Canonchet and Middlebridge in 2014 (pre-runneling) through 2019. Runneling occurred in 2015 and 2016.

(p = 0.020) at the Middlebridge site. Prior to runneling the control locations at Middlebridge had significantly greater (p = 0.006) species richness, but post runneling there was no significant difference between the runneled and control treatments. At Canonchet, the SDI increased over time in runneled but not control areas (Supplementary Table S1). At Middlebridge, the SDI was significantly greater ($p < 0.001$) at control than runneled locations.

3.2 Satellite imagery analysis

Analysis of satellite imagery suggested that fully vegetated habitat cover increased in both runneled locations, while mixed results were found in the control areas (Figure 5; Supplementary Table S2). At Canonchet, the fully vegetated area within the runneled site increased from 60.4% to 96.7% between 2014 and 2019, while in the control area the fully vegetated area decreased from 67.8% to 61.5%. Trends in open water and patchy vegetation (<25% plant cover) cover were opposite, where patchy vegetation coverage decreased from 30.8% to 3.3% in the runneled area at Canonchet, while patchy vegetation cover increased from 31.8% in 2014 to 34.9% in the control area. At Middlebridge, the area that was fully vegetated in the runneled area increased from 47.5% to 74.5% between 2014 and 2019, while in the control area, the fully vegetated area increased in extent from 52.1% to 63.8%. While the control area at

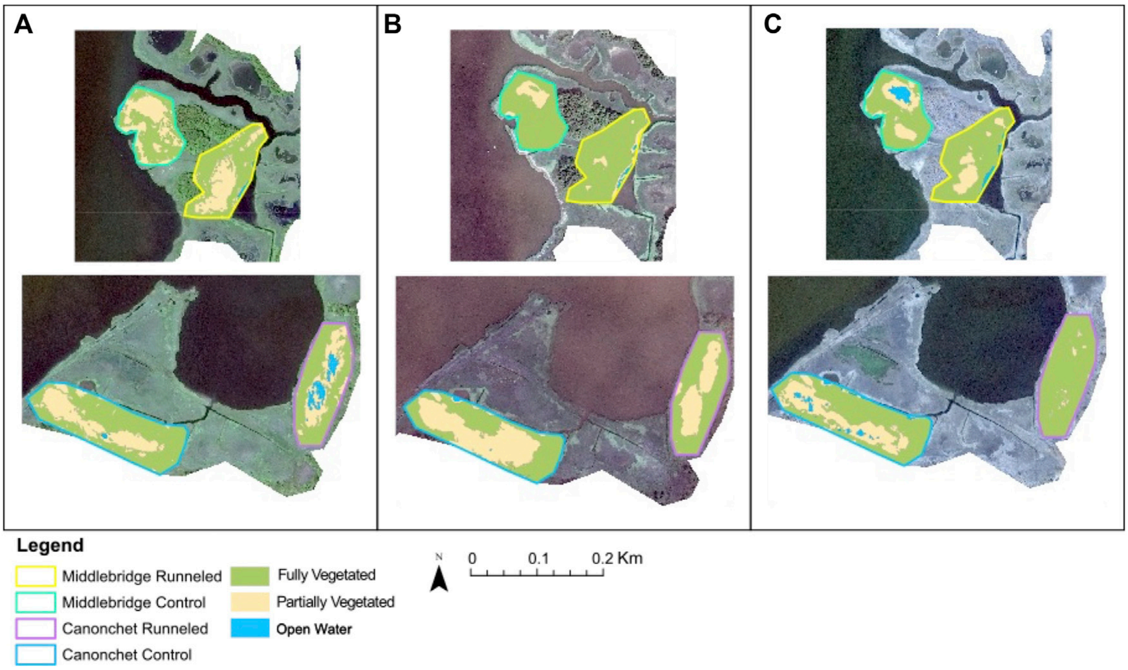

FIGURE 5
Satellite imagery analysis showing **(A)** 2014; **(B)** 2016; **(C)** 2019. The top row shows Middlebridge and the bottom shows Canonchet.

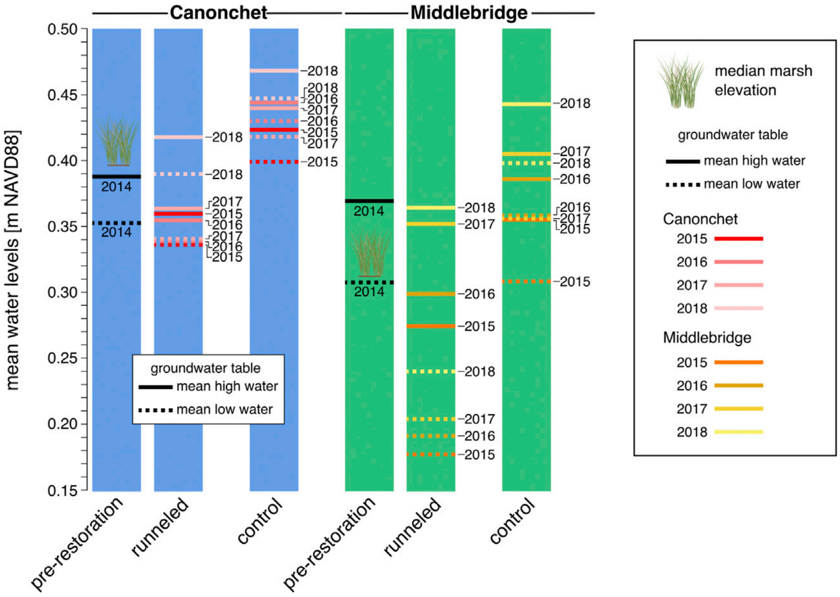

FIGURE 6
Water levels at Canonchet and Middlebridge. Mean marsh elevation is denoted on the figure using a grass icon. Overall, water levels were lower in runneled areas; at Middlebridge tidal range was also greater in runneled areas. Mean, standard deviation, and number of observations can be found in Supplementary Table S6.

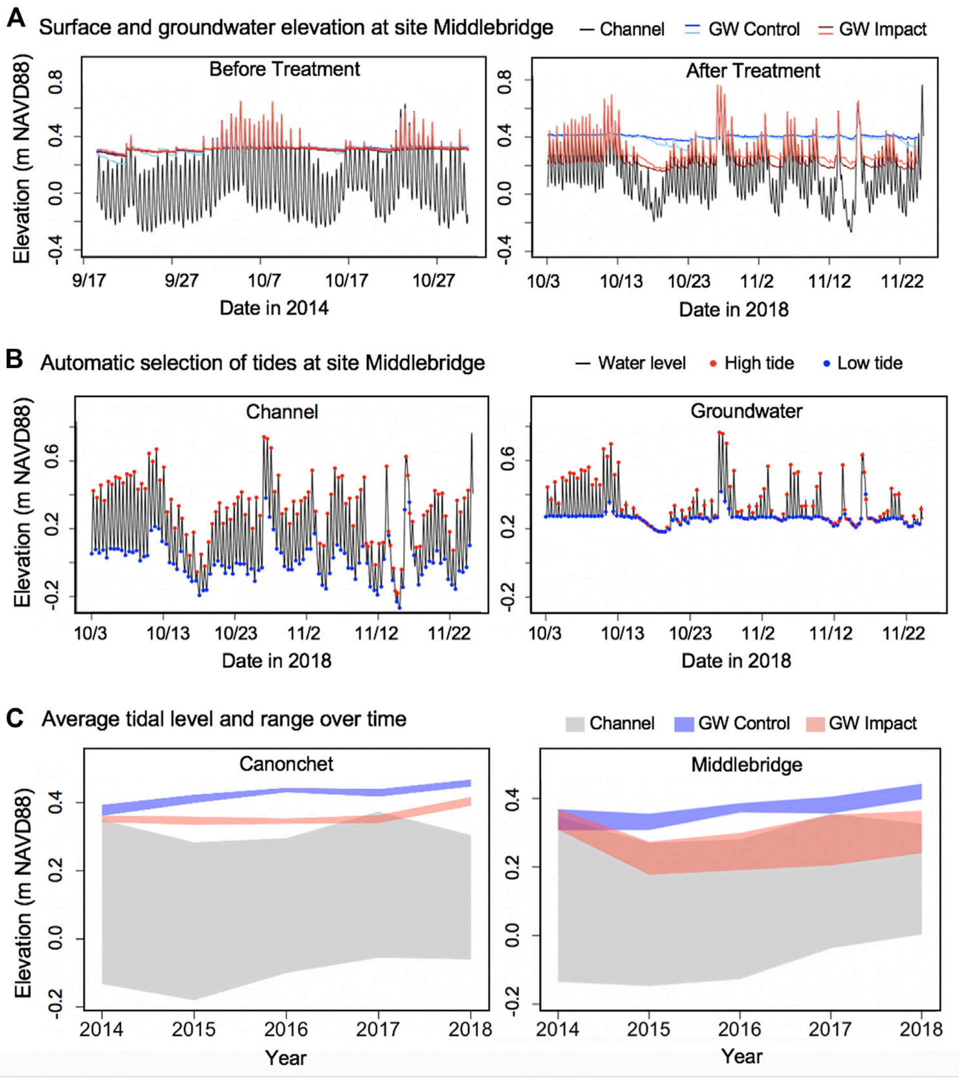

FIGURE 7
Groundwater levels before and after runnel treatment including: **(A)** Channel surface water and groundwater elevation at groundwater wells at Middlebridge marsh in the first and final year; **(B)** Example result of automatic selection of the high and low tides in the channel and the groundwater datasets using the VulnToolkit package; **(C)** Tidal level and range in the channel and the groundwater wells in the control versus runneled (or impact) treatments. The shaded ribbon represents the tidal range from the average high tide level to the average low tide level each year. The high and low tide levels of the two wells in the control treatment and the two wells in the runneled treatment were each averaged together. Surface and groundwater elevation and automatic selection of tides at Canonchet can be found in Supplementary Figure S5.

Middlebridge was found to increase in vegetation extent, the increase in full vegetation coverage was 2.3 times greater in the runneled area than the control area. Patchy vegetation coverage at the runneled site at Middlebridge decreased from 54.4% to 25.5%, while at the control site patchy vegetation decreased from 47.9% to 27.9%. Band index calculations suggested a decrease over time in open water and bare soil in the runneled but not control area at Canonchet, but no difference was found at Canonchet (Supplementary Figure S2).

3.3 Water table

The mean groundwater table elevation at Canonchet was 0.36 m NAVD88 in control and runneled areas in 2014 (Figures 6, 7). In 2015, the water levels averaged 0.40 m NAVD88 in control areas and 0.34 m NAVD88 in runneled areas; water levels on average were 6-cm lower in the runneled area. From 2015 to 2018, water levels at Canonchet averaged 7-cm lower in the runneled vs. control areas. The mean groundwater table elevation at

Middlebridge was 0.32 m NAVD88 in control and runneled areas in 2014 (Figures 6, 7). Starting in 2015, the runneled areas had water table elevations that were on average 12-cm lower in the runneled vs. control areas. Overall, there were positive upward trends in water table elevations of 1.7–1.9 cm yr^{-1} for the control areas, and the runneled areas excluding the 2014–2015 period (during which a drop in water levels was observed).

Mean amplitude ratios were 0.061 at Canonchet in 2014, meaning that the tidal range in the groundwater table was 6.1% what was observed in the tidal channel. This mean amplitude ratio averaged 0.039 in 2015 through 2018. There was no observable difference in the mean amplitude ratio between control and runneled areas at Canonchet. In contrast, there were observed differences at Middlebridge. The mean amplitude ratio was 0.106 in 2014, and the ratio averaged 0.273 in runneled areas 2015–2018, and 0.092 in the control areas, meaning the runneled area had an 18% greater amount of tidal exchange.

Hydraulic conductivity was found to vary more across Canonchet than Middlebridge, with values as high as 0.3 cm s^{-1} at two locations and as low as 0.002 cm s^{-1}. Values were higher at Canonchet than at Middlebridge, although there was heterogeneity observed within sites as well (Supplementary Figure S4; Supplementary Table S3).

Groundwater daily maximum elevation was significantly greater ($p = 0.0117$) for control than runneled locations at Canonchet but not Middlebridge (Supplementary Table S4). The main effects of treatment and time were not significantly different for groundwater daily minimum or daily mean elevation, but there were significant treatment by time interactions. Groundwater elevations were generally greater for control than runneled sites in later years at Canonchet, but no statistical differences were evident at Middlebridge (Supplementary Table S4).

3.4 Porewater salinity

There was a significant ($p = 0.020$) treatment by time effect on salinity at Canonchet (Supplementary Table S5). At both the runneled and control locations there were greater salinities post-runneling (27.7 ± 10.3) compared with pre-runneling (20.5 ± 10.5) (mean ± SD). Salinity was similar at the runneled and control locations pre-and post-runneling (29.3 ± 12.3 in runneled areas vs. 26.7 ± 9.8 in control areas). In contrast at Middlebridge, while there was no effect of time on the salinity at the runneled and control locations, the magnitude of the salinity at the control locations was significantly greater than the runneled locations prior to (33.1 ± 5.5 vs. 24.8 ± 8.7) and after (35.8 ± 6.4 vs. 25.0 ± 8.1) runneling.

4 Discussion

4.1 Runnels as a tool to build ecosystem resilience

The installation of channel extension features, or runnels, in Northeastern US marshes is an approach adapted from mosquito management techniques used in Australia to reduce mosquito populations (Dale, 2008). Runnel installation in the US Northeast has involved excavating shallow drainage features with the aim of increasing the drainage of surface water impounded by topographic highs (both natural and human made features) to allow for recolonization of vegetation, but avoiding the negative impacts that have been observed from mosquito ditching (e.g., peat oxidation, erosion, tidal water impoundment, and subsidence) (Dale and Hulsman, 1990). Runnels are different from the pervasive mosquito ditches installed in Northeastern marshes (Kennish, 2001). They tend to be very shallow, so as to prevent root oxidation (Besterman et al., 2022); although it is recognized that mosquito ditches often started out narrow and shallow as well (Penny, 2010). They are simple tidal channel extension features (Taylor et al., 2020) and work with the natural hydrology. Mosquito ditches, in contrast, often had a high channel density, were installed as linear or gridded features, and often supplanted the pre-existing tidal channel hydrology. Over the past decade, runnels have been introduced in several sites in Rhode Island, at Buzzards Bay, Massachusetts, and at Cape May National Wildlife Refuge in New Jersey (Wigand et al., 2017; Weis et al., 2021). While the Australian literature suggests runnels are a successful mosquito control technique associated with minimal marsh damage (Dale and Knight, 2006), there has not previously been strong quantitative data available to demonstrate their ability to promote positive ecosystem benefits nor effects on the marsh water table in the Northeastern US. Rather, previous work has reported somewhat ambiguous effects (Raposa et al., 2019; Besterman et al., 2022) and with lower carbon dioxide assimilation at runneled locations than for reference sites, suggesting that runnels did not fully recover ecosystem function (Perry et al., 2022).

The formation of marsh ponds and associated vegetation die-off and habitat fragmentation is a principal mode of marsh loss in the Northeastern US (Figure 1) (Watson et al., 2017), and because constructing runnels is a relatively inexpensive and low disturbance intervention, runnel installation could be successfully employed at a wide number of locations. In the present study, we focused on analyzing effects of runneling on marsh vegetation, groundwater levels, flooding, and porewater salinity. Overall, we found that the area of bare ground decreased in runneled but not control areas, and *S. alterniflora* increased at runneled but not control sites, but differences in the cover of other plant species were site specific (Figure 4, Supplementary

Figure S2; Supplementary Table S1). Overall, runnels did not consistently increase coverage of high marsh species *Juncus gerardii* or *S. patens* in this or a related study (Besterman et al., 2022). These species are restoration targets as they comprise nesting habitat for the saltmarsh sparrow (*Ammodramus caudacutus*) that is threatened with extinction (Elphick et al., 2015). Although anecdotal reports suggest use of drained areas by marsh-breeding birds (Besterman et al., 2022), it is unclear if runneling improves nesting habitat.

Prior to runnels being installed, the groundwater table at instrumented wells typically sat very near the marsh surface, increased when spring tides flooded the marsh, and decreased during neap tidal cycles when surface flooding did not replenish water lost through evapotranspiration (Figures 2, 7), which has been estimated at 3–6 mm d^{-1} for species of *Spartina, Distichlis,* and *Salicornia* (Moffett et al., 2012). The perched water table found in these marshes pre-intervention can be described as tidal overheight, or the maintenance of the groundwater table in an unconfined coastal aquifer at an elevation significantly above sea level due to increased aquifer transmissivity at high tide (Jiao and Post, 2019). Tidal overheight has been well studied in intertidal habitats, such as beaches and intertidal marsh (e.g., Turner et al., 1997; Xin et al., 2022), and the groundwater table in coastal areas can typically be expected to sit above mean sea level by 20%–25% of the tidal amplitude (Phillip, 1973), although topography and hydraulic conductivity can affect the magnitude of the overheight (Li and Jiao, 2003). This tidal overheight is substantially less adjacent to tidal channels (Figure 2; Xin et al., 2013). The pre-intervention water table condition can help explain why marsh fragmentation and loss is occurring on the marsh platform away from tidal channels, where a perched water table is associated with waterlogged conditions and plant loss. This is a crucial point as high elevation marsh is typically not considered vulnerable to SLR (Cahoon et al., 2019). Although it is ultimately topographic highs that block the exit of surface water, contributing to waterlogging and creating these unvegetated interior depressions, our results suggest that an increase in the groundwater table resulting from SLR can contribute to die-off for high elevation marsh, as the water table intersects and rises above the marsh surface.

We observed increases in the groundwater table at both runneled and unmanipulated control sites over time (Figures 6, 7). In control sites, and in the runneled sites after 2015, the high tide and low tide water table levels increased by an average of 1.7–1.9 cm yr^{-1} from 2014 to 2018. This matched the upward trend in monthly mean high water (MHW) observed at the Newport, RI tide gauge from 2014 to 2018 (1.6-cm yr^{-1}; NOAA, 2022b). This short-term increase in mean high water from 2014 to 2018 is both a function of long-term trends and shorter-term variability related to astronomical variables and interannual variability in water levels. However, the rate of rise in monthly MHW over the past 19 years at the Newport, RI tide gauge has been 0.69-cm yr^{-1} (NOAA, 2022b), which is significantly greater than the long-term SLR trend of 0.28-cm yr^{-1} (NOAA, 2022a). While our groundwater table data were not collected consistently during the same months each year, nor do they have as rigorous an elevation control as NOAA tide stations, it does suggest that salt marsh groundwater tables may be rising at a rate that exceeds that of mean sea level, and more closely approximates MHW. Increases in MHW have been observed at rates approaching 1-cm yr^{-1} over the past 19 years across the US Northeast (Courtney et al., 2020; Haaf et al., 2022).

After runnel installation, groundwater levels initially dropped in runneled locations, although they continued to increase over time at similar rates as found in unmanipulated controls (Figure 6). Mean water levels were 7-cm lower in runneled than unmanipulated controls at Canonchet, and 12-cm lower at Middlebridge. Additional differences were observed between the two sites. At Canonchet, there were no differences in the mean amplitude ratio (the fraction of the tidal range in the tidal channel that was transmitted to the marsh groundwater table) before and after runneling. However, at Middlebridge, there was an 18% increase in the in-marsh tidal range at runneled areas. This suggests that installing these small tidal channels can establish marsh hydrology similar to that seen channelside at unrunneled locations where the low-tide water table dips down towards mean sea level (e.g., Figure 2; Xin et al., 2013; Wilson et al., 2015). Because this enhanced drainage occurred in the lower elevation and more frequently inundated marsh, which also had a lower saturated hydraulic conductivity, the explanation for this difference is not straightforward. It may be that the runnels were of slightly deeper depth at Middlebridge, or had a shallowing feature at Canonchet. This deeper depth could have led to greater hydraulic gradients, more overall drainage, and depressed low tide water levels in comparison with more shallowly dug runnels at Canonchet. In fact, Besterman et al. (2022) encouraged the use of “vegetated sills” in runnels to allow for adjustments in drainage after observing effects on the landscape.

Overall, our results suggest that installation of shallow runnels in high elevation infrequently flooded marsh with heterogenous hydraulic conductivity and microtidal conditions (0.43 m daily range of tide) promoted revegetation, as measured through analysis of vegetation transects and satellite imagery analysis, although runnel installation did not clearly promote recolonization of high marsh plant species. This restoration experiment helped establish the role of a rising groundwater table in contributing to upper marsh die-off, by suggesting that the rate of rise in the water table mirrored that of MHW, which has been increasing at rates approaching 1-cm yr^{-1} in the US Northeast. This study also suggests that remediating impacts may be possible with the strategic use of surface water drainage.

TABLE 3 Assessment indicators and runneling recommendations for restoration projects.

Indicator	Goal	Methodology	Recommendation
Pond hypsometry	Compare pond bed elevations with elevations that can support vegetation elsewhere	Digital elevation model or measurements using LiDAR or elevation surveys	If pond beds are low in the tidal frame, plants will not be able to recolonize regardless of drainage. Runneling may prevent the pond from expanding. Shallow areas may revegetate
Tidal range	Assess tidal range to estimate extent of possible plant recolonization	Measure tidal range using VDATUM or deployment of in-channel loggers in a large, deep tidal channel or embayment	Very low tidal range sites have less capacity to drain. Drainage enhancements in sites with a <0.20 m tidal range may not realize improvements
Landforms and historic data	Assess past human impacts and modifications to hydrology	Historic areal imagery and ground assessments of drainage features and disturbances (e.g., stone walls, embankments, fill)	Enhance drainage using existing features. Historic imagery and surveys can reveal the origin and cause of impounded water areas
Hydraulic conductivity	To determine whether soil characteristics will enhance or obstruct drainage	Installation of shallow wells, bail down-tests. Collection of soils; measurement in lab (e.g., KSAT, Meter instruments)	Soils with high hydraulic conductivity will enhance drainage; if soils have homogeneously low hydraulic conductivity, drainage improvements may not occur
Sea level rise rate	Determine the amount of time bought by installing runnels. Consider future landscapes and marsh migration pathways	Examine mean monthly trends in MHW registered at nearest local tide gauge for the past 19 years against anticipated changes in soil flooding. Examine DEM, LiDAR, or SLAM maps	If trends in MHW are high, runnels will be a temporary solution. Consider opportunities for restoring tidal hydrology to facilitate marsh migration
Subsidence	Determine whether subsidence or peat oxidation is linked to drainage	Collect baseline elevations using appropriate survey methods (e.g., RTK or PPK GPS, or leveling to a stable upland benchmark)	This technique may not be appropriate if it is linked to significant elevation loss, and it is unknown based on this study

4.2 Recommendations for future projects

Results from this project can help suggest guidelines that may be used to improve future implementation and monitoring of runnel projects (Table 3). We review suggestions that should improve runnel implementation projects, such as inventorying site characteristics prior to deployment, and designing monitoring campaigns.

Our results suggest that this technique worked better at the higher elevation location (Canonchet), where a minor drop in the groundwater table was sufficient to allow for near-complete vegetation recolonization. On the other hand, the bottom of ponded areas that are too low in elevation to support vegetation should not be expected to recolonize (Besterman et al., 2022). The challenge is how to delineate what "too low" might mean in the US Northeast where tidal range can vary from a few cm to several meters and marsh elevations can vary by over a meter (Elsey-Quirk et al., 2022). A simple and promising indicator may be if the ponded area is recently formed (assessed using historic imagery), shallow, or somewhat ephemeral and the marsh platform has not subsided. A more rigorous assessment could involve elevation surveys or a GIS analysis using LiDAR, if the LiDAR accurately depicts pond elevations (Millette et al., 2010). If the elevation of the pond bed is below the limit for vegetation elsewhere in the marsh, surface drainage will not allow revegetation to occur in the ponded area even if surface water is drained (Mariotti, 2020), yet it can prevent further degradation of marsh vegetation surrounding the ponded area known as "pool creep."

A second suggestion is to consider additional factors associated with drainage, such as tidal range, and the hydraulic conductivity of the soil. Where tidal ranges are extremely low, gradients are similarly low and runnels may not enhance drainage to the extent that vegetation can recover significantly. In our site, the mean tidal range was ca. 0.40 m, and the water table dropped 0.07–0.12 m based on runnel installation to 0.30 m depth. To operationalize the investigation of tidal range at a candidate site, VDATUM can be used to estimate tidal range in US Northeastern marshes (Haaf et al., 2022); although data is not always available or accurate for back-barrier marshes (Cole Ekberg et al., 2017). In these cases, deployment of an in-channel water level logger for a short time period (e.g., 1–2 months) with data post-processed in R (R Core Team, 2018) using the package VulnToolkit (Hill and Anisfeld, 2021) could help establish tidal range, and can be adjusted using nearby NOAA tide gauge data (NOAA, 2003). Another factor related to tidal range that can help shape drainage in concert with runneling is hydraulic conductivity. At the PRE, we measured saturated hydraulic conductivity that ranged from 10^{-5} to $1\ \mathrm{cm\ s^{-1}}$ and values were quite heterogenous (Supplementary Figure S4). If a marsh has homogeneously fine soils with low hydraulic conductivity, these soils can act as a barrier to through-marsh drainage. Conversely, soils that are very sandy and permeable can help augment runneling to decrease water logging across the landscape. Hydraulic conductivity can be estimated using bail down tests, or through laboratory soil tests using the falling head method (Hvorslev, 1951; Hwang et al., 2017). Sandy soils may also be more conducive for plant recolonization, as they are better drained (Bradley and Morris, 1990).

An additional recommendation of items to consider in planning runneling projects is SLR rates, or how much time you are buying by installing runnels. In this study, we dropped groundwater levels by 7–12 cm in comparison with control sites. However, given that groundwater levels rose 1.7–1.9 cm yr^{-1} from 2014 to 2018, water levels in runneled sites were up to pre-runneled levels by 2018. Given the longer-term rate of MHW rise of 0.5–1 cm yr^{-1} in the US Northeast, dropping the water table by ca. 10 cm will buy 10–20 years of extra time. In this case, the time bought was only 5 years due to the exceptionally fast rate of rise in water levels 2014–2018. Another consideration is that if runnels are clogged, this could also negate the time "bought" by installing runnels. If runnels fill in with sediment or peat, they may need to be cleared to maintain drained conditions. Managers that been installing and maintaining runnels recommend that they be maintained by hand every 3 years.

The results of the present study can also inform monitoring campaign design. Pre-restoration monitoring was key in establishing impacts of runnels, and although we designed this study using a BACI design, an additional year of pre-intervention monitoring data would have been an even more helpful baseline given interannual variability in vegetation and water levels (Figure 5, Supplementary Figure S2). Our monitoring wells were established prior to knowledge of where runnels would be; in retrospect it would have been more helpful to have located wells in restoration areas that had identical proximities to tidal channel distance to help address co-variability in water levels and landscape position (Montalto et al., 2006; Wilson et al., 2015). We found that groundwater levels changed immediately after runnel installation; while vegetation changed more slowly (Figure 5, Supplementary Figure S2). Vegetation transects were helpful for monitoring changes in species cover (Figure 4, Supplementary Figure S2); satellite imagery posed more problems due to differences in tidal levels and season (Morgan et al., 2022). Ideally, drone photographic mosaics could have been used to track change over time (Haskins et al., 2021); however, policies related to the use of drones on USFWS property discouraged their use (50 CFR 27.34, 50 CFR 27.51). Finally, a previous study suggested that enhanced drainage may lead to loss of elevation (Raposa et al., 2019), perhaps due to consolidation and dewatering. While the creeks examined in that study were much deeper and wider than the small channel extension features that we focused on, the potential linkage between channel installation and subsidence is worthy of additional study (Table 3).

5 Conclusion

Our results suggest that an increase in the groundwater table resulting from SLR can contribute to vegetation die-off for high elevation marsh, as the water table intersects and rises above the marsh surface. Runnels, or the installation of channel extension features, can help mitigate this adverse effect of the water table rising and pond formation with subsequent die-off. While we acknowledge that runnels may be a temporary solution, we also found that they are also quick acting, with drops in groundwater appearing as soon as the runnels were installed, and vegetation reestablishment occurring in two to 3 years. Runnels also might be a more feasible climate change adaptation technique where sediment addition is not possible, due to cost, distance from sediment sources, or concern about disturbance. We also propose that runnels—even if they do not fully reestablish vegetation—may be helpful in reducing the amount that ponds might expand due to wind-wave erosion or excessive waterlogging. In addition, runnels may promote reductions in the presence of marsh-breeding mosquitos. We suggest that future studies include strong monitoring to guide implementation, and recommend this technique as one of the many tools that are needed to address the effects of climate change on coastal areas over the next centuries.

Data availability statement

All data is available as Supplementary Material. Inquiries can be directed to the corresponding author.

Author contributions

The study was conceptualized by WF, CW, and EW. Project administration was conducted by WF, JW, and NE. Field data collection was conducted by WF, NE, JW, and EW. BPW, HS, LC, and EW designed and produced illustrations. Data analysis was conducted by LC, CW, and HS. Remote sensing analysis was conducted by BPW. Data curation was completed by LC. Manuscript was written by EW and CW. All authors contributed to editing the manuscript.

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Conflict of interest

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Supplementary material

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Including phylogenetic conservatism of shortgrass prairie restoration species does not improve species germinability prediction

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Premise: We investigated whether phylogenetic conservatism can improve the performance of seed germinability prediction models. Previous studies in tallgrass prairie and alpine meadow revealed that seed morphological traits demonstrate phylogenetic conservatism. We hypothesized that phylogenetic conservatism in seed traits could help predict the seed germinability, under the assumption that seed traits contain phylogenetic signals.

Methods: We measured seed germination percentage and seed morphological traits (seed mass, seed height, and seed surface area) on 34 native species from shortgrass prairie in North America. We supplemented these data with similar data from the literature on 11 more species. We calculated the robustness of the phylogenetic signal of each trait to the number of species sampled. We also compressed the phylogenetic distance matrix to a two-dimensional space, and applied the Akaike information criterion to evaluate the effects of phylogeny on seed germinability prediction models.

Key results: We found weak but significant phylogenetic signals in seed mass and seed height in the full data set. These phylogenetic signals were not able to improve seed germinability prediction model performance among shortgrass prairie species. Our robustness tests of phylogenetic signals using random sub-sampling showed that the detection rate of phylogenetic signals in seed mass was increased along with the expansion of species pool, and nearly 100% at 40 species. However, the detection rate of phylogenetic signals in seed height was constantly low, around 20%.

Conclusion: When the phylogenetic signals are weak, the phylogenetic position does not improve germinability prediction model performance. Therefore, phylogenetic signals detected during a single species pool calculation may not accurately reflect the phylogenetic conservatism of the trait in a plant community. We suggest testing for robustness of phylogenetic signals using random sub-sampling tests.

KEYWORDS

ecological restoration, phylogenetic comparative method, seed germinability prediction, phylogenetic conservatism, phylogenetic signal

Introduction

The need for ecological restoration is constantly increasing. For example, the September 2014 United Nations Climate Summit suggested the need for 350 million hectares to be restored worldwide by 2030 (Bonn Challenge, https://www.bonnchallenge.org/). Tremendous numbers of native species will be needed to meet this need. Most ecological restoration projects select only a small number of species out of the community species list to conduct ecological restoration (Kiehl et al., 2010). Given the low numbers of species selected for any specific restoration project, maximizing the benefit from selected species is key. Thus, ensuring that the selected species have high final germination percentages is a high priority because seed germination ranks as one of the top restoration challenges (Larson et al., 2015). Therefore, lab assessment formulas to narrow down the restoration species list could aid species selection in many restoration projects.

Seed dormancy regulates seed germination but is complicated and hard to predict. In over 90% of species, seeds dry and start primary dormancy by the time of harvest (Finch and Leubner-Metzger, 2006; Subbiah et al., 2019). After dispersal, seeds can have secondary dormancy, a shallow physiological dormancy which is broken by responses to environmental cues (Finch and Leubner-Metzger, 2006). Multiple categorical seed dormancy types are widely represented in plant species, including morphological dormancy (MD), physical dormancy (PY), physiological dormancy (PD), and morphophysiological dormancy (MPD; Baskin and Baskin, 1998). Physiological dormancy is thought to be the ancestral state of seed dormancy and also serves as the diversification hub for different dormancy types (Willis et al., 2014). Considering the complexity of dormancy stages and the lengthy experiments needed to distinguish these types (Finch and Leubner-Metzger, 2006), it is desirable to predict seed germinability success through other related traits.

Low germination rate hinders restoration and, given limited resources, managers desire to only include species with predictably high germination rates. Several seed traits are related to seed germination and might serve as more easily measured predictors of final germination percentage. In general, mass is a good indicator of seed germination, as small seeds tend to germinate faster (Westoby et al., 2002; Barak et al., 2018), while large seeds can stay dormant longer and produce stronger seedlings after germination (Leishman et al., 2000; Westoby et al., 2002). The rationale behind this phenomenon is related to nutrition stored in the seed under either a "larger-seed-later-deployment" interpretation (Ganade and Westoby, 1999; Leishman et al., 2000; Kidson and Westoby, 2000) or "cotyledon functional morphology" hypothesis (Hladik and Miquel, 1990; Kitajima, 1996a,b). Furthermore, seed size and seed shape are also traits influencing seed germination by stimulating or delaying seed germination through wind, water, or animal dispersal (Howe and Smallwood, 1982). Large seeds generally have advantages for dispersal related to entrapment strategies, such as net trapping, surface tension, and wake trapping (Jager et al., 2019), especially for wind-dispersed species (Zhu et al., 2019). Specifically, seed morphological traits influence both seed primary dispersal (seed departure from parent plants) and secondary wind dispersal (seed lifting off the ground by wind power; Zhu et al., 2019). Primary dispersal is mainly driven by dispersal height and terminal falling velocity, which are influenced by seed morphology (Sheldon and Burrows, 1973; Jongejans and Telenius, 2001). Secondary dispersal distance strongly depends on the lift-off velocity, which is influenced by seed height and seed surface area (van Tooren, 1988; Schurr et al., 2005; Zhu et al., 2022). There are many other seed physiological traits associated with seed germination that are not commonly tested, such as base water potential, cardinal temperature, thermal time and hydrothermal time for germination (Bradford, 2002; Hardegree et al., 2013).

Seed germination trials are time consuming, therefore, predicting germinability for species without conducting such trials could benefit restoration. Seed morphology traits are potential predictors of germination rate. If dormancy and lack thereof are evolutionarily conserved, then it may be possible to predict seed germination rate of unmeasured species based on the rates of closely related taxa. A phylogenetic tree models the inferred evolutionary branching history of a group of taxa (Baum and Smith, 2013). A phylogenetically conserved trait will tend to be most similar among species close together on the phylogenetic tree. The common test for such phylogenetic signals is Blomberg's K (Blomberg et al., 2003, Revell et al., 2008), but it is also possible to include all pairwise phylogenetic distances among taxa in linear models through the method of phylogenetic residuals (Revell, 2010). Phylogenetic trait conservatism is common across many traits and clades (Bu et al., 2016; Barak et al., 2018; Duncan et al., 2019). Adding phylogenetic residuals to the generalized least square model can take the evolution of unmeasured traits into account and improve the prediction model's accuracy. This work has two major goals. The first goal is to test whether adding phylogenetic information among species (presented by x-y coordinates transferred from phylogenetic tree topology) can improve predictions of germination rate based on seed morphology. Adding phylogenetic information might improve predictions if the germination rate shows a phylogenetic signal or if the seed morphology effect on germination rate interacts with phylogeny. There is precedent for using phylogeny for this purpose: In a study of species native to tallgrass prairie, Barak et al. (2018) confirmed that adding the phylogenetic residual improved the accuracy of the seed germinability prediction model due to the phylogenetic conservatism in both seed germination and morphological traits. However, because phylogenetic tools are unfamiliar and inaccessible to restoration practitioners and due to a historical separation between evolutionary biology and applied ecology, phylogenetic methods have not been broadly applied to restoration practice (Hipp et al., 2015).

The second major goal of this work is to determine how the size of a sample of taxa from an ecological community influences the power to detect phylogenetic signals in traits. The sample size and combination of given species influence tree topology and branch length during phylogenetic signal calculation. In empirical examples, the detection of phylogenetic signals is strongly related with the number of species included, with 20 or more species usually considered sufficient for estimation of Blomberg's K (Blomberg et al., 2003). However, in phylogenetic comparative analysis aimed at answering evolutionary questions, the combination of species is commonly fixed. For applied restoration use, the practitioner will need to measure traits on some sample of species from a particular community. By examining how this sample of taxa influences the calculation of Blomberg's K, we aim to provide guidelines for estimating the robustness of this calculation.

To address these two major goals and test the potential role of phylogeny for improving restoration practice, we asked four research questions: (1) Do seed traits and seed final germination percentages exhibit phylogenetic signals? (2) Among seed traits, which one is the best predictor of seed final germination percentage? (3) Does including phylogenetic residuals improve the seed germinability prediction? (4) Do the sampling size and species composition influence phylogenetic conservatism detection in shortgrass prairie species?

Materials and methods

To determine the relationship between seed germinability and seed morphological traits, we measured seed germination percentage, seed mass, seed height, and seed surface area in 45 species which are native to the shortgrass prairie of North America (Table 1; Figure 1). All of our raw data and calculations were demonstrated in our interactive Shiny Application (Figure 2; https://chenyanniii.shinyapps.io/Phylo_Compar_Traits/).

Seed germination percentage and morphological traits measurements

Seed germination percentage was obtained from two sources: our own germination trials and previous publications. In all cases, we defined "germination percentage" as the maximum final germination percentage obtained. The germination trials followed a simple germination protocol without cold stratification or other attempts to break dormancy, which simulated minimum requirements for restoration projects. This simple protocol is essentially a measurement of lack of dormancy assuming the tested seeds were full viable. For 34 of the 45 species, we conducted new germination trials. Our new germination trials were trying to simulate the scenario that practitioners want to find some easy to use native species. Because the experiment is trying to simulate the scenario in which practitioners are attempting to find easy to use native species, we bought seeds from a local restoration seed vendor (Native American Seed), and chose species for which they offered local seed sources (and recorded the seed source), with

TABLE 1 Forty-five native species were selected in this study, which are commonly involved in restoration practice and range management in shortgrass prairie.

Species	Family
Andropogon gerardii Vitman	Poaceae
Argemone albiflora Hornem.	Papaveraceae
Aristida purpurea Hutt.	Poaceae
Asclepias asperula (Decne.) Woodson	Asclepiadaceae
Astragalus crassicarpus Nutt.[1]	Fabaceae
Bouteloua curtipendula (Michx.) Torr.	Poaceae
Bouteloua gracilis (Willd. ex Kunth) Lag. ex Griffiths	Poaceae
Callirhoe involucrata (Torr. & A. Gray) A. Gray	Malvaceae
Callirhoe leiocarpa R.F. Martin	Malvaceae
Centaurea americana Nutt.	Asteraceae
Chasmanthium latifolium (Michx.) Yates	Poaceae
Chloris cucullata Bisch.	Poaceae
Coreopsis lanceolata L.[2]	Asteraceae
Coreopsis tinctoria Nutt.	Asteraceae
Corydalis curvisiliqua Engelm.	Fumariaceae
Desmanthus illinoensis (Michx.) MacMill. ex B.L. Rob. & Fernald	Fabaceae
Digitaria californica (Benth.) Henr.	Poaceae
Digitaria ciliaris (Retz.) Koeler	Poaceae
Echinacea angustifolia DC.[2]	Asteraceae
Eragrostis trichodes (Nutt.) Alph. Wood	Poaceae
Eryngium leavenworthii Torr. & A. Gray	Apiaceae
Gutierrezia sarothrae (DC.) A. Gray	Asteraceae
Helianthus annuus L.	Asteraceae
Herbertia lahue (Molina) Goldblatt	Iridaceae
Ipomopsis rubra (L.) Wherry	Polemoniaceae
Liatris mucronata Hook. var. *mucronata* (DC.) B.L. Turner[2]	Asteraceae
Linum rigidum Pursh	Linaceae
Monarda citriodora Cerv. ex Lag.	Lamiaceae
Oenothera rhombipetala Nutt. ex Torr. & A. Gray	Onagraceae
Pavonia lasiopetala Scheele	Malvaceae
Penstemon cobaea Nutt.[2]	Scrophulariaceae
Phacelia congesta Hook.	Hydrophyllaceae
Phytolacca americana L.	Phytolaccaceae
Polytaenia nuttallii DC.	Apiaceae
Ratibida columnifera (Nutt.) Wooton & Standl.	Asteraceae
Rivina humilis L.	Phytolaccaceae
Salvia azurea Michx. ex Lam.	Lamiaceae
Salvia coccinea P.J. Buchoz ex Etlinger[2]	Lamiaceae
Salvia farinacea Benth.	Lamiaceae
Salvia lyrata L.	Lamiaceae
Schizachyrium scoparium (Michx.) Nash	Poaceae
Sorghastrum nutans (L.) Nash	Poaceae
Sporobolus airoides (Torr.) Torr.	Poaceae
Sporobolus cryptandrus (Torr.) A. Gray	Poaceae
Tradescantia occidentalis (Britton) Smyth	Commelinaceae

Most of the species were bought from Native American Seed, tested in controlled environments, 6 species were cited from Chou et al. (2012)[1] and 5 species were cited from Schwilk and Zavala (2012)[2].

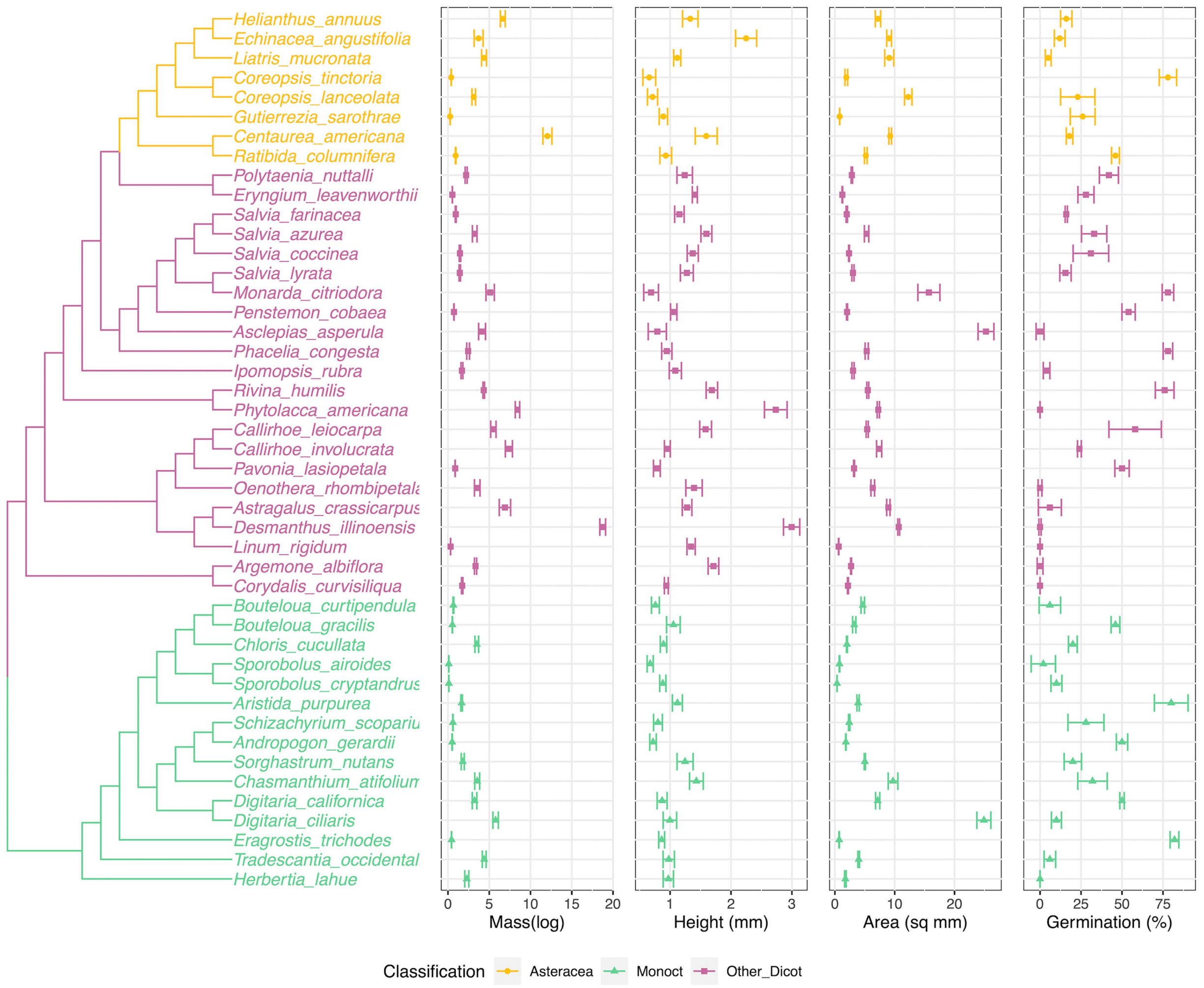
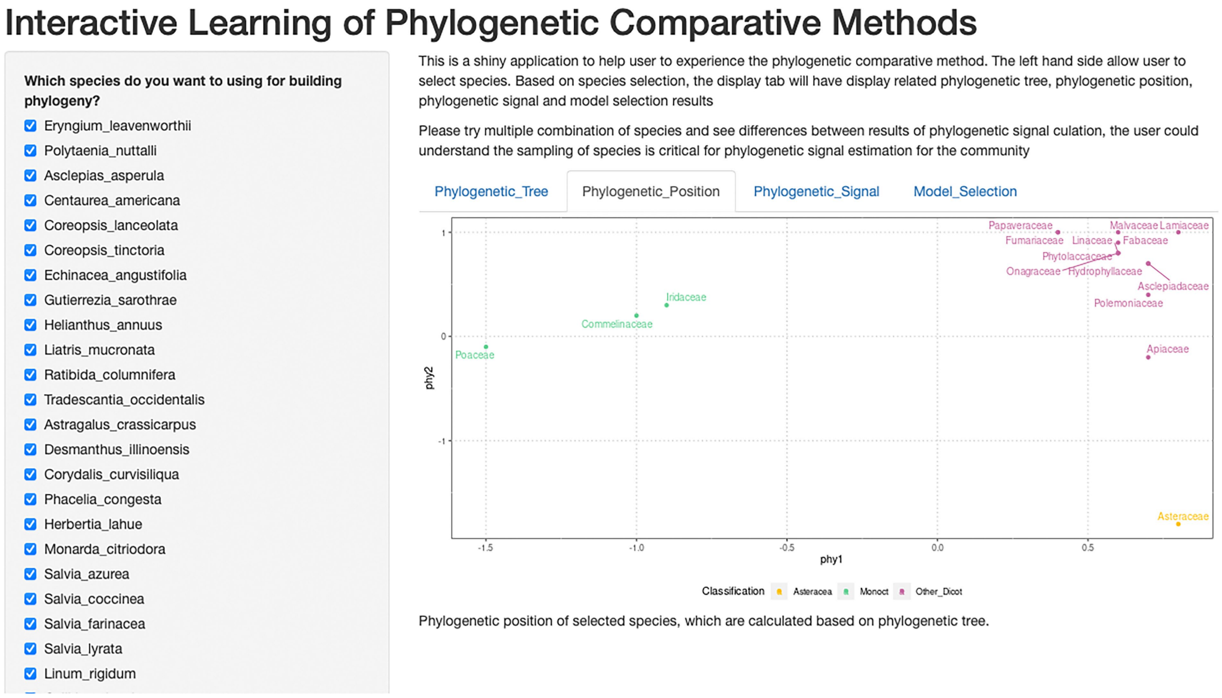


FIGURE 1
Phylogenetic tree of species and species seed traits values (seed mass, seed height) distribution along the phylogenetic tree. Phylogenetic tree was generated from the pruned Zanne et al. tree (Zanne et al. 2014), including 15 species (*Astragalus crassicarpus, Argemone albiflora, Asclepias Asperula, Callirhoe leiocarpa, Centaurea americana, Chasmanthium tifolium, Corydalis curvisiliqua, Digitaria californica, Eragrostis trichodes, Herbertia lahue, Linum rigidum, Pavonia lasiopetala, Polytaenia nuttallii, Tradescantia occidentalis, Liatris mucronata*) were placed within under the same genus/family. The center of each plot is the mean value, the other two lines are −/+ standard errors. The colors were coded corresponding to the grouping of phylogenetic positions (Figure 3).

seeds that were harvested less than 6 years ago. When seeds arrived, we stored the seeds in a dry and dark place at room temperature (20°C) until experiments started. Although it's possible that some species may exhibit dormancy, we did not use any dormancy breaking treatment, in order to simulate simple restoration practice. For the germination experiment, we used triple replicated germination trials: disposable petri dishes with lids were placed in germination chambers (20°C day and night, with 15 and 9 h day night shift). Inside a petri dish a piece of filter paper was placed to observe auto-claved water to keep the seeds moist. We checked the water sufficiency every day. In each germination trial we split a total of 50 seeds of each species into 5 petri dishes. Since our study used commercial seeds and focused on species dormancy status, we assumed our seeds will either be dormant or start germination within a month. Our observations during experiments proved this assumption. The seeds generally started germinating within 10 days or stayed dormant through the whole germination trial. Our germination trials ran until 1 week after the last seed germinated. Most of the seed germination trials finished within a month, and all the trials finished within 2 months. Three independent trials happened in July 2019, September 2019, and November 2019. For the remaining 11 species, we used final germination percentages reported in two published studies (Chou et al., 2012; Schwilk and Zavala, 2012). These two studies were originally designed for detecting smoke effects on shortgrass prairie species, but we used the control treatment data only which provided conditions similar to those in our trials (20–25°C, 12–16 h illumination).

We measured seed mass using an electronic balance (Sartorius Analytical Balance LA 230P, 0.1 mg readability) in lab conditions



Interactive Learning of Phylogenetic Comparative Methods

Which species do you want to using for building phylogeny?

☑ Eryngium_leavenworthii
☑ Polytaenia_nuttalli
☑ Asclepias_asperula
☑ Centaurea_americana
☑ Coreopsis_lanceolata
☑ Coreopsis_tinctoria
☑ Echinacea_angustifolia
☑ Gutierrezia_sarothrae
☑ Helianthus_annuus
☑ Liatris_mucronata
☑ Ratibida_columnifera
☑ Tradescantia_occidentalis
☑ Astragalus_crassicarpus
☑ Desmanthus_illinoensis
☑ Corydalis_curvisiliqua
☑ Phacelia_congesta
☑ Herbertia_lahue
☑ Monarda_citriodora
☑ Salvia_azurea
☑ Salvia_coccinea
☑ Salvia_farinacea
☑ Salvia_lyrata
☑ Linum_rigidum

This is a shiny application to help user to experience the phylogenetic comparative method. The left hand side allow user to select species. Based on species selection, the display tab will have display related phylogenetic tree, phylogenetic position, phylogenetic signal and model selection results

Please try multiple combination of species and see differences between results of phylogenetic signal culation, the user could understand the sampling of species is critical for phylogenetic signal estimation for the community

Phylogenetic position of selected species, which are calculated based on phylogenetic tree.

FIGURE 2
Shiny application of interactive learning of phylogenetic comparative methods. This is a screenshot of the shiny application. The checkbox of species could be used to choose different combinations of species and explore its impact on phylogenetic signals.

with 10 replicates of 100 seeds each per species. For species in which we could not obtain 100 seeds, we used 30 seeds per replicate.

We measured seed surface area and seed height through digital image processing with 10 replicates. The seed surface was defined by the two largest orthogonal axes, the height was defined as the third axis. We calculated the seed surface area by digital image of the maximum surface area of seeds and imaged under a stereomicroscope at 400 magnification. We transformed the images to 8-bit (black and white) and calculated the surface area using the "analyze particle" function in ImageJ (Schindelin et al., 2012). We also recorded the seeds' heights calculated by the z-stack image function and NIS-Element BR 4.60.00 software.

Species phylogenetic information

We generated a phylogenetic tree of all study species using two methods: pruning existing phylogeny (Zanne et al., 2014) and binding non-existing tips to the phylogeny based on their taxonomic information. The phylogeny (Zanne et al., 2014) we used in this study was a time-calibrated maximum-likelihood-based phylogenetic tree, built with seven genes (18S rDNA, 26S rDNA, ITS, matK, rbcL, atpB, and trnL-F) downloaded from GenBank. First, we confirmed that every genus in our study was on the Zanne phylogeny. Second, we created a function to prune species which were not on the tree, and we also swapped the species under the same genus if the exact species was not on the tree (see the function of func_prun_replac on https://github.com/chenyanniii/Traits4 repo for more detail). The results showed that 30 species on the tree and 15 missing species (*Argemone albiflora*, *Asclepias asperula*, *Astragalus crassicarpus*, *Callirhoe leiocarpa*, *Centaurea americana*, *Chasmanthium latifolium*, *Corydalis curvisiliqua*, *Digitaria californica*, *Eragrostis trichodes*, *Herbertia lahue*, *Liatris mucronata*, *Linum rigidum*, *Pavonia lasiopetala*, *Polytaenia nuttallii*, and *Tradescantia occidentalis*). After applying func_prun_replac, 13 of 15 species were placed based in their genus and only two species (*Callirhoe leiocarpa* and *Digitaria californica*) were missing. Thus, we added the missing species (*Callirhoe leiocarpa* and *Digitaria californica*) as sister tips to *Callirhoe involucrate* and *Digitaria ciliaris* under the same genus assuming that phylogenetic relationships were consistent with their taxonomic grouping. Our final tree contained all species was a dichotomous tree (Figure 1).

To incorporate phylogenetic relatedness in the general linear models, we represented the phylogeny by all pairwise phylogenetic distances across taxa. We converted the pairwise distance matrix to points distributed in a two-dimensional coordinate system, using nonmetric multidimensional scaling (NMDS; isoMDS function in the package MASS, Venables and Ripley, 2002). We evaluated phylogenetic signals for individual traits as Blomberg's K (Blomberg et al., 2003) using the phylosig function in the phytools R package (Revell, 2012). We tested for phylogenetic signal using a randomization test (phylosig function) that compared the measured value of Blomberg's K against a distribution of K calculated when trait values were randomized across the tips of the phylogeny.

Germinability prediction model selection

To generate and evaluate generalized linear models, we applied backward stepwise model comparison based on the Akaike information criterion (Akaike, 1998) using the AICc function in the AICcmodavg package (Mazerolle, 2020). We also used seed germination percentage, three seed morphological traits (seed mass, seed height and seed surface area) and phylogenetic positions to generate a global general linear model. Then, we used AIC to correct for small sample sizes (AICc) and evaluate the fitness of models. We standardized all input parameters to the mean of zero to produce standardized coefficients between parameters for numeric reasons in fitting. We also tested correlation among morphological traits (seed mass, seed height and seed surface area). All original data and scripts that we used to calculate phylogenetic signals, phylogenetic residuals, and seed germinability prediction models are available on GitHub website (https://github.com/chenyanniii/Traits4, DOI: 10.5281/zenodo.6609175).

Random sub-sampling of different species pool size

To estimate the minimum species pool size for obtaining a stable phylogenetic signal, we created 31 different species pool subsets, from 10 species to 40 species. For each pool size, we randomly withdrew 100 times at each pool size species from the whole species pool, thus generating 100 sub-pools of each species pool size by random sub-sampling. The phylogenetic signals of each sub-pool were calculated for their Blomberg's K and related p value. We analyzed the relationship between sample size and detection rate of phylogenetic signals was analyzed to evaluate the effect of sample size to estimated phylogenetic signals in traits.

Shiny application

Shiny is a web framework for displaying data. Shiny is a good data processing demonstration tool, an interactive way for users to experience how different input and procedure affect output. We designed our shiny application to import with our full dataset and display data analysis and results. Users can see our full dataset result (as default), or interactively calculate all parameters for any sub-pools using checkboxes of species (Figure 2).

Results

In this study, we used 45 commonly selected restoration species to explore the phylogenetic distance among shortgrass prairie species by pruning unnecessary species and adding desired species to the existing phylogenetic tree of flowering plants (Figure 1).

Seed final germination percentage and morphological traits measurements

When examining species' trait value with the phylogenetic tree (Figure 1), we found the phylogenetic patterns in seed mass, seed height, seed surface area and seed germination rate were varied. We were not able to germinate eight species (Figure 1, *Argemone albiflora*, *Callirhoe leiocarpa*, *Corydalis curvisiliqua*, *Herbertia lahue*, *Oenothera rhombipetala*, *Pavonia lasiopetala*, *Phytolacca americana*, and *Polytaenia nuttallii*). *Eragrostis trichodes* had the highest final germination percentage, 82%. For seed mass, *Sporobolus airoides* had the lightest weight per seed, 0.0945 ± 0.0083 mg per seed; the heaviest seed was *Pavonia lasiopetala*, 18.75 ± 0.3487 mg per seed. The seed height measurement ranged from 0.658 ± 0.1051 (*Coreopsis tinctoria*) to 2.995 ± 0.1334 mm (*Pavonia lasiopetala*); and the seed surface areas ranged from 0.361 ± 0.0083 (*Sporobolus cryptandrus*) to 25.258 ± 1.322 (*Polytaenia nuttallii*) mm^2 (Figure 1).

Species phylogenetic information

We used nonmetric multidimensional scaling (NMDS) to compress the phylogenetic distance matrix to a two-dimensional space, with a pressure of 17.86. Our results showed that 45 species were grouped into three clusters: Monocot, Asteraceae and eudicots-except Asteraceae (Figure 3). NMDS compressed phy1 (x-axis) corresponded to separating monocot and eudicots, while the phy2 (y-axis) separated Asteraceae from other families.

Our measurements of phylogenetic signals, Blomberg's K (using species shuffling method), were low for all four seed traits, indicating a departure from signal under strict Brownian motion and suggesting that these traits are evolutionarily labile. Although Blomberg's K were low, indicating a weak phylogenetic signal, we found significant phylogenetic signals for seed mass ($K = 0.07$, $p = 0.01$) and seed height ($K = 0.05$, $p = 0.05$).

Germinability prediction model selection

The full set of models built from morphological traits and phylogenetic information were evaluated using adjusted AIC (AICc). The AICc values range from 129.9 to 139.4. The best prediction model is using seed height to predict seed germination (AICc = 129.9), slightly better than the model using seed mass to predict germination (AICc = 130.5). The models with low AICc values were clustered by using one morphological trait as a predictor or the combination of two morphological traits. This indicated that morphological traits out-perform phylogenetic

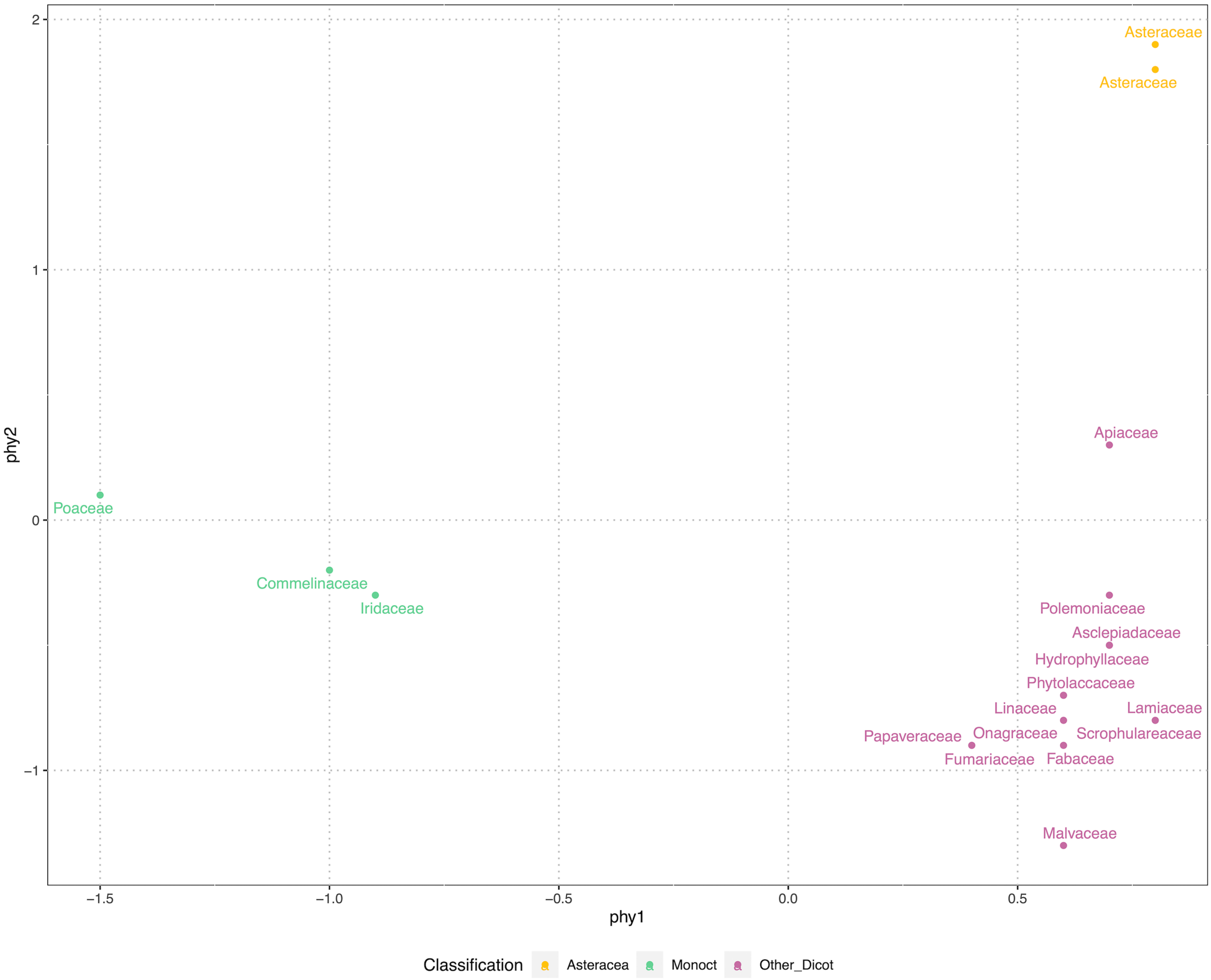


FIGURE 3
Phylogenetic position of 45 species, represented by family, were clustered in three groups. The phylogenetic positions were generated from paired-wise distances of species on the phylogenetic tree (see Figure 1). The nonmetric multidimensional scale (NMDS) was applied, at the stress of 17.86, displayed in two axes. For the convenience of display the phylogenetic positions were grouped and color coded by vision.

distance in predicting seed germination. Pearson correlation coefficient analysis revealed a strong correlation between seed mass and seed height (r = 0.66, $p < 0.01$); a medium correlation between seed mass and seed surface area ($r = 0.49$, $p < 0.01$); no correlation was detected between seed height and seed surface area (Table 2).

Random sub-sampling of different species pool size

We calculated phylogenetic signals of morphological traits (seed mass, seed height, and seed surface area) and seed germination rate of all 3,100 sub-pools. All Blomberg's K values were between 0 and 1 in all phylogenetic signal calculations, except 9 of them were larger than 1. In general, phylogenetic signals distributed widely at small species pool sizes, and became less varied while increasing species pool sizes (Figure 4). For seed height, seed surface area, and seed germination, the probability of detecting phylogenetic signals were consistently low regardless of the species pool size. This was true even for seed height, for which we detected a significant phylogenetic signal in our full dataset. In contrast, the probability of detecting the phylogenetic signal of seed mass increased with species pool size (Figure 5).

Discussion

Aiming to verify the usefulness of trait conservatism in restoration seed selection, we measured seed traits, ran seed germination tests, calculated phylogenetic signals in seed traits, and presented the phylogenetic residual in seed germinability prediction models. We quantified weak phylogenetic signals in seed mass and seed height, but we found no phylogenetic signal in seed surface area nor in seed final germination percentage. In those traits that did exhibit phylogenetic signals, the signals were weak: closely related species were more similar than expected

TABLE 2 Phylogenetic signal was tested in seed morphological traits and overall seed final germination percentage.

Trait	Blomberg's K	*p*-value
Seed Mass	**0.07**	**0.01**
Seed Height	**0.05**	**0.05**
Seed Surface Area	0.03	0.14
Seed Final Germination Percentage	0.02	0.20

Blomberg's K was used to evaluate phylogenetic signals (Blomberg et al., 2003). $K = 1$, the traits is perfectly fit with Brownian motion model. $K > 1$, the traits is more conserved than expected comparing to Brownian motion model. $K < 1$, the traits is less conserved than expected comparing to Brownian motion model. Bold indicates the trait containing phylogenetic signal ($p = < 0.05$).

under species shuffling, but more different in their trait values than expected under Brownian motion.

Phylogenetic tree

The phylogenetic tree of 45 commonly selected species in shortgrass prairie ecological restoration was clustered in Poaceae within monocots and were relatively clustered in Asteraceae and Lamiaceae within eudicots (Figure 3), which reflects that the species composition may be clustered in shortgrass prairie. The phylogenetic comparative methods displayed trait values indicated that the closely related species had similar trait values in seed mass and seed height, but not in seed germination (Figure 1). The NMDS compressing phylogenetic distance into two-dimensions shows three distinct clusters (Figure 3). The results showed that shortgrass prairie families were grouped into 3 clusters: one monocot group and two eudicot groups (Asteraceae and others, Figure 3). Meanwhile the tallgrass prairie species (Barak et al., 2018) were grouped into 4 clusters: one monocot group, three eudicot groups (Asteraceae, Fabaceae, and others).

Our development of the Shiny application demonstrated: (1) the procedure of pruning the synthetic phylogenetic tree (Zanne et al., 2014) to the desired species tree. (2) the calculation of compressing phylogenetic distance into two-dimensions. The interactive demonstration allows users to select all or a portion of desired species and understand the effect of species selection on phylogenetic calculation.

Phylogenetic signal in traits

Phylogenetic signal indicates that closely related species have more similar trait value than expected under species shuffling across tips of a phylogeny. We found significant phylogenetic signals in seed mass and seed height, but no such signals in seed surface area nor in seed final germination percentage. Although germination traits are not specific or constant in each species (but vary in space and time), since we chose seeds from the same eco-region, our results are able to represent our region and still allow generalization when considering germinability predictions. Generally, seed mass is phylogenetically conserved in sample taxas from different ecosystems (tallgrass prairie, Barak et al., 2018; alpine grassland, Bu et al., 2016; globally, Westoby et al., 2002). In our set of taxa, we found a weak but significant pattern. Seed mass often predicts energy and nutrient provisioning (Westoby et al., 2002), which increases seed germination rates and stress tolerance (Leishman et al., 2000; Moles, 2018). This assumes, however, that mass is primarily the embryo and nutrients. It is possible for a large portion of the seed mass to be seed defense structures (i.e., seed coat).

We used seed height and seed surface area as proxies for seed dispersal syndrome, because these dimensions influence primary wind dispersal (seed departure from mother plants, Sheldon and Burrows, 1973; Jongejans and Telenius, 2001) and secondary wind dispersal (seed lifting off ground by wind power, van Tooren, 1988; Schurr et al., 2005; Zhu et al., 2022). Primary dispersal is mainly related to dispersal height and terminal falling velocity, which is influenced by seed morphology (Sheldon and Burrows, 1973; Jongejans and Telenius, 2001). Secondary dispersal distance strongly depends on the lift-off velocity, which is influenced by seed height and the planform area of a seed exposed to airflow (van Tooren, 1988; Schurr et al., 2005; Zhu et al., 2022). Classically, seed shape was measured by the roundness or closeness of a seed to specific shape, such as ellipse or cardioid (Cervantes et al., 2016) and linked with seed persistence in soil seed bank (Moles et al., 2000; Laughlin, 2014). Some recent studies link seed morphological shape with evolutionary constraint and selective pressure of seeds and its potential relationship with seed germination (Bu et al., 2016; Barak et al., 2018). In our study, seed mass and seed height were positively correlated. We found a weak pattern of phylogenetic trait conservatism in two traits, but this signal did not aid in improving seed germinability prediction models.

Seed germination is a complex phenomenon. Our measure of total germination was, in effect, a dormancy proxy: high germination rates indicated a lack of dormancy in our research. Our experiment did not include any dormancy breaking retreatments, only supplying light and water during experiments to simulate practitioners' low effort practices. Seed germination can be influenced by abiotic factors, such as wetland species germination impacted by water level (Keddy, 1992); or arid zone woody species developing rapid germination in response to unpredictable rainfall (Duncan et al., 2019). Seed germination can also be influenced by biotic factors, such as small- and large-seeded species diverging in the species they associate with, regarding seed mass and understory light preference (Umaña et al., 2020). We did not detect a phylogenetic signal in germination rate indicating this trait is highly labile. This result was different from a similar study of tallgrass prairie species (Barak et al., 2018), where the authors found significant phylogenetic trait conservatism in germination percentage under control and gibberellic acid treatment, and including phylogeny improve time-to-germination (survival) model. However, the survival model (Barak et al., 2018) includes both germination time and pretreatment for germination rate and does not measure dormancy. Differing patterns in phylogenetic

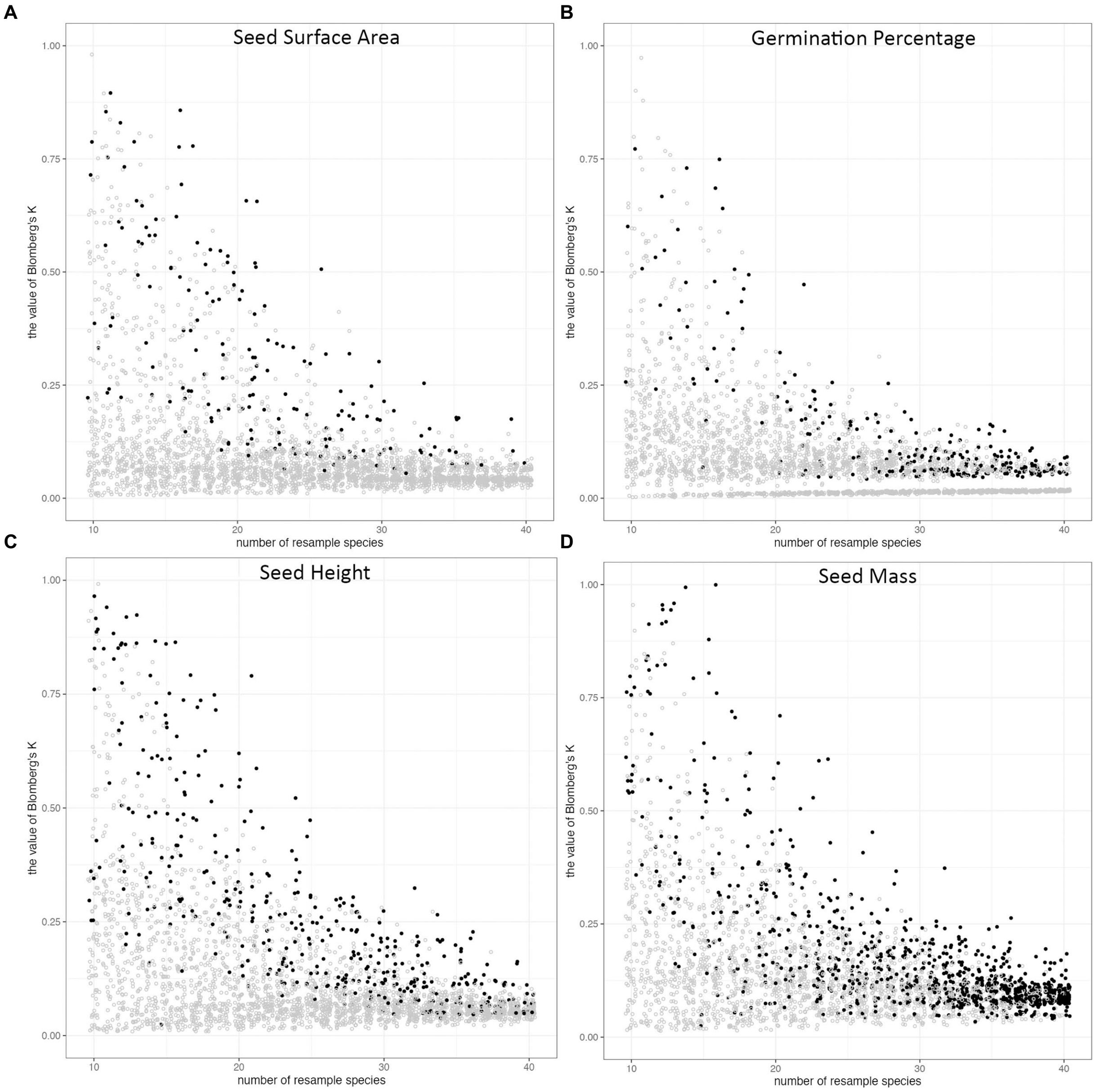


FIGURE 4
The distribution of Blomberg's K along the size of the species pool in random subsampling tests. The species were resampled 100 times from 10 species to 40 species, and phylogenetic signal (Blomberg's K) was calculated for each trait, 3100 times for each trait. Phylogenetic signals of **(A)** seed surface area, **(B)** germination percentage, **(C)** seed height, **(D)** seed mass. The dots represent the Blomberg's K value of each resampling pool. The color of dots indicates the *p*-value of Blomberg's K ($p <= 0.05$, black; $p > 0.05$, grey).

signal in germination rate of two prairie studies are reasonable, in consideration of environmental differences between two different ecosystems, and the germination experiment setting in two studies.

Germinability prediction model selection

The germinability predictive models with morphological data did not improve when adding phylogenetic information using the full dataset (Supplementary material). This means adding phylogenetic information to morphological measurements increased the complexity of models but did not increase the fitness of models. This is not surprising given that we found no phylogenetic signal in seed germination rate and only weak signals in two other traits.

Random sub-sampling of different species pool size

From the distribution of Blomberg's K, we can tell the species sample size will greatly influence phylogenetic signal calculation (Blomberg et al., 2003). Our shortgrass prairie restoration species

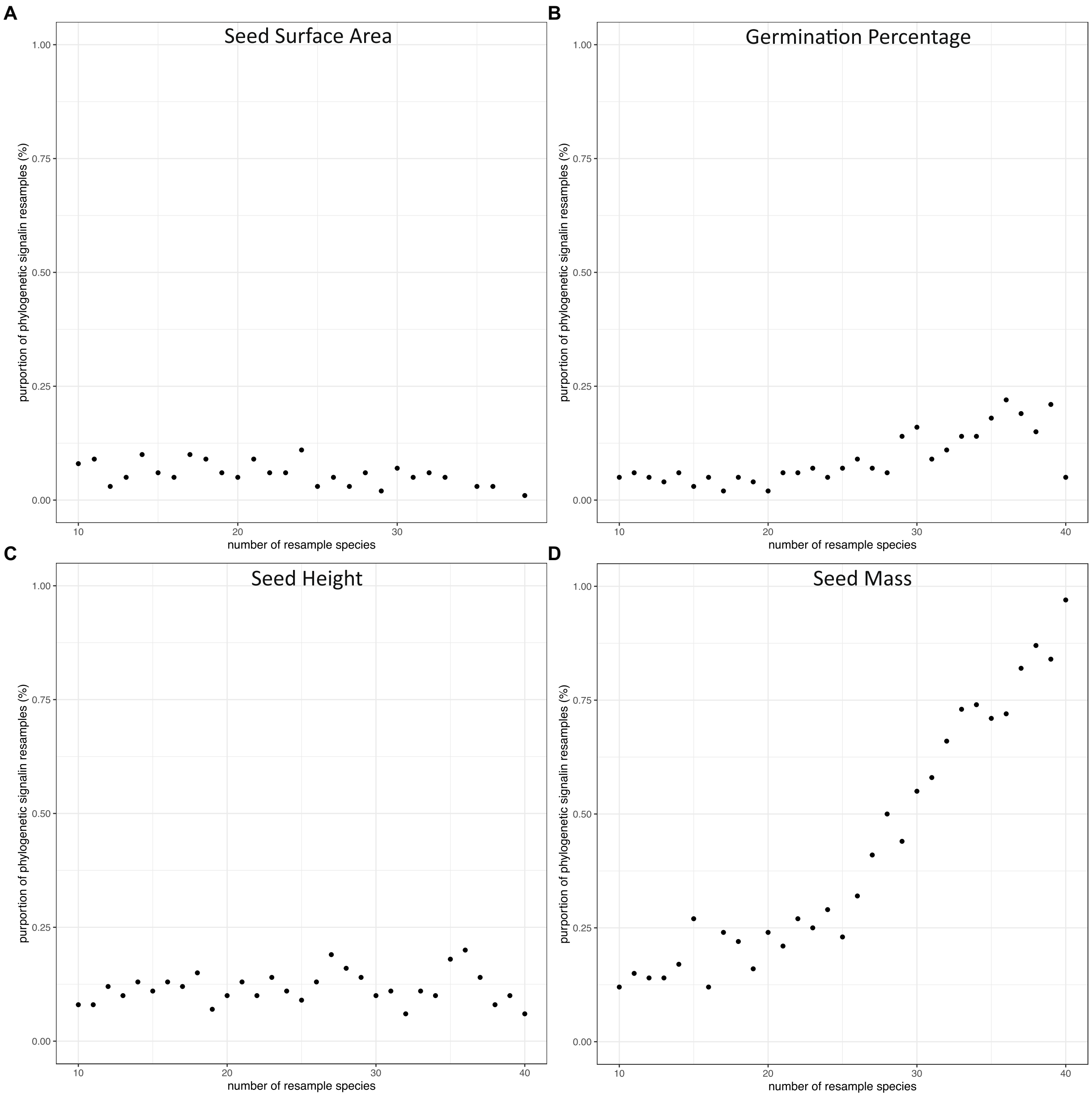


FIGURE 5
The proportion of subsamples with significant phylogenetic signals along the change of number of species in species pools. The species were resampled 100 times from 10 species to 40 species. The dots represent the proportion of Blomberg's K value (p =< 0.05) in each resampling pool: **(A)** seed surface area, **(B)** germination percentage, **(C)** seed height, **(D)** seed mass.

results showed that the phylogenetic signal would be less impacted by the species composition, and less varied with sufficient species, around 35 to 40 (Figure 4). This also indicates the 45 species we have in our study is sufficient.

In the full dataset (45 species), we were able to detect phylogenetic signals for both seed mass and seed height. However, the subsampling exploration method demonstrates that detecting a phylogenetic signal in seed height is a low probability event. On the other hand, our sub-sampling in seed mass showed that the probability of detecting a phylogenetic signal increased along with the increase in the number of species in the species pool. The Blomberg's K value is stable at 40 species, which could indicate that if researchers or practitioners have over 40 species sub-sampling of shortgrass prairie restoration species, their studies should be able to detect phylogenetic signals. The random sampling methods to verify sample size method could apply in sampling species to estimate phylogenetic conservatism in plant communities.

Shiny application

From the Shiny application, restoration practitioners could use interactive methods to explore our data and statistical

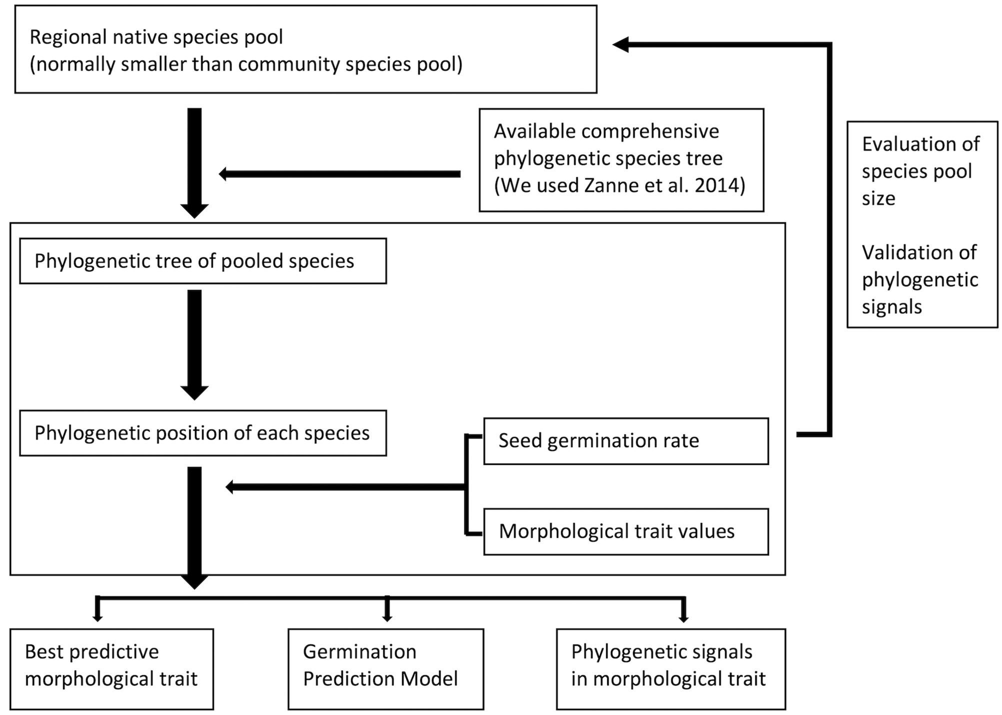


FIGURE 6
General protocol for generating a germinability prediction model with phylogenetic information for a plant community. This model needs a pool species with phylogenetic information, morphological data and germination data to build. It will be able to explore the germination pattern of the community.

analysis and results visualization. For readers who are first exposed to phylogenetic comparative methods, the interactive graphic user interface can lower the bar for exploring our data, as well as increase engagement. Our checkbox of species list allows users to design their composition of species, and to investigate the impact of species choice on phylogenetic signal and germinability prediction. Our Shiny application was published on GitHub website (https://github.com/chenyanniii/Traits_Shiny, DOI: 10.5281/zenodo.6609191) and on shinyapps.io.[1]

Comparison between tallgrass prairie and shortgrass prairie studies

Seed germination is a complex physiological phenomenon that could be studied for its optimization using dormancy breaking treatments (Barak et al., 2018), as well as could be a dormancy proxy, such as high germination rates indicated a lack of dormancy in our research. Our research can be contrasted with a similar tallgrass prairie study (Barak et al., 2018), in which: (1) the phylogenetic signals of germination were detected in morphological traits and seed germination percentage; (2) phylogenetic information improves the seed germinability prediction model. We saw the potential of applying phylogenetic information in ecological restoration, so we tested the phylogenetic application in simply restoration setting: (1) We selected regional appropriated seed sources from a local restoration vendor. (2) We estimated dormancy in seed sources by running germination trails without any dormancy breaking treatment to approximate the conditions preferred by restoration practitioners. (3) We tested our results against null models: confirming our confidence in sample size, examining the robustness of our conclusion while ensuring we can generalize results for the whole shortgrass prairie plant community. Our unique restoration scenario of shortgrass prairie showed a few advancements of knowledge. First, only seed mass and seed height detected phylogenetic signals in 45 species. The phylogenetic signal in seed mass is well preserved and can be generalized to estimate the phylogenetic signal for the shortgrass prairie plant community. On the opposite, detecting a phylogenetic signal in seed height is a low chance event that the phylogenetic signal in 45 species should not be generalized to estimate the phylogenetic signal for the shortgrass prairie plant community. Second, estimating phylogenetic signals for a plant community needs a larger sample size than a single fixed group. The shortgrass prairie plant community needs at around 40 species for detecting a general pattern (Figures 4 and 5), which is twice of the 20 species assumption in a fixed species comparative study (Blomberg et al., 2003).

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[1] https://chenyanniii.shinyapps.io/Phylo_Compar_Traits/

Conclusion and future studies

Overall, we have demonstrated that the phylogenetic signal calculation can be influenced by size and composition of seed pool. We recommend running a sub-sampling test to verify the sufficiency of species and phylogenetic conservatism in traits for a community study, and we proposed a general protocol for implementing phylogenetic conservatism in plant community restoration (Figure 6). Our Shiny application is on GitHub website[2] and on shinyapps.io,[3] using an interactive way to demonstrate how species composition directly impacts the phylogenetic signal calculation.

Our work demonstrated that some morphological traits have phylogenetic signal in shortgrass prarie (North America), although our subsampling found this to be robust to sample size only for seed mass. Yet our study could not detect the benefit of adding phylogenetic information using morphological traits to predict seed germinability (without dormancy breaking treatments). The inconsistent role of phylogeny in different ecosystems needs further exploration, especially taking advantage of large standard databases of seed traits and the tree of life.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found at: https://zenodo.org/record/6609175#.Yr3ovi-B3fY, 6609175.

Author contributions

YC and MJ: study conception and design. YC: data collection, data analysis and figures, and first draft of manuscript. DS and RC: experimental facilities. MJ: funding for supplies. All authors contributed to interpretation of results and revising the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.983192/full#supplementary-material

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[2] https://github.com/chenyanniii/Traits_Shiny,DOI:10.5281/zenodo.6609191

[3] https://chenyanniii.shinyapps.io/Phylo_Compar_Traits/

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Glossary

Phylogeny/Phylogenetic tree branching evolutionary histories / to graphs that represent these evolutionary histories. Phylogenetic tree including gene tree and species tree. In this paper, we only refer to species' tree (Baum and Smith, 2013).

Phylogenetic conservatism the hypothesis that closely related species share more traits than distantly related species (Agrawal, 2007).

Phylogenetic position the relative position between species commonly used nearest neighbor and paired-wise distance. We used paired-wise distance in our calculation.

Phylogenetic signal to describe a tendency for evolutionarily related organisms, under assumption of following a certain evolutionary model, to resemble each other (Blomberg et al., 2003).

Phylogenetic residual incorporate the phylogeny through error structure, such as estimating ancestral states, rates of evolution, phylogenetic effects (Garamszegi, 2014).

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Impacts of different fencing periods and grazing intensities on insect diversity in the desert steppe in Inner Mongolia

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For the past several decades, both species biodiversity and productivity of desert steppe have been reduced due to excessive use and climate factors. To counteract this, Chinese government has supported large-scale grassland ecological restoration programs since the year 2000. The policy needs a standard for the evaluation of the effects of such restorative measures on the grasslands after decades. Grassland insect diversity plays an important role in the maintenance of plant species and functional diversity. To understand the relation of grazing management and insect diversity, we use a complete two factor design, two fencing periods (3 or 7 years) and three grazing intensities (0, 6, or 12 sheep per ha), to examine the response of the insect diversity to fencing and grazing in desert steppe. We found almost no significant differences in either plant or insect species diversity between the sites fenced for 3 and 7 years, as the pressure of grazing increased, insect diversity decreased to a greater extent at 7-year enclosure sites than at 3-year sites. We recommend the most suitable grazing intensity for the sustainability of biodiversity of the desert steppe in Inner Mongolia is light grazing (8 sheep/ha 0.5 yr^{-1}), and the most suitable fencing period is three years, which suggest that policies that remove livestock from the desert grassland for long periods (7 + years) are not beneficial for maintaining insect diversity, and heavy grazing lead ecological environment weaker and insect diversity decreasing. Thus, periodic livestock grazing is important in the design of management actions to preserve biodiversity.

KEYWORDS

enclosure, livestock grazing, arid steppe, China, insect community biodiversity

Introduction

The "desert steppe" is a transitional region between the desert and traditional grassland steppes on the Inner Mongolia plateau and is particularly vulnerable to desertification (Yong et al., 2021). The region is dominated by *Stipa klemenzii* Roshev. (Poaceae) and is important for the livelihood of pastoral communities (Ren et al., 2011). However, for the past several decades, both species' biodiversity and grassland productivity have been reduced, causing serious damage to the ecology of the region (Zhang et al., 2010, 2020). Overgrazing is the main factor that accelerates steppe degradation (He et al., 2019). The Chinese government has supported an integrated portfolio of large-scale grassland ecological restoration programs since 2000 to counteract grassland degradation, mainly involving fencing for grazing control, increased numbers of protected areas, and other forms of support to local communities (Cheng et al., 2016). However, the policy lacks a general standard for the evaluation of the effects of such restorative measures on grasslands. Insects are the most biologically diverse group of animals and are important primary consumers (pests), secondary consumers (natural enemies), and decomposers (carrion and fecal insects) in grassland ecosystems, playing an important role in maintaining healthy grassland ecosystems (Yang and Yuan, 2019). Insects have been used in a wide range of ecological and environmental applications as they occupy almost every type of terrestrial and aquatic habitat and are extremely sensitive to environmental change (Gerlach et al., 2013). Therefore, an increasing number of studies are using insects as indicator species for the assessment of the success of grassland restoration (Alison et al., 2013; Alignan et al., 2018; Dröse et al., 2021). Studies assessing the impact of grazing, as the main utilization of grassland, have used insect diversity as an indicator with inconsistent results. Compared with grazing exclusion, light or moderate grazing results in high insect diversity, whereas heavy grazing results in low insect diversity (Ma et al., 2017), some studies reported that grazing increased insect diversity (Jerrentrup et al., 2014; Johansson et al., 2017; Zhu et al., 2017, 2020a), while others showed reduced or no significant effects on insect diversity in response to grazing (Wardle et al., 2001). Factors that may have influenced these inconsistent results may include differences in the type of grassland and grazing pattern, including both grazing intensity and the size of the herbivores and insect groups present (O'Neill et al., 2010; Zhu et al., 2015; Ma et al., 2017). In this study, we sampled fields in the desert steppe region of Inner Mongolia with different fencing periods and grazing intensities. We measured insect diversity to provide a reference evaluation of the recovery of the steppes and a scientific basis for the relationship between insect communities and the steppe environment. We hypothesized that insect diversity in pastures that had been fenced longer would be reduced compared with those fenced for shorter times as a result of the negative influence of fencing and, in addition, that the insect diversity would be higher in lightly grazed pastures compared with those subjected to no grazing or heavy grazing. We also expected changes in the species abundance distribution, with reductions in species evenness in longer-fenced pastures compared with those fenced for shorter times as the most competitive group will tend to increase its dominance in the process of community succession. We also hypothesized that there would be variations in the group proportions as some groups would be more affected by grazing than others.

Materials and methods

Study area

The study was conducted at Sonid Right Banner (42°47′19″N, 112°40′20″E, 972 m a.s.l.) and Sonid Left Banner (43°42′44″N, 113°36′12″E, 1070 m a.s.l.) temperate desert steppe in Inner Mongolia, China. This region conforms to a typical arid and semiarid temperate continental climate with rich heat and is characterized by a mean annual temperature of 3.1°C and a mean annual precipitation of 180 mm, with the growing season mainly from May to September (Ren et al., 2011). Evaporation (between 0.15 and 0.30) is several dozen times more than the "precipitation and moisture index." According to the Chinese Soil Database, the main soil types are chestnut soil, brown soil, and sierozem (China Soil Database, Institute of Soil Science, Chinese Academy of Sciences, 2019[1]). The soil has a thickness of 15–25 cm, with a thin layer of humus. The vegetation is dominated by *Stipa klemenzii* Roshev., *Cleistogenes songoric*a Roshev., and *Artemisia frigida* Willd. The grass is sparse and short with less than 30% of coverage, a height of 20–30 cm, and low primary production (Tana et al., 2011).

Design of experiment

We used two periods of fencing enclosures and three grazing intensities in a complete randomized block design to create a total of six treatments (**Supplementary Table 1**). Two fencing periods, i.e., 3 and 7 years, were selected. For each fencing period, three 45-ha plots (six in total) were established under the same conditions. In each plot, three 15-ha sections (18 in total) were divided and treated with three grazing intensities, i.e., no grazing (CK), light grazing (8 sheep/ha; LG), and high grazing (15 sheep/ha; HG). All the sample plots were enclosed all year round, and the CK plots were not used for grazing, while the LG and HG treatment areas were grazed from May to October every year.

Vegetation and identification

The vegetation of each paddock was surveyed. Three 1 × 1-m^2 quadrats were then randomly placed within each sample plot replication, and the vegetation composition and average height and coverage were recorded. The average height of the vegetation was measured. The coverage of the sward was assessed as the percentage of aboveground vegetation within the boundaries of the quadrat. Plants were identified to the species or morphospecies level using specialized literature (Cao, 2017), and the numbers were recorded.

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[1] http://vdb3.soil.csdb.cn/

Insect sampling and identification

We surveyed insects using three randomly located 20 × 20-m^2 quadrats within each sample plot replication. There were 54 quadrats in total. Insects were sampled between July and August 2012 using a checkerboard sweep net method (38 cm in diameter), whereby samples were collected by making a total of 250 sweeps, with five vertical sweeps (every 5 m) and five horizontal sweeps (every 80 cm) (Andreas and Teja, 2002). The sampled insects were stored in plastic bags with ethyl acetate, followed by preservation in 95% ethanol before sorting into taxonomic groups. We identified insects to the species or morphospecies level according to appropriate identification keys (Nonnaizab et al., 1988, 1999).

Phototropic insects, such as Lepidoptera, were attracted using a white tent (1 × 1 × 2 m) and a high-pressure mercury lamp (250 W). For insect collection, killing jars supplied with a small amount of ether were used. All samples were sorted to the species or morphospecies level in the field and kept in glassine envelopes. Sampling was carried out from 9.00 to 12.00 p.m. between July and August 2012. All specimens were identified in consultation with taxonomic experts.

Data analysis

All statistical analyses were conducted in R version 4.1.3 (R Core Team, 2022). Differences in plant cover, plant height, plant Shannon–Wiener index, and plant Simpson index among the two fencing periods and three grazing intensities were analyzed using linear mixed-effects models with the "lme" function of the nlme package. Linear mixed-effects models were followed by the analysis of variance (ANOVA, with the "anova" function) and Tukey tests using the multcomp package.

The insect diversity index was calculated by Past 4.08 software (Hammer et al., 2001). To assess insect community diversity patterns in different grazing intensities and fencing years, principal coordinate analysis (PCoA) with Bray–Curtis distances was used in the vegan package (Oksanen et al., 2018). Permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2017) was used to evaluate differences in communities using the "adonis" function in the vegan package (Oksanen et al., 2018).

To analyze the relationships between grazing intensities and fencing years (fixed effects) and insect abundance, richness, Shannon diversity, and Simpson diversity (response variables), we created generalized linear mixed models (GLMMs) using the glmmTMB function in the glmmTMB package with the model: diversity measure ∼ grazing × fencing + (1| grazing/plot). This was followed by the R^2 explained by fixed and random factors using the "r.squaredGLMM" function of the MuMIn R package. A Poisson link was used for species richness, whereas a Gaussian link was used for the other measures of diversity. Log transformation of data was used in cases where improvement was required for model fit. Redundancy analysis (RDA) was used to visualize the associations between the abundances of insect orders and the plant attributes, using the rda package. Ordination plots were compiled for insect order abundance in relation to plant variables, including plant species richness, cover, height, and plant Shannon–Wiener index, using the "envfit" function of the vegan package with 999 permutations.

Results

The total number of plant species found in the plots was as follows: 47 species in no grazed pastures, 48 species in lightly grazed pastures, 41 species in heavily grazed pastures, 47 in 3-year fencing grasslands, and 48 species in the 7-year fencing grasslands (**Supplementary Table 2**). In a comparison of the two types of fencing grasslands, 33 plant species were found in both treatments, 14 plant species were found only in the 3-year fencing treatment, and 15 plant species were exclusive to the 7-year fencing treatment (**Supplementary Figure 1**). No differences in plant species richness, plant Shannon diversity, plant cover and plant height were found ($P > 0.05$, **Table 1** and **Supplementary Figure 2**). The ungrazed (CK) sites had a higher Shannon diversity than the heavily grazed (HG) sites ($P < 0.05$), which did not differ from the lightly grazed (LG) sites ($P > 0.05$, **Supplementary Figure 3**). Plant species richness showed no differences between the three grazing intensity sites. Significant differences were found for plant cover and plant height, which were highest in the CK sites, lowest in the HG sites, and intermediate in the LG sites (**Supplementary Figure 3**).

In total, 2601 individuals were collected from all sites, which belonged to 165 species of 53 families of eight orders (**Supplementary Table 3**). Cicadellidae, Gomphoceridae,

TABLE 1 ANOVA tables of mixed-effects models with plant species richness, plant Shannon diversity, plant height, and plant cover as dependent variables in two fencing periods in a desert steppe: 3-year enclosure and 7-year enclosure. The plant cover was log-transformed.

	numDEF	denDG	*F*-value	*P*
Plant species richness				
Intercept	1	47	46.99667	<0.0001
Fencing	1	4	2.52735	0.1871
Plant Shannon diversity				
Intercept	1	47	357.8773	<0.0001
Fencing	1	4	0.3729	0.5744
Plant cover				
Intercept	1	47	681.7816	<0.0001
Fencing	1	4	0.0950	0.7733
Plant height				
Intercept	1	47	161.18649	<0.0001
Fencing	1	4	0.01679	0.9032

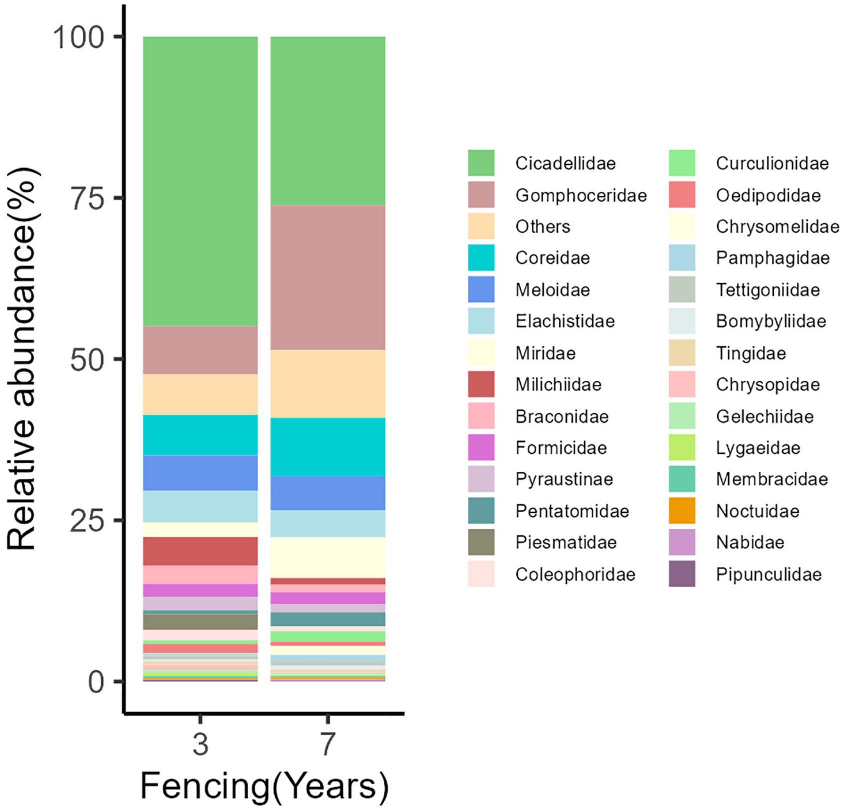

FIGURE 1
Proportional abundance of insect species collected from two fencing periods in a desert steppe.

Coreidae, and Meloidae represented most of the collected insects (Figure 1), accounting for 35, 15, 7.7, and 5% of the total abundance, respectively (Figure 1). Cicadellidae was the most abundant family in 3-year enclosure sites, representing 45% of the total abundance, followed by Gomphoceridae with 7.5% of the total abundance. In the 7-year enclosure sites, the proportion of Cicadellidae decreased to 26%, while Gomphoceridae increased to 22% of the total abundance (Figure 1). Overall, the species composition differed significantly between the different enclosure sites and different grazing sites (grazing: $R^2 = 0.03$, $P = 0.048$; fencing: $R^2 = 0.07$, $P = 0.001$). Our PERMANOVA pairwise comparisons indicated that all pairs of grazing intensity sites differed from each other, and the PCoA ordination plot showed clear distinctions, especially between insect communities from 3-year and 7-year enclosure sites (Figure 2). Among the 7-year enclosure sites, CK sites were markedly more distant from the LG and HG sites, which were closer to each other. This was also the case for the 3-year enclosure sites.

Insect abundance was higher in the CK sites than in the HG sites ($P < 0.05$), whereas there was no difference between the CK and LG sites ($P > 0.05$, Table 2 and Figure 3A). This was consistent with the trend of insect species richness (Table 3 and Figure 3B). However, there were no differences in insect Shannon and Simpson diversity indices between the CK and LG sites and between the CK and HG sites (Tables 4, 5 and Figures 3C,D).

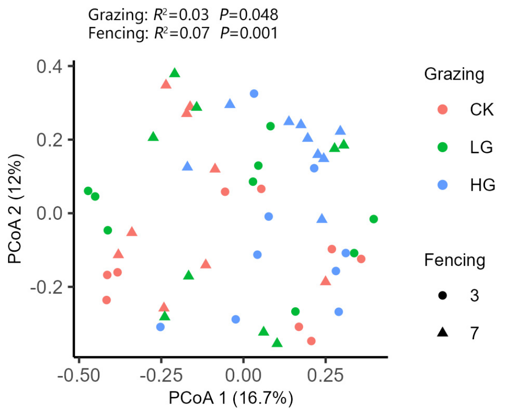

FIGURE 2
Principal coordinate analysis (PCoA) of insect communities across two fencing periods and three grazing intensities. PCoA was generated by the Bray–Curtis dissimilarity method.

TABLE 2 Results of generalized linear mixed models (GLMMs) for species abundance of insects sampled after 3 or 7 fencing years in three grazing treatments in a desert steppe: Ungrazed plot (CK, used as reference), light grazed (LG), and heavily grazed (HG).

	Estimate	Std. error	*Z*-value	*P*
Grazing				
Intercept	67.778	15.166	4.469	$<0.0001^{****}$
LG	−16.778	21.448	−0.782	0.4341
HG	−48.583	21.578	−2.251	$<0.05^{*}$
Fencing				
7	10.445	21.448	0.487	0.6263
Interaction				
LG × 7	−6.084	30.332	−0.396	0.6924
HG × 7	−12.000	30.424	−0.200	0.8415

Variance explained by fixed effects: Marginal $R^2 = 0.34$. Variance explained by the entire model: Conditional $R^2 = 0.77$. $^{****}P < 0.0001$, $^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$.

There was no difference in insect abundance between the 3- and 7-year enclosure sites ($P = 0.6236$, Table 2 and Figure 4A). We also found no significant interactions between grazing and fencing in relation to insect abundance (Table 2 and Supplementary Figure 4A). Higher insect abundance was seen in the LG sites, compared with the CK and HG sites in the 3-year enclosure sites, while the CK sites showed the highest abundance in the 7-year enclosure sites (Supplementary Figure 4A). Insect species richness did not differ between the two enclosure times (Table 3 and Figure 4B). However, we found a significant relationship between species richness and both grazing and fencing (Table 3 and Supplementary Figure 4B). In 7-year enclosure sites, species richness was significantly higher in the CK sites than in the LG and HG sites (Table 3 and Supplementary Figure 4B). Therefore, grazing strongly reduced species richness in the 7-year enclosure sites. The Shannon and Simpson diversity indices varied with the different lengths of fencing without showing any obvious trend (Tables 4, 5 and Supplementary Figures 4C,D). Diversity was higher in the 3-year enclosure sites than in the 7-year sites (Supplementary Figures 4C,D), implying that the longer fencing time did not significantly improve the

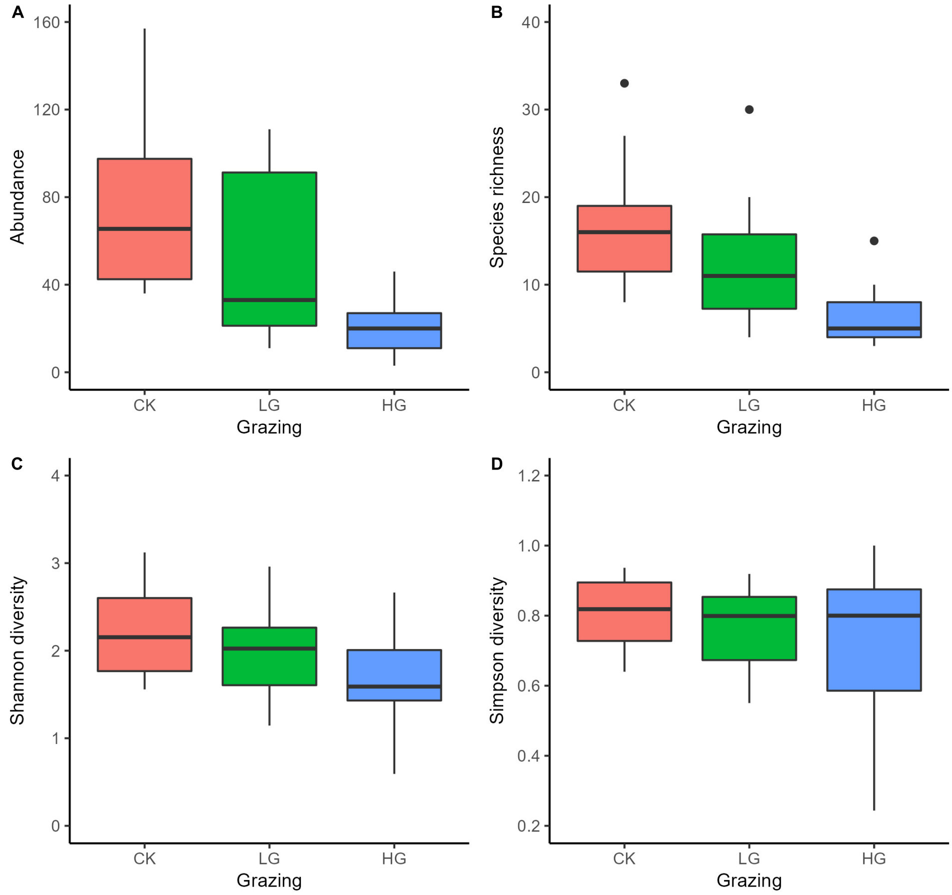

FIGURE 3
Boxplots of insect species abundance **(A)**, richness **(B)**, Shannon diversity **(C)**, and Simpson diversity **(D)** in three grazing intensities in a desert steppe: Ungrazed plot (CK), light grazed (LG), and heavily grazed (HG).

insect diversity. Grazing reduced both Shannon and Simpson diversities, although not significantly (**Tables 4**, **5**).

About 2.87% of the insect composition variation was explained by plant attributes ($F = 2.56$; $P = 0.001$) in the RDA model (**Figure 5**). Most of the variation in abundance was explained by axis 1, which was negatively associated with all the plant attributes, the same as the second axis of the RDA. Axis 1 separated the CK sites from the LG and HG sites while axis 2 separated the LG sites from the CK sites and some of the HG sites for all plant attributes. Hemiptera were found to be more abundant in the localities with higher plants while Orthoptera were more abundant in areas with lower plants. Coleoptera, Hymenoptera, and Lepidoptera were negatively associated with all plant attributes. In the CK sites fenced for 3 years, Neuroptera was strongly related to plant cover.

Discussion

In this study, we investigated the effects of fencing and grazing and their interactions on the structure of the insect communities of the desert grassland. Fencing represents one of the restoration measures applied in grassland areas to mitigate the negative effects of grazing on productivity and the ecosystem. In contrast to our expectations, we found almost no significant differences in either plant or insect species diversity between the sites fenced for 3 and 7 years. This showed that the fenced pastures established similar biological communities, irrespective of the fencing period, suggesting that fencing was successful in terms of community recovery (Steiner et al., 2016). Furthermore, fencing was found to have a significant effect on vegetation. For a certain period of time, enclosure eliminates disturbances to plant community structures produced by livestock trampling and foraging and enhances seedling germination, conducive to the recovery of plant productivity and the succession of community structures (Wang et al., 2020). Grazing can also alter the structures of plant communities by reducing species dominance and promoting the restoration of rare species (Pulungan et al., 2019). Our results showed that grazing significantly affected both plant height and cover, although it had no significant effect on the plant species diversity.

Our study showed varying degrees of change in the dominant insect group in relation to the different fencing periods. The proportion of the dominant insect family—Gomphoceridae—was found to be quite different in each plot, becoming more dominant as the time of enclosure increased, while that of Cicadellidae declined (**Figure 1**). This illustrates that extended fencing periods, together with pasture enclosure, away from grazing cattle and other large animals, allow previously less abundant insect groups to assume positions of dominance in the community in contrast to others (Zhao et al., 2010). Biotic organisms have been found to vary in their sensitivities to grassland restoration and degradation (Helbing et al., 2021), and our findings support this opinion (**Figure 4**). Besides direct effects, livestock grazing can also affect insect diversity indirectly in many cases. These indirect effects mainly include changes in vegetation, the spatial heterogeneity of the community, and microclimatic conditions resulting from grazing (Jerrentrup et al., 2014; Zhu et al., 2020b). We observed that the abundance of Orthoptera was negatively associated with vegetation height in the pastures. This may be due to the supply of oviposition sites, with more new growth providing greater numbers of sites and changes in microclimate favoring locust hatching following grazing (Zhu et al., 2020b).

TABLE 3 Results of generalized linear mixed models (GLMMs) for species richness of insects sampled after 3 or 7 fencing years in three grazing treatments in a desert steppe: Ungrazed plot (CK, used as reference), light grazed (LG), and heavily grazed (HG).

	Estimate	Std. error	*Z*-value	*P*
Grazing				
Intercept	2.6635	0.1293	20.604	< 0.0001****
LG	−0.1379	0.1276	−1.081	0.2798
HG	−0.6411	0.1534	−4.180	< 0.0001****
Fencing				
7	0.2337	0.1783	1.311	0.1898
Interaction				
LG × 7	−0.3770	0.1805	−2.089	< 0.05*
HG × 7	−0.5669	0.2237	−2.535	< 0.05*

Variance explained by fixed effects: Marginal $R^2 = 0.60$. Variance explained by the entire model: Conditional $R^2 = 0.69$. $^{****}P < 0.0001$, $^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$.

TABLE 4 Results of generalized linear mixed models (GLMMs) for species Shannon diversity of insects sampled after 3 or 7 fencing years in three grazing treatments in a desert steppe: Ungrazed plot (CK, used as reference), light grazed (LG), and heavily grazed (HG).

	Estimate	Std. error	*Z*-value	*P*
Grazing				
Intercept	0.30875	0.05813	5.312	< 0.0001****
LG	−0.01484	0.08220	−0.180	0.857
HG	−0.04892	0.08288	−0.590	0.555
Fencing				
7	0.05054	0.08220	0.615	0.539
Interaction				
LG × 7	−0.09490	0.11625	−0.816	0.414
HG × 7	−0.19157	0.11673	−1.641	0.101

Variance explained by fixed effects: Marginal $R^2 = 0.27$. Variance explained by the entire model: Conditional $R^2 = 0.69$. $^{****}P < 0.0001$, $^{***}P < 0.001$, $^{**}P < 0.01$, $^{*}P < 0.05$.

According to previous studies, different grazing management strategies significantly influences the composition of grassland insect communities (Poyry et al., 2005; KÅrösi et al., 2012). Our study showed that different fencing periods and grazing intensities had different effects on the insect community. We observed that light grazing maintained insect variety in areas fenced for shorter times while the variety decreased with

TABLE 5 Results of generalized linear mixed models (GLMMs) for species Simpson diversity of insects sampled after 3 or 7 fencing years in three grazing treatments in a desert steppe: Ungrazed plot (CK, used as reference), light grazed (LG), and heavily grazed (HG).

	Estimate	Std. error	*Z*-value	*P*
Grazing				
Intercept	−0.352163	0.143320	−2.457	< 0.05*
LG	0.022559	0.202685	0.111	0.911
HG	0.005291	0.205029	0.026	0.979
Fencing				
7	0.082218	0.202685	0.406	0.685
Interaction				
LG × 7	−0.215199	0.286640	−0.751	0.453
HG × 7	−0.400665	0.288302	−1.390	0.165

Variance explained by fixed effects: Marginal R^2 = 0.15. Variance explained by the entire model: Conditional R^2 = 0.52. ****$P < 0.0001$, ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

increased grazing intensity in pastures fenced for longer time periods (**Supplementary Figure 4**). We could see that species diversity and insect richness did not increase as the fencing period increased. It was, thus, possible to reach a maximum insect diversity during the restoration. As the pressure of grazing increased, insect diversity decreased to a greater extent at 7-year enclosure sites than at 3-year sites, suggesting that fencing for 7 years had no significant advantage, even in the presence of interference by large animals, probably because the long-term enclosure promoted the status of dominant species and the vegetation structure became progressively homogenized (Karg et al., 2015). These changes in the vegetation community led to a decline in the variety of insects. In contrast, in the plots fenced for 3 years with light grazing, species richness did not differ significantly from sites without grazing, demonstrating that light disturbances benefited both the number and diversity of insects due to the maintenance of high plant diversity (Koch et al., 2016; Ferreira et al., 2020). We found no significant effects of the fencing period and grazing intensity on insect Shannon and Simpson diversity. Similar to insect species richness, after the inclusion of grazing, the insect Shannon diversity decreased to a greater extent for 7-year of enclosure than for 3-year of the

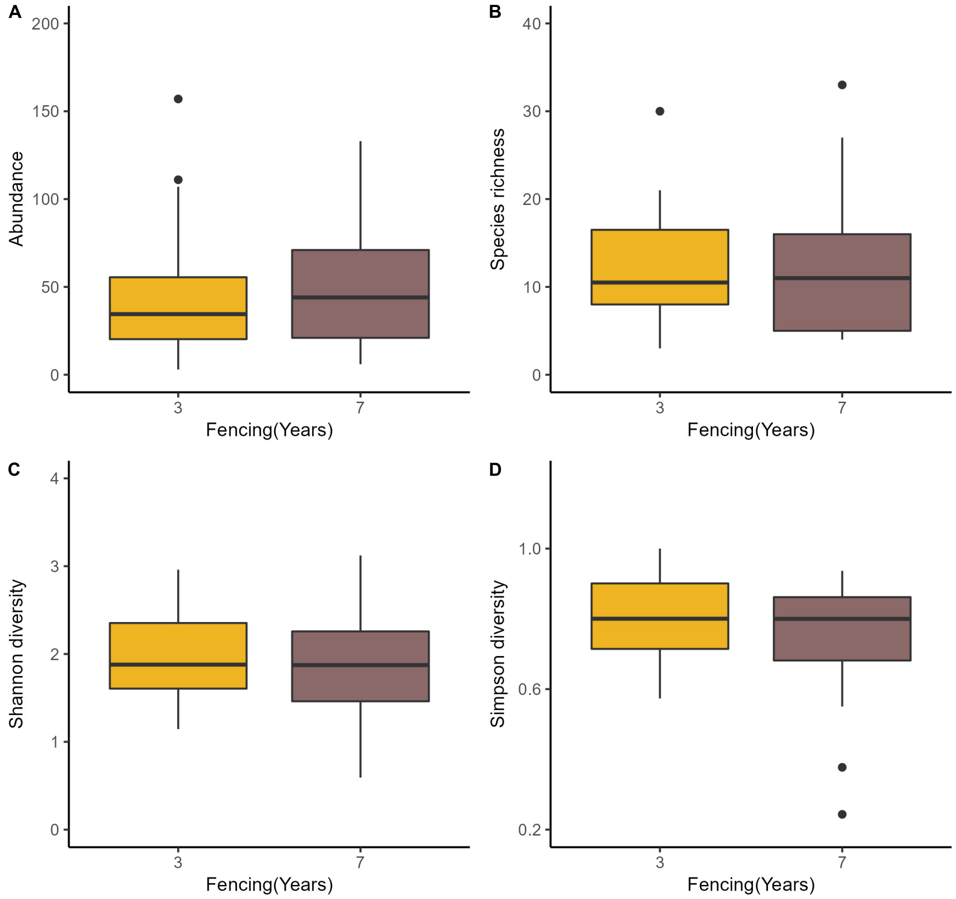

FIGURE 4
Boxplots of insect species abundance **(A)**, richness **(B)**, Shannon diversity **(C)**, and Simpson diversity **(D)** in two fencing periods in a desert steppe: 3 fencing years and 7 fencing years.

enclosure. This further demonstrated that extending the fencing period does not contribute significantly to the maintenance of biodiversity. Hence, grasslands, where grazing has been prohibited, should gradually be restored according to the policy of "rotation grazing."

It was found that under the same fencing period, the ungrazed plots showed the highest diversity, with light grazing showing the second highest diversity, and heavy grazing the lowest diversity. This indicated that an increase in grazing stocking rates altered the abiotic and biotic properties so that the dominance of more competitive or disturbance-tolerant species was favored, thus reducing insect diversity (Gossner et al., 2016). It has been found that when the grazing system was changed, by allowing disturbance by sheep in the desert steppe, the plant species, insect species, soil, and environment changed as a result (Deng et al., 2014; Zhou et al., 2017). Previous research has shown that factors such as biomass, coverage, and species composition affect indicators such as the diversity and richness of insects (Zhu et al., 2012; Jerrentrup et al., 2014). These findings were supported by our RDA results (**Figure 5**). Orthoptera was favored by a low cover and low height of plants in the HG sites, indicating that Orthoptera species were influenced by grazing through modifications in the plant community structures, which is consistent with the results of recent findings (Schwarz and Fartmann, 2022). In contrast, Diptera and Hymenoptera were more strongly influenced by plant height as they tend to have specific habitat requirements, such as for refugees or oviposition (Morris, 2000).

In the present study, the results may have been influenced by the climate at the time of sampling as during the months from April to August 2010, the rainfall recorded was less than that at other times over the Sonid Right Banner and the Sonid Left Banner in Inner Mongolia, and the critical period for herbage growth was during June, July, and August. Continuous drought and less rainfall, in addition to the higher-than-average temperatures, may have affected both the growth of herbage and the accumulation of grass productivity. This is likely to have decreased the insect diversity of the grassland, especially in the plots with slight disturbance. Thus, further research on fencing and grazing, together with continuous monitoring of insect diversity, and the study of the influence of environmental factors such as climate are of great importance

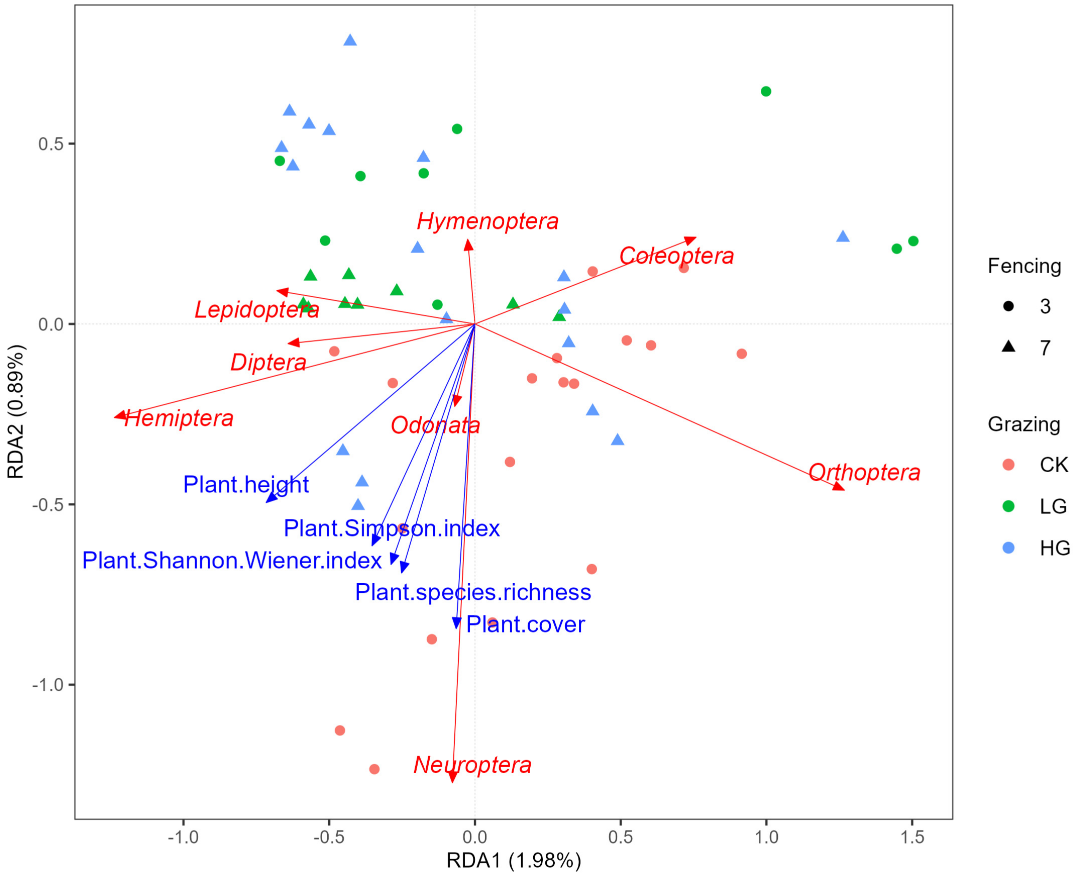

FIGURE 5
Effects of plant attributes on insect abundance based on redundancy analysis (RDA).

to gain a deeper and more comprehensive understanding of the regulatory mechanisms underlying environmental influences on the recovery of insect diversity.

Data availability statement

The original contributions presented in this study are included in the article/**Supplementary material**, further inquiries can be directed to the corresponding author.

Ethics statement

The animal study was reviewed and approved by the Ethics Committee of the Chinese Academy of Agricultural Sciences.

Author contributions

NW and XS conceived and designed the methods and framework, analyzed and interpreted the data, wrote the manuscript, and discussed the results. JW contributed to the collection and interpretation of the data and discussion of results. LW conducted the analyses and wrote the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.1021677/full#supplementary-material

SUPPLEMENTARY FIGURE 1
Venn diagrams of differences in the plant species in two fencing periods **(A)** and differences in the plant species in three grazing intensities **(B)**.

SUPPLEMENTARY FIGURE 2
Boxplots of plant species richness (number of species, **A**), plant Shannon diversity **(B)**, plant cover **(C)**, and plant height **(D)** in two fencing periods in a desert steppe: 3 fencing years and 7 fencing years.

SUPPLEMENTARY FIGURE 3
Boxplots of plant species richness (number of species, **A**), plant Shannon diversity **(B)**, plant height **(C)**, and plant cover **(D)** in three grazing intensities in a desert steppe: Ungrazed plot (CK), light grazed (LG), and heavily grazed (HG).

SUPPLEMENTARY FIGURE 4
Boxplots showing monthly variations of insect species abundance **(A)**, richness **(B)**, Shannon diversity **(C)**, and Simpson diversity **(D)** in two fencing periods in a desert steppe: Ungrazed plot (CK), light grazed (LG), and heavily grazed (HG).

SUPPLEMENTARY TABLE 1
Experimental design of grazing trial.

SUPPLEMENTARY TABLE 2
Plant species in each plot in a desert grassland in Inner Mongolia.

SUPPLEMENTARY TABLE 3
Insect species and abundances in each plot in a desert grassland in Inner Mongolia.

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Patch-level processes of vegetation underlying site-level restoration patterns in a megatidal salt marsh

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Vegetation patterns during salt marsh restoration reflect underlying processes related to colonization, reproduction, and interactions of halotolerant plants. Examining both pattern and process during recovery is valuable for understanding and managing salt marsh restoration projects. We present a decade of vegetation dynamics during salt marsh restoration (2011–2020) at a study site in the Bay of Fundy with megatidal amplitudes, strong currents, cold winter temperatures, and ice. We mainly investigated reproduction (asexual and sexual) and associated spread rates of *Spartina* grasses, and their health-related states (stem density, canopy height, and percent flowering) which help inform the probability of processes occurring. We also estimated modes of colonization and began quantifying the effects of interspecific interactions and environmental conditions on plant state. *Spartina pectinata* was the only pastureland plant to survive dike-breaching and saltwater intrusion in 2010; however, it was stunted compared to reference plants. *Spartina pectinata* patches remained consistent initially, before decreasing in size, and disappearing by the fifth year (2015). This early dynamic may provide initial protection to a developing salt marsh before *Spartina alterniflora* becomes established. *Spartina alterniflora* first colonized the sites in year 2 (2012), likely *via* deposition of rhizomal material, and then spread asexually before seedlings (sexual reproduction) appeared in year 4 (2014). Vegetation cover subsequently increased greatly until near-complete in year 9 (2019). The early successional dynamics of *S. pectinata* and *S. alterniflora* occurred spatially independently of each other, and likely contributed to sediment retention, creating an improved environment for *S. patens*, the dominant high marsh species in our region. *Spartina patens* have been slowly spreading into restoration sites from high elevation areas since year 6 (2016). We expect that competition between *S. alterniflora* and *S. patens* will result in the typical distinct zonation between high and low marsh zones. A next study will use the quantified processes for spatial-explicit modeling to simulate patterns of vegetation recovery, and to evaluate different salt marsh restoration strategies for the Bay of Fundy and elsewhere. Thus, proper identification and quantification of pattern-building processes in salt marsh vegetation recovery, the focus of our present study, was an essential step.

KEYWORDS

pattern-building, process quantification, spread rate, density, canopy height, Bay of Fundy, *Spartina*, *Sporobolus*

Introduction

Community patterns are the result of underlying, patch-level processes of individual species (Levin, 1992; Tilman and Kareiva, 1997; Liu et al., 2016). Patch-level processes can be generally defined as small-scale ecological changes in species that, when acting in unison with others and through time, affect larger-scale distributions of the communities in a defined area (Wu and Loucks, 1995). During ecological restoration, changes in vegetation community patterns reflect changes in species abundance and distribution (Radeloff et al., 2001; Peng et al., 2012; Virgin et al., 2020), and quantitatively analyzing processes related to colonization, reproduction, and interactions of these species can elucidate the trajectory (structure and rate of change) of the patterns (Hupp, 1992; Bergen et al., 2000). In addition, monitoring health-related states (live stem density, canopy height, and percent of live stems flowering) of vegetation at the patch-level informs the probability of processes occurring (Briske et al., 2005). Ecological studies that examine pattern, process, and state are valuable for understanding and managing ecosystems (Levin, 1999).

After tidal flow to salt marsh restoration sites is reestablished, the vegetation community undergoes substantial changes in its pattern, including extirpation of terrestrial or freshwater vegetation, decreased abundance of brackish vegetation, and increased abundance of halotolerant vegetation, which is typically led by those most tolerant of saltwater inundation and followed by those that are superior competitors at higher elevation (Sinicrope et al., 1990; van Proosdij et al., 2010; Virgin et al., 2020). The rate of vegetation recovery (i.e., rate of change of the vegetation community patterns) of salt marshes varies depending on several conditions including sediment deposition and edaphic characteristics; the species of terrestrial, freshwater, and semi-halotolerant vegetation present prior to restoration; proximity to sources of reproductive material of halotolerant vegetation; and patch-level processes and states of vegetation (Broome et al., 1988; Warren et al., 2002). For the present salt marsh restoration study (Aulac, New Brunswick, Canada), community patterns following saltwater intrusion after breaching an agriculture dike (formerly protecting pasture land from tidal influence) and die-off of pastureland vegetation were: decline of the on-site semi-halotolerant *Spartina pectinata* (freshwater cordgrass, syn. *Sporobolus michauxianus*), establishment and spread of *Spartina alterniflora* (saltwater cordgrass, syn. *Sporobolus alterniflorus*; Peterson et al., 2014; Bortolus et al., 2019), and establishment of a high marsh (dominated by salt marsh hay *Spartina patens*, syn. *Sporobolus pumilus*), resulting in a salt marsh with distinct zonation (Boone et al., 2017; Virgin et al., 2020).

Processes contributing to site-level community patterns observed during the Aulac salt marsh restoration project may have been driven by physiological thresholds, ecological interactions, or a combination of both. *Spartina pectinata* is a semi-halotolerant species with a salinity tolerance up to 0.2 M NaCl (12 ppt; Warren et al., 1985). Although spread rates of *S. pectinata* have been measured in a wet prairie ecosystem (up to 3 m y^{-1}, Fraser and Kindscher, 2005), they have not been rigorously measured within the context of salt marsh restoration. In contrast, rates of *S. alterniflora* spread have been well studied in salt marshes throughout the world because of its capacity as an invasive species (Taylor and Hastings, 2004; Zhang et al., 2017). It is well-adapted to frequent flooding by saltwater, being tolerant of high salinities including 0.6 M NaCl (35 ppt; Vasquez et al., 2006) and above (Webb, 1983). Furthermore, it displays tall and short phenotypes, with the short phenotype likely reflecting less favorable environmental conditions (Anderson and Treshow, 1980; Zerebecki et al., 2021). *Spartina alterniflora*'s asexual spread rates when colonizing intertidal soft sediments can be vigorous (134 ± 28 m y^{-1}; Callaway and Josselyn, 1992), and its seeds can disperse up to hundreds of km *via* tidal currents (Morgan and Sytsma, 2013). Seedlings typically need more than one growing season to become as tall as mature plants (Redfield, 1972), and in appropriate elevations and edaphic conditions, they are more successful growing in bare spaces than under mature canopies (Metcalfe et al., 1986). *Spartina alterniflora* can tolerate low elevation marsh conditions (i.e., longer inundation) that other species cannot, which leads to strong vegetation zonation with *S. patens*. *Spartina patens* typically occupy high elevation areas in mature salt marshes. This zonation is controlled by abiotic stress on the seaward side and competitive stress on the landward side (Bertness, 1991). *Spartina patens* displays dense, clonal morphology, has a very high salinity tolerance (up to 60 ppt, Hester et al., 1996), and spreads slower than *S. alterniflora* (~1 m y^{-1} estimated from Ayres et al., 2004). Frenkel and Boss (1988) (Oregon, United States) reported that *S. patens* did not begin to spread at an apparent exponential rate until three decades after its colonization. Overall, substantial research on processes affecting site-level patterns in salt marshes has been conducted (see citations included earlier in this paragraph), but more is needed to better understand them during restoration. Research on recovery dynamics of salt marshes is essential, because of historical high losses of salt marshes due to human activity (Gedan et al., 2009) and the relatively recent realization of their contribution to important ecosystem services, including protection of coastal infrastructure (Costanza et al., 2008), carbon sequestration (Mcleod et al., 2011), and providing habitat for fish, birds, and invertebrates (Minello et al., 2003).

The objective of the present study was to identify and quantitatively analyze patch-level processes of vegetation community change that explain the site-level patterns observed during salt marsh restoration on a megatidal (semi-diurnal tidal amplitudes in the study area reach ~14 m; Fisheries and Oceans Canada, 2022a) and ice-influenced coastline. Our study examined plant dynamics annually from 2011 to 2020, following a managed realignment that started in Fall 2010 in the upper Bay of Fundy. We investigated the health-related states and spread rates of *Spartina* grasses (*S. pectinata*, *S. alterniflora*, and *S. patens*), and modes of reproduction and seedling performance of *S. alterniflora*. Vegetation reproduction (mostly asexual) was the process that was quantified in the most detail during our study, but we also provided our best estimate regarding colonization, and began quantifying the effects of biotic and abiotic interactions on health-related vegetation states. We first present patterns of vegetation community change at the site level and then describe, in detail, patch-level dynamics including plant health-related states (stem density, canopy height, and percent flowering) and spread rates. We subsequently discuss ecological insights and restoration implications and describe how our process-related results can be used to model spatial dynamics of vegetation.

Materials and methods

Study area

The sites of the salt marsh restoration project are located in Aulac, New Brunswick (Figure 1). The restoration project began in 2009 and is led by Ducks Unlimited Canada (DUC) and partners (Millard et al., 2013; Boone et al., 2017). Before the old dike was breached in fall 2010, the geomorphology of the site was assessed, and hydrodynamic modeling was done to encourage the reestablishment of salt marsh. The project consists of two restoration sites (Restoration East and West) and two established salt marsh sites (Reference East and West). The restoration is a managed realignment, where the agricultural dike bordering pastoral land was no longer feasible to maintain due to wave action, erosion, and sea level rise (Boone et al., 2017; Virgin et al., 2020). A new dike was constructed ~100 m landward of the old agricultural dike; the latter was later breached to encourage the development of salt marsh in front of the new dike which should prolong its lifespan. Two breaches were excavated from the seaward dike of Restoration East and one breach for Restoration West. The Reference sites are mainly high elevation salt marsh with *S. patens* dominating (typical of Bay of Fundy salt marshes; Virgin et al., 2020) and *S. alterniflora* restricted to the creek and seaward edges. The initial elevation disparity between Restoration and Reference sites was as much as 2 m in some areas, and Restoration West (~11.0 ha in size) was ~0.43 m higher than Restoration East (~5.5 ha in size; Virgin et al., 2020). The Restoration sites are typically inundated twice in a 24-h period, following the tidal regime of the region (Desplanque and Mossman 2004), with inundation times varying depending on the tidal amplitudes (Higher High Water Mean Tide is 11.66 m for nearby tidal station Pecks Point; Fisheries and Oceans Canada, 2022b). In the pre-breach sampling of the sites to be restored (summer 2010), the vegetation community was terrestrial with some semi-aquatic plants, notably *S. pectinata* (Virgin et al., 2020). *Spartina pectinata* was the only plant species that survived tidal inundation following breaching.

Vegetation dynamics at the site level

To determine large-scale vegetation patterns in Restoration sites, we subdivided each site into five strata and visually estimated and sketched percent cover of vegetation and the spatial distribution of the different sized plant patches (monospecific groups of stems; see Figure 1, panels 2011–2014) in July. The strata dividing the Restoration sites ran perpendicular to the shoreline and were 100–180 m long and 135–160 m wide. Vegetation cover was estimated visually by standing on the new landward dike midway through each stratum. From 2011 to 2014, before patches started merging, the number of patches per stratum was counted per size class. There were five size classes depending on patch diameter; they were < 0.1 (1), 0.1–0.5 (2), 0.5–1 (3), 1–2 (4), and > 2 m (5). In 2013–2014, the species of *Spartina* (either *S. pectinata* or *S. alterniflora*) in these patches was recorded in three randomly selected half-strata censused on foot.

Dynamics of *Spartina* patches in restoration sites

To determine the details of plant spread and state (stem density, canopy height, and percent flowering), we haphazardly selected and monitored five replicate patches per species (*S. pectinata* and *S. alterniflora*) per site, every 2–4 weeks from mid-June until fall 2011–2020. Note that after winter, the plants first appear above ground in late May–early June. A patch selected for study was initially defined as a monospecific group of five or more stems that was at least 2 m away from the next closest patch; in 2014, this separation distance was reduced to 50 cm (the length of a rhizome; Bertness, 1991). From 2011 to 2014, new patches were selected, and their GPS location recorded at the beginning of each growing season. In contrast, from 2015 to 2020, the locations of patches selected in 2015 were monitored across subsequent years because the vegetation had largely coalesced into a meadow of *Spartina*. Patches were classified based on their attributes at the time of selection, hereafter referred to as patch type. Patch types were: *S. pectinata* (0.24–4.25 m starting diameter); Large *S. alterniflora* (8–20 m starting diameter) and Small *S. alterniflora* (0.28–2.06 m starting diameter); Seedling

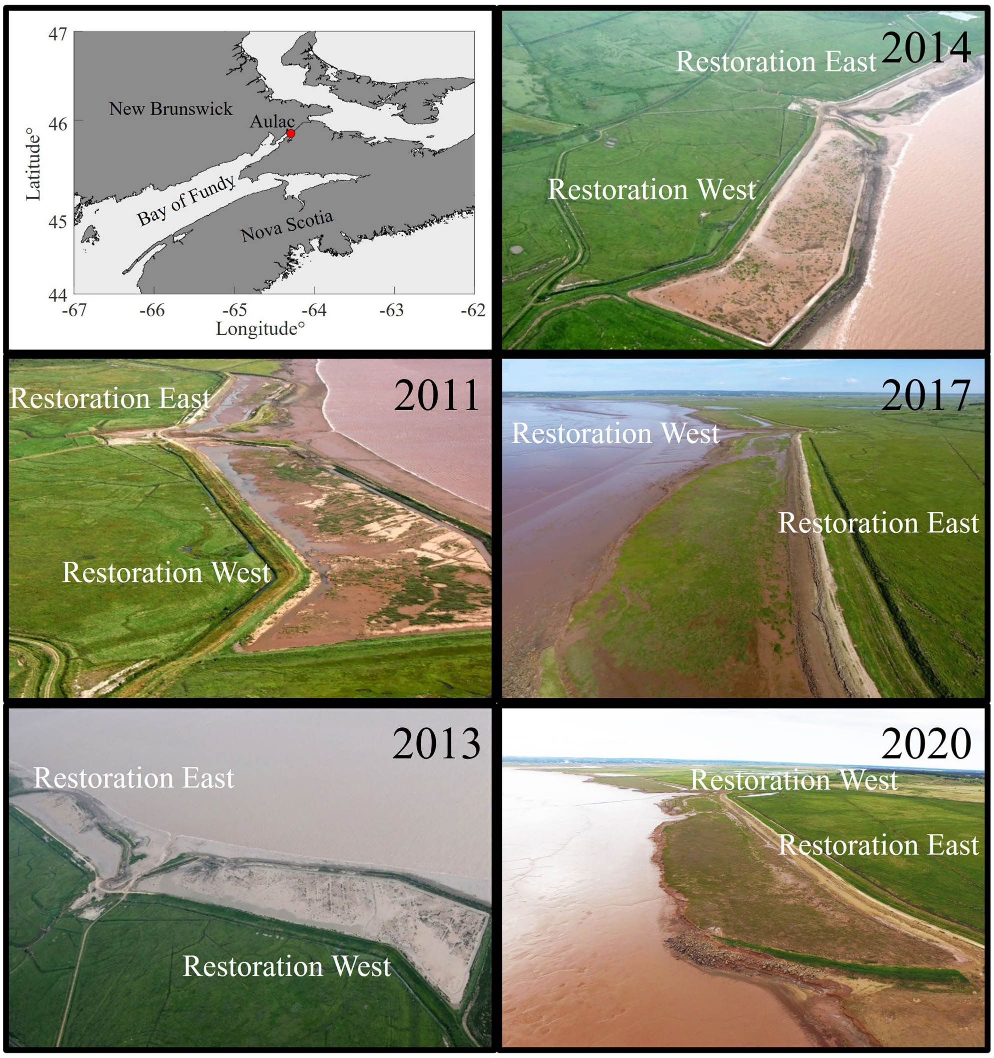

FIGURE 1
Location of the Aulac (Fort Beauséjour) salt marsh restoration project in New Brunswick, Canada (top left); the study area is in Cumberland Basin in the upper Bay of Fundy. Aerial photographs to show changes in vegetation cover in the two Restoration sites (see also Virgin et al., 2020). Photographs courtesy of Ducks Unlimited Canada (August 2011, July 2013, July 2014), Sebastian Richard (July 2017), and GSN (June 2020).

S. alterniflora (young-of-the-year), first observed onsite in 2014; and *S. patens* located along dike edges or found within the Restoration sites (first observed in 2016 in Restoration West; see Supplementary Figure 1.1 for example year of patch locations). For each patch, the number of live and flowering stems were counted, and the first and fifth tallest plant heights were measured; the tallest stem was canopy height, and the fifth tallest was measured to detect possible presence of tall outliers. When patch diameter was larger than 1 m or if it merged with other patches, plant counts and height measurements were done within a quadrat (0.5 m × 0.5 m) near the middle of the patch. Patch area was estimated as an ellipse, for *S. pectinata* and *S. alterniflora* from 2011 to 2015 and for within-site *S. patens* from 2017 to 2020, using the longest patch diameter and the diameter perpendicular to the longest. Each patch was photographed on each monitoring date with a ruler as a scale to complement field data.

Spartina in reference sites

In the Reference sites, *Spartina* spp. "patches" (i.e., GPS locations marked with a survey flag, Supplementary Figure 1.1) were monitored for plant counts and heights as in the section "Dynamics of *Spartina* patches in restoration sites" using a 0.25-m^2 quadrat. Three to five replicate "patches" per site for each patch type included both phenotypes of *S. alterniflora*, the tall form bordering protected creeks within the marsh (Creek type) and the short form located along the exposed seaward edge of the marsh (Edge type); *S. pectinata* near the terrestrial border in

Reference East (none present in Reference West); and *S. patens* in the high marsh zone. Note that the *S. alterniflora* edge patches in Reference East were omitted from analysis, because new patches (which were of mixed species composition and stressed) needed to be selected yearly due to the high erosion of that shoreline (Virgin et al., 2020).

Spartina patens encroachment onto restoration sites proper

To record the spread of *S. patens* from the new dike onto the Restoration sites, we monitored six *S. patens* patches ($n = 3$ Restoration site^{-1}) per year from 2017 to 2020. These patches were selected based on their stem density and canopy height (approaching that of Reference sites: e.g., 418 ± 40 live stems m^{-2} and 29 ± 2 cm tall; mean ± SE, $n = 10$ reference patches on 23 June 2017), size (>1 m longest diameter), and integrity. A gridded 1.0 m × 0.6 m quadrat, divided into 375 4.0 cm × 4.0 cm cells using monofilament line, was positioned such that ~10 cm of the seaward edge of the *S. patens* patch was within the quadrat on the first deployment date and its spread seaward could be recorded (see Supplementary Figure 2.1 for photograph of quadrat). Permanent bamboo stakes were inserted into sediment under the corners of the quadrat so that it could be placed into the same position at every sampling date. On each date, the seaward edge of the *S. patens* patches was carefully drawn on a gridded datasheet, as well as photographed. The distance advanced of the patches' edge onto the Restoration sites proper was measured for each from the drawings, with the first drawing in mid-June representing a start distance of 0 cm.

Data analysis

To evaluate large-scale patterns, percent vegetation cover in Restoration sites was analyzed using ANOVA (Minitab 18 Statistical Software, 2015) with Year (10 levels: 2011–2020) and Site (two levels: Restoration East and West) as fixed factors, and Stratum (five levels, nested in Site) as a random factor. Dynamics of the distribution of patch sizes (five size classes, with resemblance matrix constructed using Euclidian distance) were analyzed using Permutation Multivariate ANOVA (PRIMER with PERMANOVA add-on, v. 6; Anderson et al., 2008) with Year (four levels: 2011–2014) and Site as fixed factors, and Stratum as a random factor.

To determine change in *Spartina* patch area over a growing season, we first estimated area of each patch after a standardized period of 90 days by using simple linear regression of patch area versus days since the first sampling date (usually mid-June). Percent areal growth was then calculated by dividing by initial patch area and multiplying by 100. This was done for each patch of *S. pectinata* in 2011–2014, *S. alterniflora* in 2012–2015, and non-dike *S. patens* in 2017–2020. For *S. pectinata* and *S. alterniflora*, percent areal growth was analyzed using ANOVA with Year (three levels: 2012–2014) and Species (two levels) as fixed factors. Data obtained in 2011 for *S. pectinata* and 2015 for *S. alterniflora* were graphed but not included in the analysis.

To estimate encroachment of *S. patens* in dike patches onto the Restoration sites, we quantified incremental distance advanced after each sampling round, standardized for 2-week periods, during the growing seasons in 2017–2020. Specifically, using the grid drawings mentioned above, we selected (in a stratified random manner) five measures of the leading patch edge per drawing, converted them to standardized incremental advance, and used ANOVA, with Year (four levels: 2017–2020) and Round (six levels: June–September) as fixed factors, and Patch (six replicates; nested in Year) as a random factor. Note that we assumed edaphic conditions within Restoration sites were suitable for *S. patens* when *S. patens* patches had positive annual spread.

To examine differences in plant states of *S. pectinata* and *S. alterniflora*, live stem density, canopy height, and percent of live stems flowering were analyzed using ANOVA or PERMANOVA (which can be used for univariate analysis; Anderson et al., 2008) using Euclidian distance. For *S. pectinata* in 2013–2014, which is when we had a complete dataset, Year (two levels) and Site type (two levels: Restoration and Reference) were fixed factors, and Patch (3–10 replicates) was a random factor (the error term). For *S. alterniflora* in 2015–2020, which is when we repeatedly monitored the same patches, Year (when used, six levels) and Patch type (four or eight levels, described in the section *Spartina* in reference sites) were fixed factors, and Patch (5–10 replicates; nested in Patch type) was a random factor. More explicitly, the analyses that spanned 6 years (2015–2020, ~third week of August for each year) included the *S. alterniflora* patch types: Restoration Large, Restoration Small, Reference Creek, and Reference Edge; while the analyses conducted for an example year (namely 22 August 2017) to compare all patch types included the aforementioned patch types as well as young-of-the-year patches from 2014 to 2017. Planned contrasts in the PERMANOVAs focused on differences in vegetation states of the patch types sampled on 22 August 2017 to determine how patch types in Restoration sites compared to patch types in Reference sites, as well as how many years it took for patches established by seedlings to be similar to mature patches.

For univariate analyses, assumptions of homogeneity of variance and normality of residuals were assessed using Cochran's C test and visual examination of residuals, respectively. Dependent variables were transformed as necessary using logit for percent, square root for counts, and $\log_{10}$ for measurements (indicated in the tables). Construction of F-ratios and Pseudo F-ratios were as per Underwood (1997). Tukey's *post hoc* comparisons were conducted where appropriate to help interpretation and are presented as Supplementary material. Means ± SE are presented throughout the results, unless indicated otherwise.

Results

Site dynamics

Mean vegetation cover in Restoration sites was low to moderate in the first-year post breach (July 2011: Restoration East: 25 ± 6% and Restoration West: 51 ± 5%, $n = 5$ strata) and decreased (by 22% in Restoration East and 28% in Restoration West) from 2012 to 2013. From 2014 to 2019 however, vegetation cover rapidly increased (by 93% in Restoration East and 71% in Restoration West) before plateauing in 2019–2020; Figures 1, 2; Supplementary Table 1.1. Furthermore, the two Restoration sites differed (significant Year*Site interaction, $p < 0.001$; Table 1; Supplementary Table 1.1) in that the East site typically had less vegetation cover than the West site, but by 2019–2020 both sites had essentially complete cover (~95%; Figure 2).

Initially, *Spartina* vegetation cover was in the form of almost circular patches. Patches of *S. alterniflora* expanded rapidly (see the section *Spartina* spread rates) before eventually merging and empty space was mainly in-filled by *S. alterniflora* seedlings. The patch size distribution was dominated by small patches (<0.5 m diameter) in the early years (particularly 2012; Figure 3), with a few large *S. pectinata* patches (>1 m diameter) in the higher elevation areas in the sites. Patch size distribution shifted to mid and large sized patches in 2013, large patches (mostly *S. alterniflora*) dominated in 2014, and there was widespread merging of patches (all *S. alterniflora*) in 2015 (Table 1; Figure 2; Supplementary Table 1.2; Supplementary Figure 1.2). Very small patches (<0.1 m) were abundant in 2014, reflecting en masse appearance of *S. alterniflora* seedlings that year. The two sites again showed differences (significant Year*Site interaction, $p = 0.001$; Table 1), with the West site having relatively more of certain sized patches than the East site in some years (Figure 3).

Spartina spread rates

Focal *Spartina pectinata* patches, which survived the dike-breaching, were small in the first year of restoration (1.3 ± 0.4 m^2 on 13 July 2011; $n = 10$ patches). In subsequent years (2012–2014), annually selected patches were 4.3 ± 1.2 m^2 in mid-June. *Spartina pectinata* patches moderately increased in area (mean change: 75 and 45% over 90 days) in the early years' growing seasons (2011–2012), and mostly decreased (mean change: −65 and −35%) afterwards, becoming extirpated from Restoration sites by 2015 ($p = 0.001$ for Year effect; Table 2; Figure 4; Supplementary Table 2.1; Supplementary Figure 2.2).

Spartina alterniflora appeared in the Restoration sites in the second-year post breach (2012) as small patches (1.7 ± 0.2 m^2 in mid-June 2012, Figure 3). In subsequent years (2013–2015), annually selected patches were 3.3 ± 0.5 m^2 in mid-June. In contrast to *S. pectinata*, *Spartina alterniflora* patches greatly increased in area during every growing season from 2012 to 2015 ($p < 0.001$ for Species effect; Table 2; Figure 4). Specifically, the increase in patch area for *S. alterniflora* was initially very high (mean change: ~330% in 2012) then lower in subsequent years (mean change: ~230% in 2013, ~200% in 2014, and ~ 175% in 2015) as space became limited and patches began merging in 2015

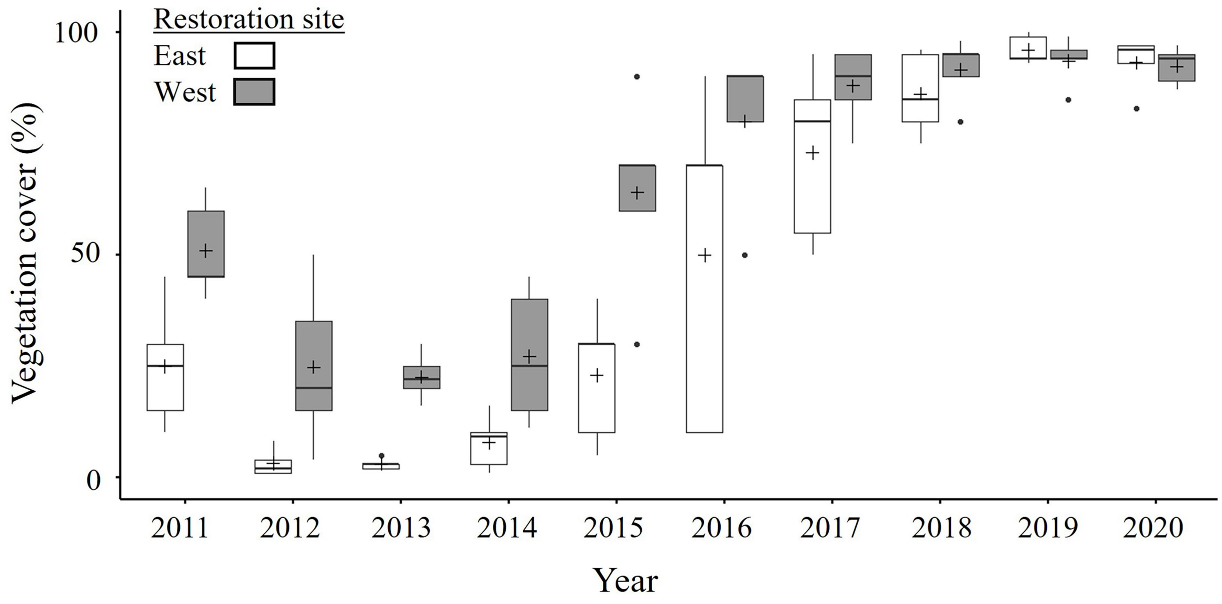

FIGURE 2
Estimated percent cover of vegetation in the Restoration sites in late July from 2011 to 2020 for the Aulac salt marsh complex. n=5 strata. For boxplots, midline represents the median, + the mean, box edges the first and third quartiles, whiskers±1.5*interquartile range, and dots outliers. See Table 1 for ANOVA and Supplementary Table 1.1 for pairwise comparisons.

TABLE 1 Results for percent vegetation cover (ANOVA) and size distribution of plant patches (<0.1, 0.1–0.5, 0.5–1, 1–2, and >2m in diameter; PERMANOVA) of *Spartina* spp. in the Restoration sites (East, West; each with five replicate strata) of the Aulac salt marsh complex from 2011–2020 and 2011–2014, respectively.

Dependent variable	Source	*df*	MS	*F*	*p*	perm
Vegetation cover	Year	9	11,344	96.63	<0.001	
	Site	1	7,656	8.10	0.022	
	Year*Site	9	469	4.00	**<0.001**	
	Stratum(Site)	8	947			
	Year*Stratum(Site)	72	117			
Patch size distribution	Year	3	8,821	28.61	0.001	999
	Site	1	5,758	7.49	0.015	126
	Year*Site	3	2,138	6.93	**0.001**	999
	Stratum(Site)	8	770			
	Year*Stratum(Site)	24	308			

Significant and interpretable value of *p*s (≤0.05) of fixed effects is bolded. For the PERMANOVA, *F*-value is a Pseudo-*F*, value of *p* was obtained by permutations, and perm = number of permutations. See Figures 2, 3 for boxplots of vegetation cover and patch size distribution, Supplementary Table 1.1 for pairwise comparisons of vegetation cover, and Supplementary Table 1.2 and Supplementary Figure 1.2 for analyses of patch size distribution per species.

($p = 0.001$ for Year effect, Table 2; Figure 4; Supplementary Table 2.1; Supplementary Figure 2.2).

Spartina patens appeared on the side of the dike in 2012 (Supplement 4 in Virgin et al., 2020) but did not start to spread onto the Restoration sites proper until 2016. During the 2017–2020 growing seasons, incremental encroachment rate of dike patches of *S. patens* varied among years and sampling rounds (significant Year*Round interaction, $p < 0.001$, Table 3; Figure 5; Supplementary Table 2.2; Supplementary Figure 2.1 for photographs). The annual spread rate was highest and most consistent in 2017 (5.2 ± 1.3 cm 14 days^{-1}, $n = 36$ patch-round combinations). In other years, dike patches slowly advanced (0.6 ± 1.1 cm 14 days^{-1} in 2018, 2.3 ± 1.2 cm 14 days^{-1} in 2019, and 4.2 ± 2.5 cm 14 days^{-1} in 2020).

In 2016–2017, two isolated *S. patens* patches were discovered within Restoration West proper (none in Restoration East), which were ~ 2.3 m^2 in mid-June 2017. One isolated *S. patens* patch was discovered in Restoration East in Fall 2020, and many more patches were found in Restoration West in 2021. During the 2017–2022 growing seasons, isolated patches moderately increased in area by 50 ± 11% over 90 days (mean ± SE, $n = 15$ patch-year combinations; range-15–149%; Supplementary Figure 2.3).

Spartina pectinata plant dynamics

In the first year post-breach, *Spartina pectinata* plants in Restoration sites had live stem densities (303 ± 54 stems m^{-2} measured on September 8, 2011, $n = 10$ patches) and percent flowering (25 ± 7%) similar to those generally observed in the Reference site [e.g., 210 ± 14 stems m^{-2} and 15 ± 3%, $n = 4$ patches, measured a later year (on 19 August 2014); Figure 6] but were stunted at ~50 cm height (MA Barbeau, personal observation). In subsequent years, live stem density and percent flowering of restoration *S. pectinata* greatly decreased [e.g., 61 ± 10 stems m^{-2} ($p < 0.001$ for year effect) and 4 ± 1% ($p = 0.023$), respectively, on August 19, 2014], being lower than in the Reference site in 2013–2014 (Table 4, Figure 6, Supplementary Tables 3.1–3.5, Supplementary Figure 3.1). Canopy height of *S. pectinata* remained stunted at ~1/3 that in reference locations (e.g., 40 ± 3 cm vs. 111 ± 7 cm tall on August 19, 2014). *Spartina pectinata* in the Restoration sites were exposed to much higher soil salinity (51 ± 3 mg salt cm^{-3} dry sediment; estimated at 43 ppt based on water content of collected sediment cores, $n = 24$ patches) than those growing in the Reference sites (11 ± 2 mg salt cm^{-3} dry sediment; estimated at 7 ppt, $n = 6$ patches; measured in 2013, $p < 0.001$ for Patch type effect, Supplement 5), likely contributing to their stressed condition. In addition, examination of *S. pectinata* root masses in 2013 indicated more dead roots per unit volume of sediment, and so a lower live to dead root ratio, for patches in Restoration sites (3.6 ± 0.8 mg dead roots cm^{-3}, and a ratio of 1.3 ± 0.4:1, $n = 6$ patches) than in the Reference site [2.6 ± 0.7 mg dead roots cm^{-3} ($p = 0.007$ for Patch type effect) and a ratio of 5.2 ± 2.5:1 ($p < 0.001$); Supplement 6].

Spartina alterniflora plant dynamics

In the earlier years of restoration (2012–2015), small patches of *S. alterniflora* had lower live stem densities (e.g., 202 ± 91 stems m^{-2} on August 12, 2014, $n = 10$ patches) and lower or similar percent flowering (11 ± 3%) than reference plants [whether creek: 471 ± 38 stems m^{-2} and 12 ± 2% ($n = 8$ patches), or edge patches: 544 ± 51 stems m^{-2} and 35 ± 14% ($n = 4$ patches), $p = 0.048$ for Year*Patch type interaction], and a canopy height (80 ± 6 cm) that was intermediate between the reference creek plants (tall-form, 107 ± 6 cm) and edge plants (short-form, 50 ± 7 cm; $p < 0.001$ for Patch type effect; Supplementary Tables 3.1, 3.6; Supplementary Figure 3.2). In later years (2016–2020), live stem density (e.g., 210 ± 10 stems m^{-2} on August 22, 2017, $n = 10$ patches) and canopy height (115 ± 8 cm) of restoration patches that were small in 2015 reached the density (180 ± 12 stems m^{-2}, $n = 10$ patches) and canopy height (102 ± 3 cm) of reference tall-form plants (significant Year*Patch type interaction for all response variables, $p < 0.001$, Table 4; Figure 7; Supplementary Table 3.9; Supplementary Figure 3.2). The reference short-form plants had higher live stem densities (264 ± 30 stems m^{-2}, $n = 5$ patches) and shorter canopy heights (32 ± 4 cm). Large patches, which appeared and became common in the mid-years (2014–2015), within the Restoration sites were similar to reference tall-form plants in 2015–2016 (e.g., 237 ± 9 stems m^{-2} and 94 ± 6 cm on August 13, 2015). However, they started to approach the short-form state as live stem density increased (e.g., 254 ± 23 stems m^{-2} on August 12, 2019) and canopy height decreased (57 ± 3 cm) in the later years

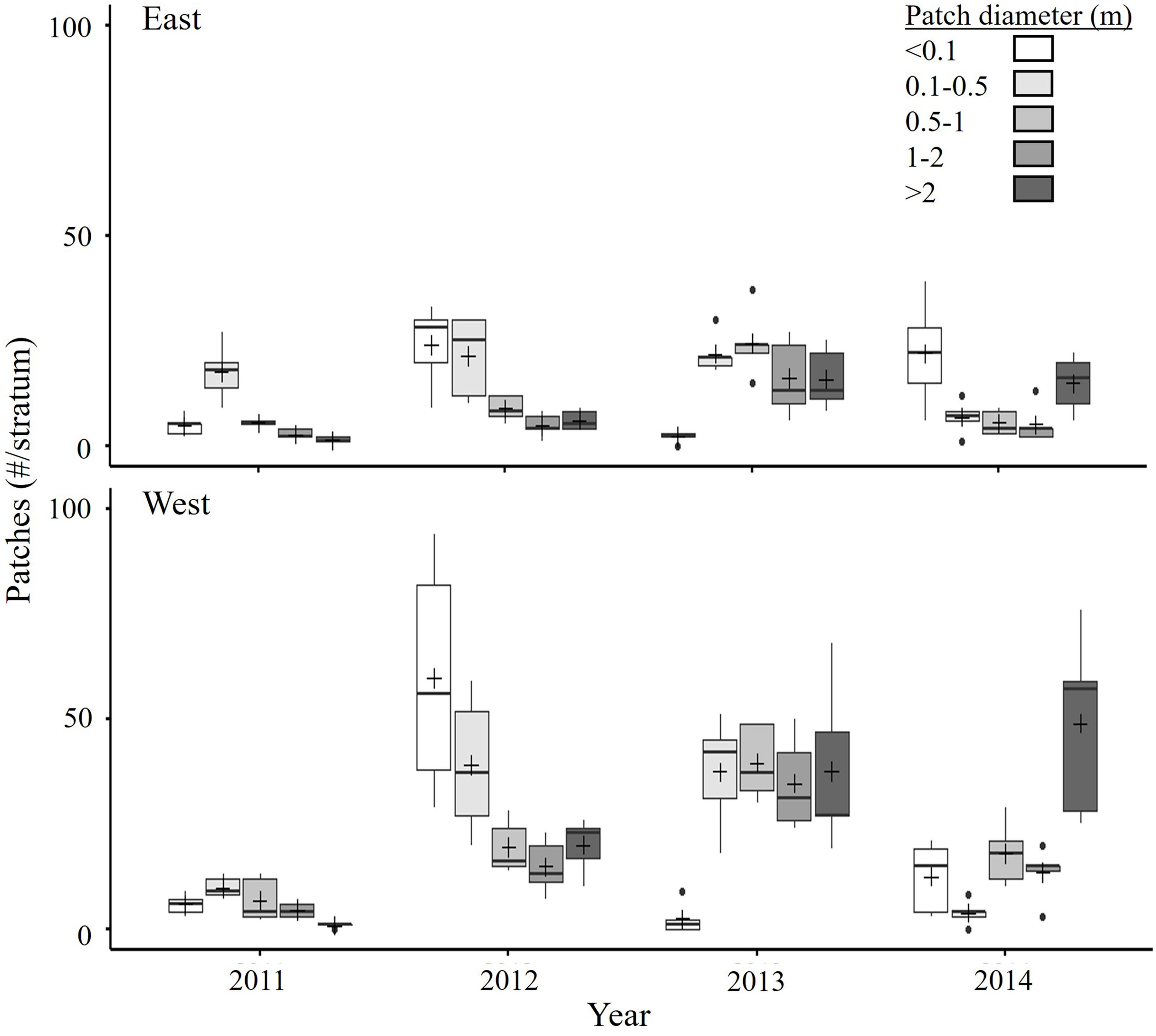

FIGURE 3
Estimated number of different sized patches of *Spartina* spp. in late July from 2011 to 2014 in the Restoration sites (East and West) of the Aulac salt marsh complex. *n*=5 strata. See Figure 2 for explanation of boxplots and Table 1 for permutation Multivariate ANOVA (PERMANOVA).

TABLE 2 ANOVA results for asexual growth of plant patches (% change in area) of *Spartina pectinata* and *S alterniflora* over a 90-day growing period in the Restoration sites of the Aulac salt marsh complex in June–August 2012–2014.

Source	*df*	MS	*F*	*p*
Year	2	2.759	7.66	**0.001**
Species	1	35.485	98.52	**<0.001**
Year*Species	2	0.766	2.13	0.129
Error	54	0.360		

Significant and interpretable *p* values (≤0.05) are bolded. Data were transformed using the logit function prior to analysis. See Figure 4 for boxplots and Supplementary Table 2.1 for pairwise comparisons.

(2017–2020), which is associated with shorter distances from the seaward edge of the marsh (Supplement 7). Note that the large patches tended to be located more seaward on the Restoration sites than small patches, and so more exposed to wave and wind stress since the almost complete erosion of the old dike in 2016. Percent flowering of small and large restoration patches in 2016–2020 showed variation but were within the range of reference plants (restoration: 32 ± 4 and 29 ± 3% flowering for small and large patches, respectively, averaged over mid-to late August 2016–2020; reference: 35 ± 3 and 15 ± 2% flowering for creek and edge patches, respectively).

Spartina alterniflora seedlings (Supplementary Figure 3.3) first appeared en masse in 2014 in the Restoration sites, reflecting increased seed supply from locally established patches, and availability of suitable space (with appropriate marsh surface elevation, Supplement 8). Seedings continued to appear in good numbers until 2017, when availability of free space greatly diminished (Figures 1, 2). Young-of-the-year *S. alterniflora* had lower live stem densities (1/3–2/3 lower, e.g., 114 ± 14 stems m^{-2}

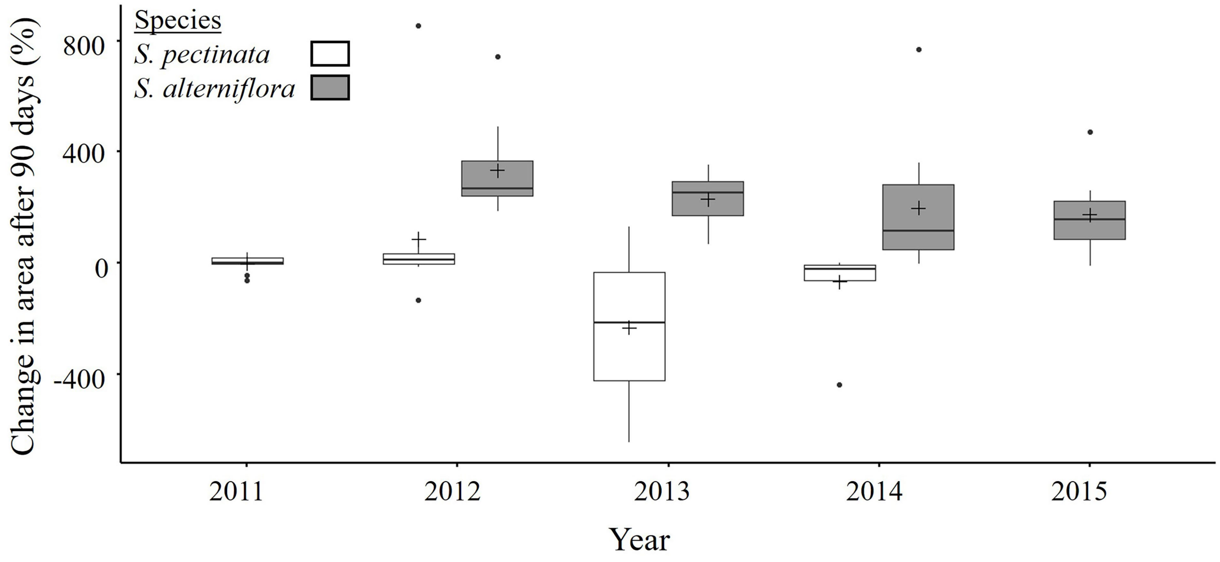

FIGURE 4
Change in patch area of *Spartina pectinata* (2011–2014) and *S. alterniflora* (2012–2015) in the Restoration sites of the Aulac salt marsh complex. n=10 patches. See Figure 2 for explanation of boxplots, Table 2 for ANOVA, and Supplementary Table 2.1 for pairwise comparisons.

TABLE 3 ANOVA results for incremental distance advanced (cm 14day^{-1}) by dike patches of *Spartina patens* into Restoration sites of the Aulac salt marsh complex from June–September in 2017–2020.

Source	*df*	MS	*F*	*p*
Year	3	636.6	3.49	0.035
Round	5	155.2	0.35	0.881
Year*Round	15	935.9	2.12	**0.015**
Patch(Year)	20	182.4	2.38	<0.001
Round*Patch(Year)	100	442.1	5.78	<0.001
Error	576	76.5		

Significant and interpretable p values (≤0.05) of fixed effects are bolded. See Figure 5 for graph and Supplementary Table 2.2 for pairwise comparisons.

on August 22, 2017, $n = 10$ patches; Figure 8) during the growing season than established restoration patches and reference patches ($p < 0.001$ for Round*Patch type interaction, Supplementary Tables 3.4, 3.8; $p < 0.001$ for Year*Patch type interaction, Supplementary Tables 3.9, 3.10; Supplementary Figures 3.2, 3.4). Canopy height of seedling patches near the end of the growing season (e.g., 49 ± 4 cm on August 22, 2017) was similar to reference short-form plants, and about half that of established restoration patches and of reference tall-form plants. Furthermore, young-of-the-year plants did not flower. By the fall, collected specimens indicated that most started to reproduce asexually (Supplementary Figure 3.3). Early in their second year (June), the young plants are easily distinguishable from new seedlings and from older plants, because they are both robust-looking and singlets (Supplementary Figure 3.3). They had a live stem density (e.g., 193 ± 15 stems m^{-2} on August 22, 2017) and canopy height (98 ± 6 cm) approaching that of established restoration patches and reference tall-form plants, but their percent flowering was on average lower (1/3–1/2 lower; 28 ± 5% on 22 August 2017; Figure 8; Supplementary Tables 3.4, 3.8–3.10; Supplementary Figures 3.2, 3.4). By their third year, former seedling plants were similar in stem density (e.g., 204 ± 11 stems m^{-2} on August 22, 2017), canopy height (100 ± 5 cm), and flowering (62 ± 6%) to established restoration patches and reference tall-form plants.

Dynamics over a growing season (presented for 2016 and 2017 as examples) showed that live stem density for plants that were not young-of-the-year started relatively high in mid-June (e.g., 613 ± 135 and 649 ± 114 stems m^{-2} for restoration small and large patches, respectively, measured in June 2016, $n = 10$ patches:), decreased over the growing season (325 ± 42 and 357 ± 53 stems m^{-2} for restoration small and large patches measured on August 24, 2016), likely due to self-thinning (Roderick and Barnes, 2004), and had a small peak in early fall (338 ± 32 and 396 ± 52 stems m^{-2} for restoration large and small patches measured on 24 September 2016) with appearance of small stems that were produced asexually (significant Round*Patch type interaction, $p < 0.001$; Supplementary Table 3.4; Supplementary Figure 3.4). Young-of-the-year began the growing season with low live density (e.g., 90 ± 18 stems m^{-2} measured in mid-June 2016) and increased over the growing season as new seedlings continued to emerge in the summer (164 ± 24 stems m^{-2} measured on 24 August 2016), and as asexually produced stems started to appear in early fall (302 ± 23 stems m^{-2} measured on 24 September 2016; Supplementary Figure 3.3). The stems and leaves of all plant types senesced and died in mid to late fall (see also Baerlocher and Moulton, 1999). Canopy height for plants that were not young-of-the-year rapidly increased from June (e.g., 36 ± 4 cm and 33 ± 3 cm

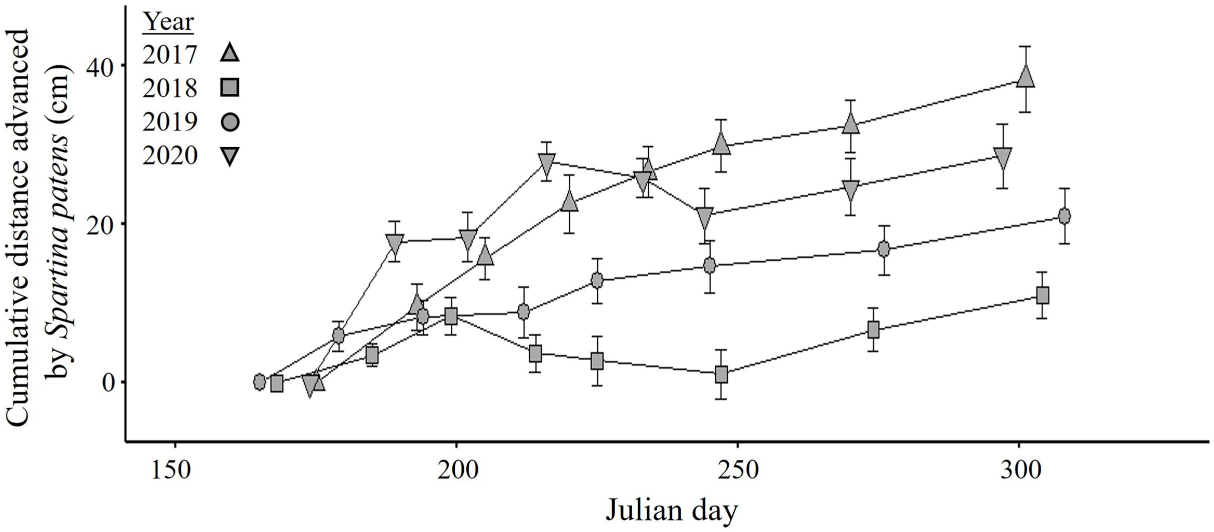

FIGURE 5
Mean (± SE, n=6 patches) cumulative distance advanced of *Spartina patens* from the landward (new) dike onto Restoration sites of the Aulac salt marsh complex from 2017 to 2020. See Table 3 for ANOVA and Supplementary Table 2.2 for pairwise comparisons.

for restoration small and large patches in 2016) to July (72 ± 6 cm and 59 ± 3 cm of restoration small and large patches) and leveled off in August (98 ± 7 cm and 86 ± 8 cm for restoration small and large patches; significant Round*Patch type interaction, $p < 0.001$; Supplementary Tables 3.4, 3.8; Supplementary Figure 3.4). Young-of-the-year grew sigmoidally (6 ± 0.5 cm in mid-June 2016), surpassed the height of reference short-form plants by end of August (47 ± 6 cm measured), and leveled off in September (55 ± 4 cm measured). All plant types showed a decreased canopy height in mid-fall as taller shoots died and remaining live shoots were measured. Flowering typically started toward the end of July, peaked in late-August/early-September (e.g., 60 ± 7 and 52 ± 10% of live stems flowering of small and large patches measured in early September 2016), and was finished by end of September. Two-year old plants started to flower in August and flowered less than more established plants (~130% less than four-year-old plants in August 2017). Note that reference short-form (edge) patches had high yearly variation in percent flowering (Supplementary Figure 3.4); in 2016 and 2017, percent flowering was relatively low.

Spartina alterniflora root masses in 2013 had a higher live to dead root ratio in Restoration sites (12.9 ± 4.5:1 on August 20, 2013, $n = 6$ patches; at the time, *S. alterniflora* patches were all small) than reference creek (1.0 ± 0.1:1) and edge (2.1 ± 0.4:1) patches ($p < 0.001$ for Patch type effect; Supplementary Tables 6.1, 6.2). Restoration live root mass per unit volume of sediment (2.7 ± 0.8 mg cm^{-3}) was equivalent to reference tall-form (creek) plants (2.7 ± 0.8 mg cm^{-3}), and dead root mass was lower (0.4 ± 0.1 mg cm^{-3}) than both reference patch types (2.3 ± 0.6 and 5.9 ± 2.0 mg cm^{-3} for creek and edge, respectively; $p = 0.002$ and 0.007 for Patch type effect when testing differences in live and dead root masses, respectively; Supplementary Tables 6.1, 6.2). *Spartina alterniflora* was growing in sediments (measured in 2013) with somewhat higher salt content in the restoration patches (50 ± 4 mg salt cm^{-3} dry sediment; estimated at 41 ppt; $n = 12$ patches) than in reference creek patches (40 ± 3 mg salt cm^{-3} dry sediment, estimated at 29 ppt; though the salinity difference was not significant, Supplementary Tables 5.1, 5.2).

Spartina patens plant dynamics and possible interaction with *Spartina alterniflora*

Spartina patens growing along the dike (observed since 2012) were well-established and resembled reference *S. patens* in live stem density (e.g., 3,376 ± 537 and 3,275 ± 217 stems m^{-2}, respectively, $n = 6$–10 patches, measured in August 2018), canopy height (66 ± 6 cm and 54 ± 2 cm), and percent flowering (3 ± 2 and 4 ± 1%) when measured in August 2017–2020 ($p > 0.30$ for Patch type effect on stem density and percent flowering; *post-hoc* $p > 0.05$ for Patch type effect on canopy height; Supplementary Tables 3.11, 3.12; Supplementary Figure 3.5). The isolated *S. patens* patches discovered growing within Restoration West (in 2016–2017) tended to have lower live stem density (e.g., 2,360 ± 584 stems m^{-2} in August 2018, $n = 2$ patches, though not significant) and had shorter canopy height (37 ± 9 cm; $p < 0.001$ for Patch type effect) for plants growing in their center than *S. patens* growing on the dikes and in Reference sites (Supplementary Tables 3.11, 3.12; Supplementary Figure 3.5).

Shoots of *S. patens* growing along the inner edges of *S. patens* dike patches and isolated patches, where they could be interacting with *S. alterniflora*, had similar live stem densities [1,179 ± 388 and 1,616 ± 688 stems m^{-2} in August 2018 for inner

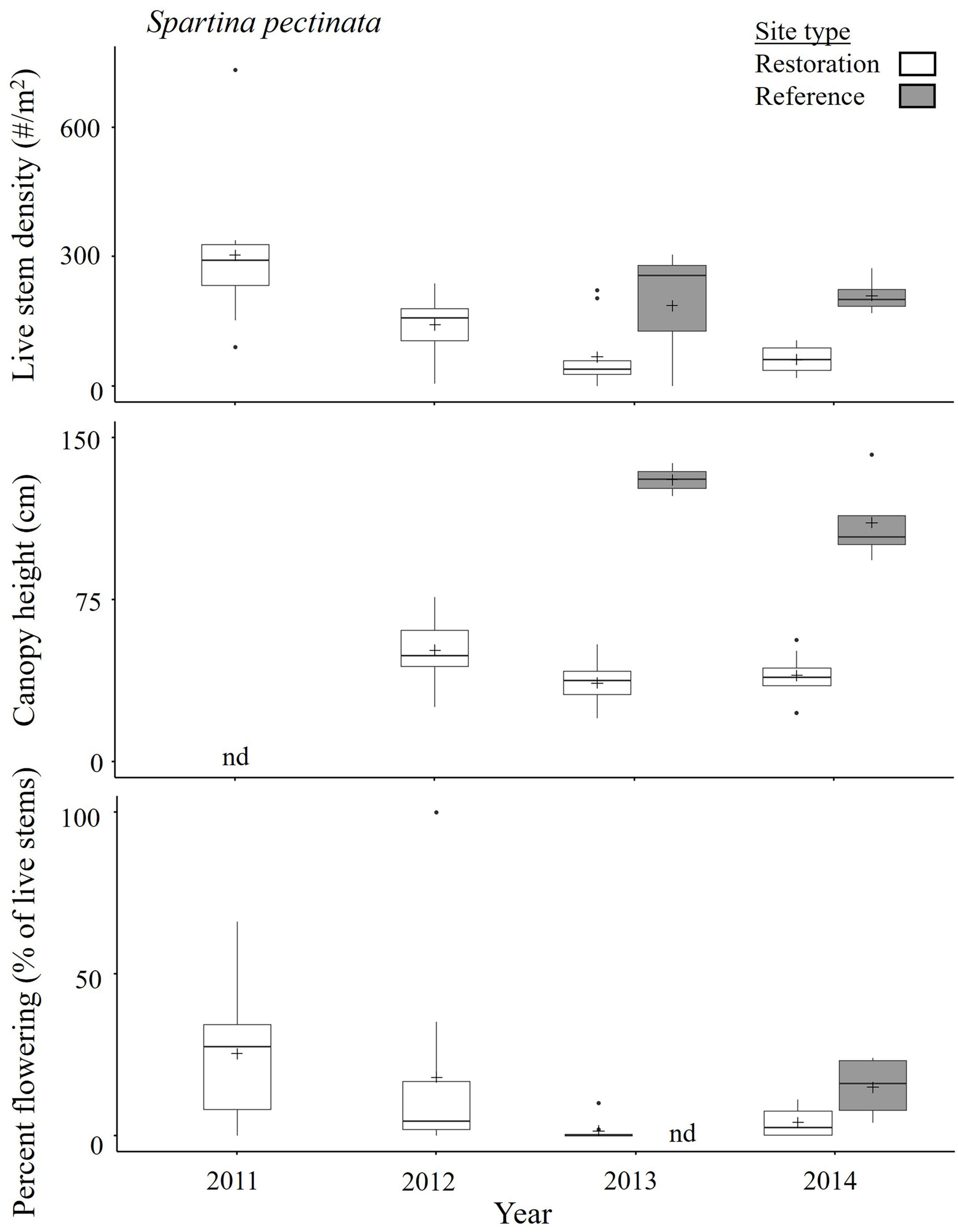

FIGURE 6
State of *Spartina pectinata* in late August/early September in the Restoration and Reference sites of the Aulac salt marsh complex from 2011–2014. In Restoration sites, n=8–10 patches; for Reference sites, n=3–4 patches; nd=no data. *Spartina pectinata* was not monitored in the Reference sites in 2011–2012, and canopy height was not recorded in the Restoration sites in 2011. See Figure 2 for explanation of boxplots, Table 4 for ANOVAs, and Supplementary Table 3.3 for pairwise comparisons.

edges of dike patches ($n=3$) and inner edges of isolated patches ($n=2$), respectively], canopy height (58 ± 7 cm and 43 ± 9 cm), or percent flowering (1 ± 1 and 4 ± 4%) compared to shoots growing more centrally in the patches (3,056 ± 371 and 2,360 ± 584 stems m^{-2}, 58 ± 5 and 37 ± 9 cm, and 0 ± 0 and 16 ± 16%, for dike and isolated patches, respectively; Supplementary Tables 4.1, 4.2; Supplementary Figure 4.1). The *S. patens* shoots growing just beyond the outside edges of the isolated patches, compared to shoots growing on the inside edges mentioned above, had lower live stem density (216 ± 64 stems m^{-2}), were shorter (35 ± 7 cm), and did not flower ($p=0.005$ and $p<0.001$ for Round*Patch type for live stem density and canopy height, respectively; Supplementary Tables 4.1, 4.2; Supplementary Figure 4.1). *Spartina alterniflora* plants growing along the edges of the dike patches and isolated patches of *S. patens* generally had lower live stem densities (89 ± 8, 148 ± 60, and 164 ± 28 stems m^{-2}), shorter

TABLE 4 ANOVA results for live stem density (# stems m^{-2}), canopy height (cm), and percent flowering (% of live stems flowering) of *Spartina pectinata* and *S. alterniflora* in Restoration and Reference sites (i.e., two site types) in the Aulac salt marsh complex over years.

Species	Dependent variable	Source	*df*	MS	*F*	*p*
S. pectinata	Live stem density (square root)	Year	1	21.09	1.05	0.316
		Site type	1	163.80	8.11	**0.009**
		Year*Site type	1	8.05	0.40	0.533
		Error	23	20.07		
	Canopy height (log_{10})	Year	1	9.80 E-04	0.08	0.784
		Site type	1	1.06	83.56	**<0.001**
		Year*Site type	1	1.52 E-02	1.19	0.289
		Error	20	1.27 E-02		
	Percent flowering (logit)	Site type	1	2.11	5.12	**0.043**
		Error	12	4.12 E-01		
S. alterniflora	Live stem density (square root)	Year	5	192.12	48.96	<0.001
		Patch type	3	272.19	26.09	<0.001
		Year*Patch type	15	18.33	4.67	**<0.001**
		Patch(Patch type)	31	10.42		
		Year*Patch (Patch type)	155	3.92		
	Canopy height (log_{10})	Year	5	3.59 E-02	6.72	<0.001
		Patch type	3	1.09	62.86	<0.001
		Year*Patch type	15	3.21 E-02	6.01	**<0.001**
		Patch(Patch type)	31	1.74 E-02		
		Year*Patch (Patch type)	155	5.35 E-03		
	Percent flowering	Year	5	5.52 E-01	24.28	<0.001
		Patch type	3	2.41 E-01	5.31	0.005
		Year*Patch type	15	1.07 E-01	4.72	**<0.001**
		Patch(Patch type)	31	4.56 E-02		
		Year*Patch (Patch type)	155	2.27 E-02		

For *S. pectinata*, data were collected in late August/early September in 2013–2014 (live stem density, canopy height) or 2014 (percent flowering); *n* = 8–10 for Restoration sites, and *n* = 3–4 for Reference sites. For *S. alterniflora*, data for multiple patch types were collected in mid-August from 2015–2020; Patch types include small and large patches in Restoration sites, and creek and edge patches in Reference sites; *n* = 10 patches per type, except *n* = 5 for edge patches. Significant and interpretable *p* values (≤0.05) of fixed effects are bolded. Data transformation prior to analysis indicated in parenthesis. See Figures 6, 7 for boxplots of *S. pectinata* and *S. alterniflora*, respectively, Supplementary Tables 3.3, 3.7 for pairwise comparisons.

canopy height (52 ± 13 cm, 67 ± 6 cm, and 58 ± 4 cm), and less percent flowering (0 ± 0, 8 ± 1, and 9 ± 3% for patches on the dike edges, the inner edges of isolated patches, and the outer edges of isolated patches, respectively, in August 2018) than those growing in monoculture *S. alterniflora* areas (183 ± 20 and 292 ± 40 stems m^{-2}, 92 ± 6 and 70 ± 7 cm, and 26 ± 9 and 14 ± 4% percent of live stems flowering, for restoration small and large patches in Restoration West, respectively; $n = 10$ patches; $p = 0.006$, $p = 0.003$, and $p < 0.001$ for Round*Patch type for live stem density, canopy height, and percent flowering, respectively; Supplementary Tables 4.1, 4.3; Supplementary Figure 4.2).

Discussion

We collected detailed measurements over 10 years of *Spartina* plant states and patch dynamics that underlie vegetation recovery patterns at two sites in the Aulac salt marsh restoration project in the upper Bay of Fundy. We estimated modes of colonization of *S. alterniflora* and *S. patens*, measured asexual spread of *S. pectinata, S. alterniflora*, and *S. patens*; monitored seedling production of *S. alterniflora*; began quantifying interactions between *S. alterniflora* and *S. patens*; and began exploring how spatial distribution within the sites affected *S. alterniflora* health-related states. In the following discussion, we first briefly examine the observed site-level patterns, and then discuss the patch-level processes in terms of dynamics, ecological insights, restoration implications, and planned research.

Recovery patterns of the salt marsh vegetation community in Aulac

Following breaching of the old agriculture dike in 2010 (Boone et al., 2017; Virgin et al., 2020), site-level vegetation patterns reflected initial persistence, then decline, and disappearance of *S. pectinata* in under 5 years, followed by spread of *S. alterniflora* in the mid years, and of *S. patens* in the later years (Virgin et al., 2020). Vegetation recovery has followed secondary, progressive succession where site-level community changes are expected to eventually result in spatial distributions of the vegetation communities observed in the reference sites (i.e., climax condition of salt marshes in the region). During other salt marsh restoration projects in New England and the Bay of Fundy, freshwater and brackish vegetation typically disappears quickly (<6 years; Burdick et al., 1996; van Proosdij et al., 2010; Smith and Warren, 2012). Increasing cover of halotolerant vegetation during salt marsh restoration typically begins with species that are more tolerant to inundation and salinity (e.g., *S. alterniflora,* but also succulent forbs including *Suaeda* and *Salicornia* spp.; Virgin et al., 2020), followed by species less tolerant to both (e.g., *S. patens*; Redfield, 1972; Mossman et al., 2012). In Aulac, *S. alterniflora* most likely colonized the restoration sites *via* rhizomal material brought into the sites by the tide and ice blocks during winter (based on observations of ice blocks and their content; van Proosdij et al., 2006; Boone et al., 2017) and lack of observed seedlings in the early years. After the sites were colonized, *S. alterniflora* spread asexually before seedlings were observed in the project's fourth year (2014).

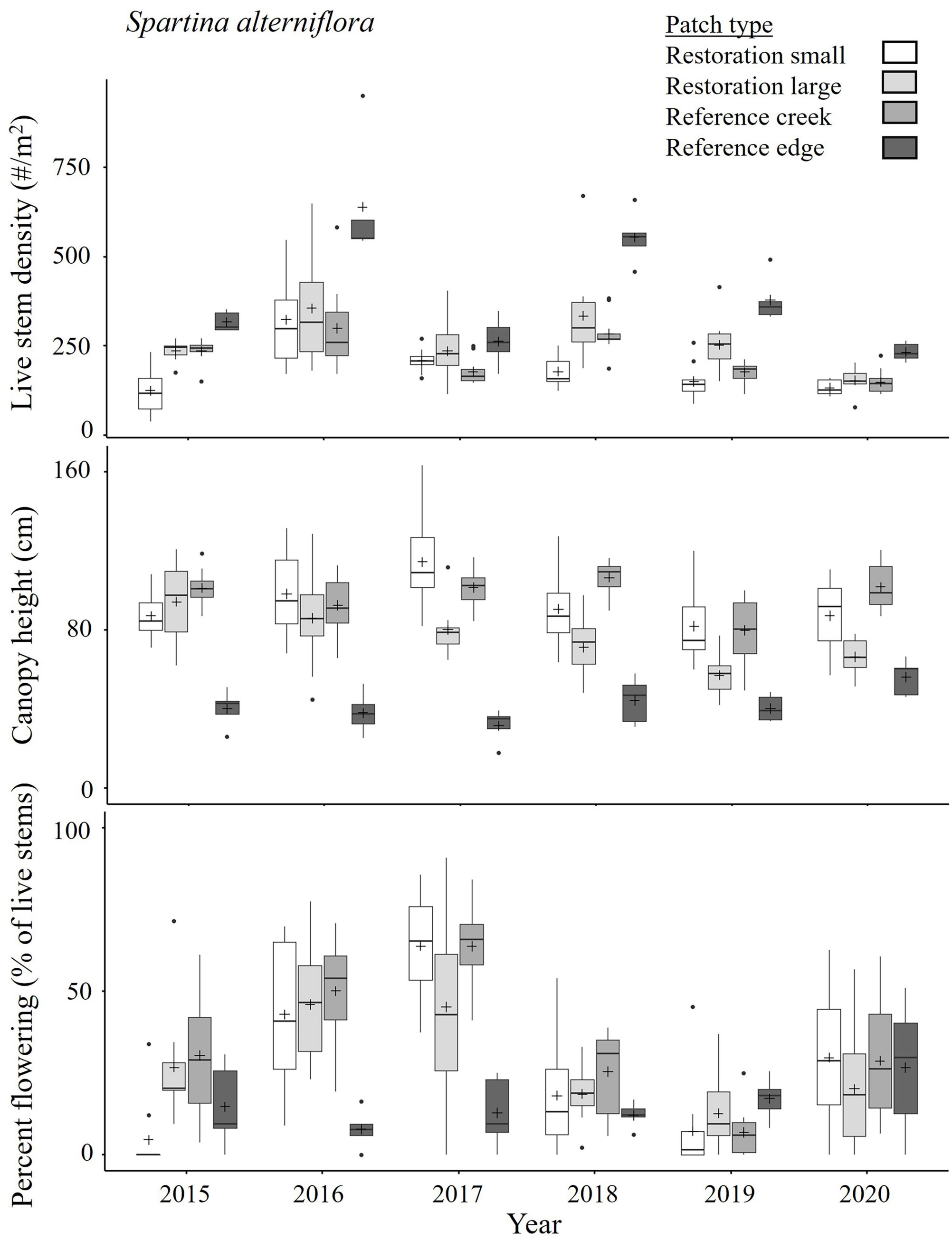

FIGURE 7
State of *Spartina alterniflora* in mid-August in established patches in Reference and Restoration sites of the Aulac salt marsh complex from 2015 to 2020. *n*=10, except *n*=5 for Reference edge patches. See Figure 2 for explanation of boxplots, Table 4 for ANOVAs, Supplementary Table 3.7 for pairwise comparisons, and Supplementary Figure 3.2 for more detailed plant dynamics.

Asexual spread was rapid during our project (nearing complete cover after 9 y) as has been reported in regions where *S. alterniflora* is considered native (Trilla et al., 2009) and invasive (Taylor and Hastings, 2004; Zhang et al., 2017). While recovery of vegetation communities was rapid in both Aulac restoration sites, differences in site dynamics likely reflected an initial lower surface elevation of the East site (Boone et al., 2017) and differing (though high) rates of sediment deposition (Virgin et al., 2020); this demonstrates that subtle differences in site conditions can affect vegetation recovery dynamics. A restoration project in Maine, United States, reached 70% of halotolerant vascular plant cover in 6 years (Burdick et al., 1996), and another in the Bay of Fundy reached 100% cover in 3 years (van Proosdij et al., 2010). Attaining high salt marsh vegetation percent cover is quite fast in the Bay of Fundy (<6 years), likely due to high deposition of sediment and

TABLE 5 PERMANOVA results for effect of patch type on each of live stem density (# stems m^{-2}), canopy height (cm), and percent flowering (% of live stems flowering) of *Spartina alterniflora* in Restoration and Reference sites in the Aulac salt marsh complex on 22 August 2017.

Dependent variable	Source	df	MS	Pseudo *F*	*p*	perm	*p*(MC)
Live stem density	Patch type	7	16,132	6.58	**<0.001**	979	0.001
	Small vs. Large	1	3,699	0.86	0.386	91	0.372
	Small vs. Creek	1	4,500	3.54	0.063	58	0.069
	Large vs. Edge	1	2,466	0.38	0.533	165	0.558
	Small vs. s2014, s2015	1	564	0.54	0.490	111	0.459
	s2015 vs. s2016	1	627	0.36	0.562	67	0.563
	s2016 vs. s2017	1	31,363	15.56	0.001	86	**0.002**
	Error	67	2,449				
Canopy height	Patch type	7	6089.7	25.13	**<0.001**	999	0.001
	Small vs. Large	1	5923.7	16.28	**0.001**	645	0.001
	Small vs. Creek	1	838.5	2.56	0.128	573	0.132
	Large vs. Edge	1	7857.0	60.31	**0.002**	693	0.001
	Small vs. s2014, s2015	1	3617.7	9.93	**0.005**	638	0.006
	s2015 vs. s2016	1	22.9	6.73 E-02	0.825	574	0.801
	s2016 vs. s2017	1	11756.0	41.39	**0.001**	702	0.001
	Error	67	242.4				
Percent flowering	Patch type	7	5.96 E-01	19.86	**<0.001**	997	0.001
	Small vs. Large	1	1.74 E-01	3.15	0.093	992	0.108
	Small vs. Creek	1	4.08 E-06	2.13 E-04	0.989	988	0.984
	Large vs. Edge	1	3.50 E-01	5.44	**0.047**	800	0.034
	Small vs. s2014, s2015	1	6.27 E-04	2.28 E-02	0.873	995	0.883
	s2015 vs. s2016	1	5.85 E-01	17.56	**0.002**	993	0.002
	s2016 vs. s2017	1	3.80 E-01	25.60	**0.001**	597	0.001
	Error	67	3.00 E-02				

Patch types are small, large, seedling 2014 (s2014), seedling 2015 (s2015), seedling 2016 (s2016), and seedling 2017 (s2017) patches in Restoration sites, and creek and edge patches in Reference sites; $n = 10$ patches (except $n = 5$ for edge patches). *p* values were obtained by permutation, and perm = number of permutations; note that those obtained by Monte Carlo simulations [*p*(MC)] should be used when perm is low (<100). Significant and interpretable *p* values (≤0.05) are bolded. Planned contrasts examined differences of interest between patch types. See Figure 8 for boxplots.

vegetation propagules (van Proosdij et al., 2010; Roman and Burdick, 2012; Virgin et al., 2020) resulting from large tidal amplitudes. Furthermore, in this and other restoration projects to date in the Bay of Fundy (Bowron et al., 2012; Norris et al., 2020), it has been observed that recovery of vegetation appears most rapid if the tidal waters move over established marsh before entering a site to be restored, likely because this is a direct source of vegetation propagules. In other geographic locations, especially in areas with small tidal amplitudes, high vegetation percent cover may take more than 10 years (Burdick et al., 1996; Garbutt et al., 2006; Weinstein et al., 2019). Currently, we are observing a gradual spread of *S. patens* into the restoration sites from high elevation areas, including the dike edge and isolated patches within the sites. We forecast continued spread and eventual dominance of *S. patens,* coinciding with ongoing sediment deposition and elevation increase, which will competitively displace *S. alterniflora* to lower elevation areas (Bertness, 1991) and lead to the expected plant zonation of *S. alterniflora* occupying low elevation marsh areas and *S. patens* dominating higher elevations.

Processes underlying the early phases of salt marsh restoration and their implications

Development of vegetation patterns during salt marsh recovery can be described in phases, which is useful when examining underlying patch-level processes. The first and second phases of salt marsh restoration in Aulac were the high initial sediment deposition occurring immediately after breaching (phase 1, year 1) and the loss of *S. pectinata* and colonization and spread of *S. alterniflora* (phase 2, years 2–5; see Virgin et al., 2020). Competition between brackish and halotolerant species (e.g., *Phragmites* sp. and *Typha* sp. vs. *S. alterniflora*; Roman et al., 1984; Barrett and Niering, 1993) has played a substantial role in successional dynamics of vegetation communities during previous salt marsh restorations. During the second phase of our salt marsh restoration project, the disappearance of *S. pectinata* and proliferation of *S. alterniflora* was the probable result of inappropriate environmental conditions for the former species, and ample suitable habitat for the latter, rather than interspecific competition. Soil water salinity of the sites was considered lethal

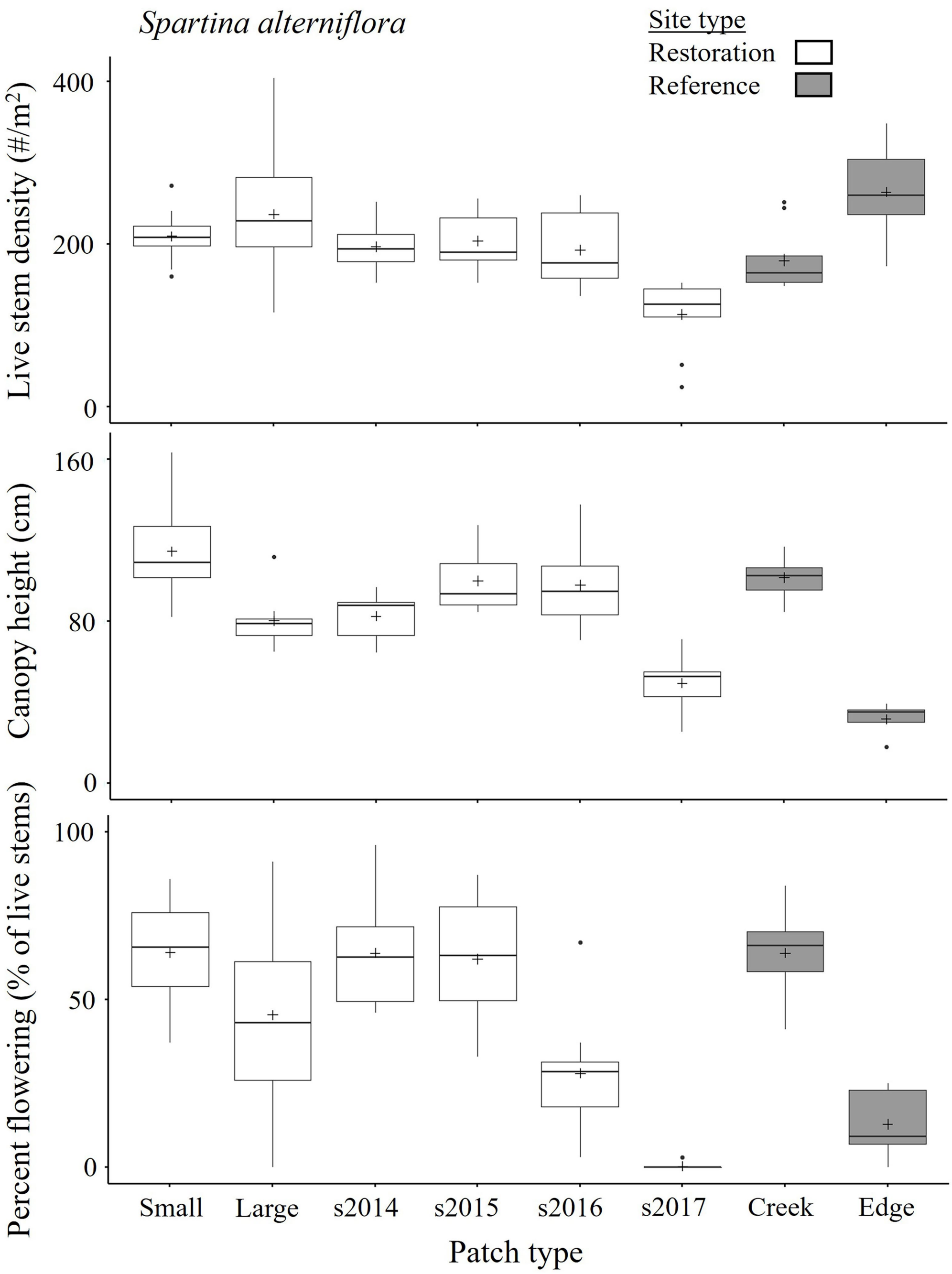

FIGURE 8
State of *S. alterniflora* in established and seedling patches in the Restoration and Reference sites of the Aulac salt marsh complex on August 22, 2017. Patch types labeled as a year (e.g., "s2014"–"s2017") are young-of-the-year from said year. *n*=10 patches, except *n*=5 for Reference edge patches. See Figure 2 for explanation of boxplots, Table 5 for PERMANOVAs, and Supplementary Figures 3.2, 3.4 for more detailed plant dynamics.

for *S. pectinata* (>0.2 M NaCl or 12 ppt; Warren et al., 1985), but suitable for *S. alterniflora* (Webb, 1983; Betzen et al., 2019). Furthermore, the availability of empty and suitable habitat would have minimized competition between *S. pectinata* and *S. alterniflora* (Craine and Dybzinski, 2013). The two species were located far apart in the restoration sites, with surviving *S. pectinata* occupying the high elevation areas of the sites (see year 1 aerial photograph in Figure 1; marsh surface elevation profiles presented in Supplementary Figure S1.1 of Virgin et al., 2020), and *S. alterniflora* colonizing bare areas at intermediate elevations. Thus, conversion from *S. pectinata* to a *S. alterniflora*-dominated area was driven by interactions with their environment (or edaphic conditions), and not by competitive interactions between species.

We initially expected the colonization and spread of *S. alterniflora* would be from high elevation dike edges, because

S. alterniflora grows most successfully in non-halophytic conditions with little competition (Bertness, 1991). Instead, we observed circular colonies (patches) of *S. alterniflora* dotting the sites, which had the tall-form phenotype when they matured. The vigorous spread by *S. alterniflora* was possible likely due to appropriate elevational range of most of the sites' surface (Proffitt et al., 2003) and high nutrient content of the soil (Keizer et al., 1989; Langley et al., 2013). The *S. alterniflora* seedlings in 2014 (year 4) must have been produced by the healthy-looking mature plants in the restoration sites in 2013, which we observed bearing seeds in addition to dense batches of seeds on the mud surface. Other studies have reported seedling colonization in the first-year post-restoration (van Proosdij et al., 2010), although seedling establishment of *Spartina* spp. can be erratic (Callaway and Josselyn, 1992). Clonal species are more often thought to transition from mostly sexual to asexual reproduction when establishing in a new site (Silvertown, 2008), which is opposite to what we observed during the Aulac restoration. In contrast to sites that are up tidal channels or are landward of established salt marshes, the Aulac sites face the open Bay of Fundy (Cumberland Basin), and we suspect that seeds would not have been readily brought in by tidal water. Furthermore, the Aulac sites' surface elevation may not have been suitable for the successful germination of seeds until the fourth year of the project. Indeed, we observed that seedlings in 2014 occurred within a narrow range of elevation (Supplement 8). Also, very high sedimentation rates in the early years [as much as 50 cm in the first year, averaging 18.3 ± 3.8 cm (mean ± SE, $n = 20$ plots) in Restoration East and 10.8 ± 1.4 cm ($n = 27$ plots) in Restoration West; Virgin et al., 2020] may have contributed to lack of germination if seeds were present; *S. alterniflora* germination rates decrease when buried under too much sediment (Zhao et al., 2020). In addition, our later monitoring of *S. alterniflora* patches that started from young plants indicated that it takes 2–3 years for the plants to flower substantially, supporting the claim that onsite plants would have started producing substantial amounts of seeds only at the end of the 2013 growing season. As the typical ecosystem engineer species of salt marsh on the east coast of North America, the colonization and initial asexual and sexual spreads of *S. alterniflora* were considered crucial for the successful development of salt marsh habitat during our restoration project.

Our process-related observations and attendant ecological insights during the early phases (particularly phase 2, Virgin et al., 2020) of the restoration suggest three restoration implications. First, the initial presence of *S. pectinata* onsite (present before and after the breaching), along with *S. alterniflora* which appeared a year later, likely aided in binding sediments (Neumeier and Ciavola, 2004) and preventing erosion, which has been reported during failed restoration projects where retrogressive succession results in the failure of salt marsh establishment (French et al., 2000). *Spartina pectinata* has not previously been thought of as a good temporary species facilitating the initial development of a salt marsh. Due to its potential value as a facilitator and lack of competition with *S. alterniflora*, we propose that *S. pectinata* is a good temporary plant when initiating a salt marsh restoration and assists in salt marsh development in the first 3–4 years. This idea should be tested in a field experiment conducted concurrently with a planned restoration, in which presence/absence of *S. pectinata* is manipulated. Second, the appearance of *S. alterniflora* at our Aulac sites was delayed compared to other salt marsh restoration projects in the Bay of Fundy. When considering where to breach an old dike, we suggest that the presence of an established salt marsh seaward of the restoration site should be included in the list of criteria of the breach (see Boone et al., 2017). This would provide an immediate source of vegetation propagules brought in by tidal water. This idea could be tested further by studying the effect of breach location relative to surrounding established salt marsh on initial vegetation recovery, as well as in a spatial modeling exercise examining the importance of input rate of *S. alterniflora* propagules relative to other processes in the vegetation recovery. Third, at north temperate latitudes, ice blocks are a vector of colonization for various organisms as well as a source of sediment transport (van Proosdij et al., 2006; Macfarlane et al., 2013; Lundholm et al., 2021). The importance of ice blocks for sediment transport had been considered in planning the breaches in Aulac (i.e., by making the breaches large enough to allow ice in; Boone et al., 2017). However, we had not originally considered ice blocks to be a primary mode of *S. alterniflora* colonization for our sites. This idea could be assessed by quantifying density of ice blocks appearing on site and proportion of ice blocks with marsh plant rhizomal material. This information could then be used to parameterize the input rate of *S. alterniflora* propagules in a spatial model. The size distribution of plant patches outputted from the model and observed in the field could then be compared. To summarize, three implications were suggested during the early restoration phases (particularly phase 2, the decline and eventual disappearance of *S. pectinata* and colonization and spread of *S. alterniflora*) which, if considered while planning future restoration projects, could speed the appearance of the later phases.

Processes underlying the later phases of salt marsh restoration and their implications

The third phase (years 6–10) of salt marsh restoration in Aulac was characterized by the dominance of *S. alterniflora* with the continued merging of patches and infilling by seedlings, resulting in decreased spatial variation and homogenization of vegetation density and diversity (Supplementary Figure 1.3; Virgin et al., 2020). The production of *S. alterniflora* seeds and subsequent germination into seedlings were important processes underlying the spatial vegetation pattern up until year 8 (2018), at which time free space became vanishingly small, and very low densities of seedlings were observed, mostly interspersed among mature plants. We stopped establishing and monitoring new seedling patches that year (2018) because there were almost none. Mature plants were still producing seeds, but sexual reproduction was no longer an important process affecting spatial patterns. Seeds likely had low germination success because of light and space limitations, i.e., intraspecific competition with established plants (Metcalfe et al., 1986). Our results suggest that successful spread by sexual reproduction of *S. alterniflora* was related to availability of space, in addition to appropriate edaphic conditions. Any spread of *S. alterniflora* in the later part of the third phase appeared mostly through asexual production of shoots either from plants in the older established patches or from past seedlings which were creating shoots asexually starting in their second year of life. Thus, the two modes of reproduction (asexual and sexual) were highly complementary with their relative importance changing as the recovery proceeded and led to the rapid spread and domination of *S. alterniflora* throughout the sites. A restoration implication of this is that transplanting *S. alterniflora* tillers or plugs of seedlings (e.g., grown in greenhouse) upon initiating a restoration may not contribute much to the recovery of vegetation cover in site situations like ours, i.e., within an elevation range of a low marsh zone, and where sediment deposition is high and passive establishment of the primary ecosystem engineer species (*S. alterniflora* in our case) is prompt. In other situations, such as in a high marsh zone (even in the Bay of Fundy; Rabinowitz et al., 2022) or other geographic locations (Travis et al., 2002; Novy et al., 2010), transplanting tillers and/or seedlings has been shown to be worthwhile.

Aside from their influence on site-level spatial patterns, which was presented as part of our current study, a potential restoration implication and likely consequence of the high number of seedlings appearing during recovery (from 2014 to 2017, or end of phase 2 and start of phase 3) that requires investigation is the potential increase in *S. alterniflora* genetic diversity. Indeed, we did collect plant samples for genetic analysis in 2016–2017, but still need to process them. Restoration projects elsewhere did observe that natural levels of genetic diversity in *S. alterniflora* can develop quickly through passive colonization if a ready source of propagules is available (Louisiana; Travis et al., 2002). Genetic diversity in *S. alterniflora* can influence many aspects affecting recovery dynamics, including plant performance and spread rates (Seliskar et al., 2002; Wang et al., 2012), germination response (Seneca, 1974; Travis et al., 2002), flowering phenology (Somers and Grant, 1981), adaptability (Travis et al., 2002), and interactions with other species, such as competition, facilitation, and resistance to consumer pressure and fungal infection (Travis et al., 2002; Proffitt et al., 2005; Zerebecki et al., 2017). With the return to mostly asexual reproduction in *S. alterniflora* once a marsh site is fully vegetated, genetic diversity is expected to decrease as certain competitively superior genotypes begin to dominate the maturing marsh (Travis et al., 2004); this should be tested at our sites in the future. Overall, the third phase of restoration was defined by the natural proliferation and success of *S. alterniflora* until its near complete cover of the restoration sites.

The Aulac salt marsh restoration is now just starting the fourth phase (years 10+), distinguished by the development of the *S. alterniflora* short phenotype, spread of *S. patens*, and likely interaction between *S. alterniflora* and *S. patens* (Virgin et al., 2020). During earlier phases, mature *S. alterniflora* plants throughout the restoration sites were the tall phenotype (similar in canopy height to those growing in creeks of reference sites), indicating that they were healthy and not stressed by intraspecific competition, nutrient limitation, or abiotic conditions (Anderson and Treshow, 1980; Zerebecki et al., 2021). However, at the beginning of the fourth phase, *S. alterniflora* growing close to the seaward edge of the restoration sites began to resemble the short-form plants of the reference marshes. Bay of Fundy salt marshes typically have a scarped seaward edge, which is elevated compared to the sides of the creeks within the marshes where tall-form *S. alterniflora* grows. This seaward edge is exposed to environmental stress (including tidal, wind, and wave action), and is occupied by short-form *S. alterniflora*. Our recent observations of spatial heterogeneity in canopy height in the restoration sites, with short *S. alterniflora* plants seaward in more elevated and older vegetated areas, and tall *S. alterniflora* plants landward in the lower elevation, protected and more newly vegetated areas (including the borrow pits), are approaching the reference condition. The transition in phenotype from tall form to short form in the seaward area of our sites may be due to increasing intraspecific competition among these older *S. alterniflora* plants (Wang et al., 2005), decreasing edaphic conditions with accreting marsh surface elevation and presumably less tidal flushing (resulting in the delivery of less fresh sediment and nutrients; Mendelssohn and Seneca, 1980), and/or environmental stress in the form of mechanical action by high tidal, wave, and wind energy (e.g., causing high rates of plant mass loss, particularly in apical sections of leaves; Baerlocher and Moulton, 1999). We suspect that a combination of the above is involved because the old seaward dike (breached in 2010 in demarcated locations) protected the developing marsh until it was essentially fully eroded after winter 2016 (Virgin et al., 2020); this resulted in much higher environmental stress on the young marsh. However, we only started detecting the short phenotype in 2019 (Figure 7). Targeted research is needed to disentangle the cause(s) of the change in phenotype, since proximity to the seaward marsh edge and age of the *S. alterniflora* patches are confounded in our study, and this is further confounded by the effect of the yearly increased accretion of the marsh surface (mean accretion ± SE between 2010 and 2020: 0.57 ± 0.05 m, $n = 45$ GPS locations, range: 0.13–1.25 m). Note that although our restoration sites have accreted substantially, their surface elevation in 2020 (mean ± SE: 5.92 ± 0.04 m CGVD28, $n = 45$ locations) still has much accretion to do to reach the elevation of reference sites (6.83 ± 0.07 m CGVD28; $n = 7$ locations; data from J. Ollerhead). Two restoration implications arise from our above observations. First, dike-breaching plans need to consider the duration of protection provided to the developing young marsh. This duration partly depends on the state of the old dike when breached. For the Aulac project, although a new (managed realignment) dike was built in 2006, dedicated plans for breaching were done in 2009, and the breaching occurred in 2010, when the old dike had already started to erode (Boone et al., 2017). Implementing the breaching sooner would have given the developing marsh more time to develop while being protected. Second, conversion of *S. alterniflora* patches from tall form to short form is indicative of the increased maturity of the restoring marsh, heading toward the reference condition, and is an easy metric to monitor. Overall, development of distinct *S. alterniflora* phenotypes is a key indicator of the fourth phase of restoration in Aulac, as is the spread of *S. patens*.

Just before and at the start of the fourth phase, *S. patens* began spreading into the restoration sites from the higher elevation dike areas as well as from individual patches within the restoration sites proper. We predicted spread from dike edges would be the primary mode of spread because *S. patens* performs best in high elevation salt marsh areas (Bertness, 1991). Like *S. alterniflora*, we did not expect that *S. patens* would colonize and begin spreading in relatively high elevation areas in the middle of the restoration sites. We suspect that these isolated, circular, within-site, *S. patens* patches originated from rhizome material or turf deposited by ice blocks during the winter in a similar manner to *S. alterniflora* (Lundholm et al., 2021), since the isolated *S. patens* patches were already substantial in size (1–2 m in diameter) when we found them (one in 2016 and one in 2017 in Restoration West, one in fall 2020 in Restoration East, and ~ 20 in 2021 in Restoration West). Based on the morphologies of the grasses, namely the long rhizomes of *S. alterniflora* and dense clonal morphology of *S. patens*, we think that *S. alterniflora* mostly colonized as rhizome material and *S. patens* as turf, but this needs to be investigated by inspecting ice blocks in winter. Thus far, we have only detected asexual colonization and spread of *S. patens*, and not by sexual reproduction although *S. patens* patches in restoration and reference sites do flower. There is reduced need for planting tillers or seedlings in sites like ours since plant material readily colonizes a restoration area passively. After colonizing the restoration sites, the increase in *S. patens* has been relatively slow compared to that of *S. alterniflora* earlier in the restoration.

Spartina patens encroachment has been slow likely due to the plant's dense clonal morphology, gradually improving edaphic conditions, and possible interactions with *S. alterniflora* (Bertness, 1991; Pennings et al., 2005). Based on *S. patens* dynamics to date and as mentioned above, only recently has the marsh surface likely reached high enough elevation (and consequent appropriate inundation conditions) that enabled *S. patens* to spread. More years of monitoring are needed to determine if an increasing rate of spread will occur (Frenkel and Boss, 1988). In the upper Bay of Fundy (such as our Aulac sites), appropriate edaphic conditions for *S. patens* develop naturally since sedimentation rates are very high (Virgin et al., 2020). Other regions may require anthropogenic intervention to improve edaphic conditions for high elevation marsh species including *S. patens* (Fearnley, 2008), which when not appropriate, negatively influence plant performance (Anastasiou and Brooks, 2003; Merino et al., 2010) and prevent colonization (Gleason and Zieman, 1981). In addition, other regions may require planting of tillers or seedlings if plant material does not readily colonize a restoration area passively as it does in the upper Bay of Fundy. As edaphic conditions for *S. patens* continue to improve in Aulac, we expect that *S. patens* will competitively displace *S. alterniflora* (Bertness, 1991). Recently, *S. alterniflora* plants adjacent to *S. patens* patches appeared to be experiencing competitive stress, based on their observed lower stem densities and canopy heights than further away from these patches. It is not clear if *S. patens* are experiencing stress from adjacent *S. alterniflora*. Continued monitoring as well as experimentation on interspecific interactions between *S. patens* and *S. alterniflora* are needed to quantify plant states and spread rates in this situation, and to better understand processes underlying the fourth phase of salt marsh restoration during our project.

Conclusion

We conducted a decade-long study to quantify plant states and patch-level processes that lead to changes in vegetation community patterns during salt marsh restoration in the upper Bay of Fundy. Our focus on processes enabled us to better understand the phases of salt marsh restoration pattern change identified by Virgin et al. (2020). We found that *S. pectinata*, surviving after the dike breaching, was stressed, growing in sediment of high salinity, and declined because of these environmental conditions rather than competition with *S. alterniflora*. We also suggest that *S. pectinata* has potential in protecting a new restoration site, facilitating sediment retention. *Spartina alterniflora* initially colonized the restoration sites 2 years post-breach (in 2012), we think *via* deposited vegetative material, and soon after displayed the tall phenotype and rapid asexual spread. After the appearance of *S. alterniflora* seedlings in 2014 as well as continued asexual spread, the percent cover of vegetation in the restoration sites became greater than 90% by 2019. Seedlings took 2 years to reach mature live stem density and canopy height, and 3 years to reach mature percent flowering. As the restoration site aged, we began observing evidence that the short form phenotype of *S. alterniflora* was forming near the seaward scarped edges of the sites. We also observed S. *patens* slowly spreading from high elevation dike areas into the restoration sites and outward from isolated patches within-site. We expect these processes to continue until the restoration sites resemble established salt marshes by displaying distinct zonation between high and low marsh zones, and with tall and short phenotypes of *S. alterniflora*. In a future study, we plan to use our patch-level process information to estimate parameters for spatial-explicit modeling to examine patterns of percent vegetation cover and patch size distributions at the site level and to compare against observed patterns (complemented with recent and on-going remote sensing of salt marsh vegetation at our sites; Norris et al., 2022). Once developed, the modeling exercise will be used to evaluate different restoration strategies and help plan future restoration projects in the Bay of Fundy. Aside from contributing to a future modeling exercise, our study also provided relevant, detailed-oriented information and insight for salt marsh restoration strategies.

Data availability statement

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

Author contributions

MB and DS conceived the main study design. MB oversaw the research. GN, SV, EM, DS, JW, KM, LH, and MH led year-specific sampling designs, data collection, processing, and reporting of the project. GN analyzed the overall dataset. GN and MB wrote and edited the manuscript. SV and DS also edited the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.1000075/full#supplementary-material

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Variation in resource use between adult and juvenile Semipalmated Sandpipers (*Calidris pusilla*) and use of physiological indicators for movement decisions highlights the importance of small staging sites during southbound migration in Atlantic Canada

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Semipalmated Sandpipers (*Calidris pusilla*) are Arctic-breeding shorebirds that use staging sites in Atlantic Canada during their annual migration to South America. The Bay of Fundy has long been recognized as a critical staging site for migrating Semipalmated Sandpipers and supports a large prey base. The diet of adult sandpipers in the Bay is flexible but the diet of juveniles, which arrive later, is not well documented. Comparatively little is known about the prey base and how it is utilized by sandpipers at sites in Atlantic Canada outside the Bay. Plasma metabolite measures can provide useful insight to assess habitat quality for sandpipers and have not yet been measured in Semipalmated Sandpipers in Atlantic Canada. To address these knowledge gaps we sampled shorebird habitat to estimate invertebrate availability in the Bay of Fundy and the Northumberland Strait. Concurrently, we collected blood samples from adult and juvenile sandpipers for analysis of plasma metabolite levels and isotopic estimates of dietary niche in both regions. We found that sites on the Northumberland Strait hosted a more diverse and variable prey base than sites within the Bay of Fundy, and that sandpipers were selective when foraging there, appearing to prefer bivalves. Juveniles may occupy a broader dietary niche than adults along the Northumberland Strait, though appear to gain weight as efficiently. Sandpipers sampled along the Northumberland Strait had higher plasma triglyceride concentrations than those within the Bay of Fundy, which may suggest differences in fattening rate or dietary fat intake. Sandpipers that had lower triglyceride concentrations on the Northumberland Strait were more likely to move into the Bay of Fundy, while sandpipers with high triglyceride values tended to remain on the Strait. These data suggest that sandpipers made movement decisions within the region depending on their physiological state. Our results suggest adult and juvenile Semipalmated Sandpipers successfully use a variety of staging habitats in Atlantic Canada. This is an encouraging finding for sandpiper conservation in the region, but also indicates that maintaining access to a broad variety of staging habitats is critical, supporting calls for stronger conservation measures throughout the region.

KEYWORDS

Semipalmated Sandpiper, *Calidris pusilla*, migratory physiology, habitat selection, shorebird conservation, automated radio-telemetry, dietary niche, stable isotopes

1 Introduction

Shorebird populations throughout the western hemisphere are in decline. This is especially true for long distance migrants (North American Bird Conservation Initiative Canada, 2019), which are known to stage at a number of sites to refuel during their migration (Warnock, 2010; Ma et al., 2013). Birds choose staging sites based on a variety of factors including food availability (Hicklin and Smith, 1984; Goss-Custard et al., 1991; Ydenberg et al., 2002; Hamilton et al., 2003; Sprague et al., 2008) and site safety (Ydenberg et al., 2002; Sprague et al., 2008). High-quality staging sites are thus essential for successful migration (McGowan et al., 2011) and maintaining the integrity of these sites is a conservation priority. Often these are coastal sites that are experiencing erosion and habitat loss, risking their future availability for shorebird use (Galbraith et al., 2002). For species in which individuals stage at just one or two sites to refuel during their migration, particular areas can take on even greater importance [e.g., Delaware Bay for Red Knots (*Calidris canutus rufa*); Morrison and Harrington, 1992]. The rate of refueling at these sites can determine migration speed and success (Lyons et al., 2008), thus a healthy prey base and safe environment are essential.

Fat is the main energy source used on migration, as it has the most energy per unit mass (Ramenofsky, 1990; McWilliams et al., 2004). Thus, an ability to gain fat efficiently at staging sites is critical to successful migration. Previous studies have found a positive correlation between plasma triglyceride concentrations and fattening rates (Jenni-Eiermann and Jenni, 1994; Williams et al., 1999), making triglyceride measures a good index of fattening rates and potentially site quality (Lyons et al., 2008). In contrast, when energy use is higher than intake, lipids are burned as an alternative fuel source (Ramenofsky, 1990). β-OH-butyrate is indicative of fat catabolism and can therefore indicate fasting, restrictive feeding, or long endurance flights (Jenni-Eiermann and Jenni, 1994; Stevens, 1996). Previous studies have examined plasma metabolite levels in migrating juvenile and adult shorebirds. Guglielmo et al. (2002) found no difference in plasma triglyceride levels between adult and juvenile Western Sandpipers (*Calidris mauri*) during staging, but there was some evidence that juveniles may have higher β-OH-butyrate levels than adults. Another study in the prairie pothole region found that adult Semipalmated Sandpipers (*Calidris pusilla*) had higher plasma triglyceride levels and lower β-OH-butyrate levels than juveniles (Thomas and Swanson, 2013).

Semipalmated Sandpipers migrate annually from their Arctic breeding grounds to winter in South America. The species has experienced widespread declines, with losses observed on breeding, staging, and non-breeding sites (Jehl, 2007; Andres et al., 2012; Gratto-Trevor et al., 2012b; Morrison et al., 2012). The Bay of Fundy, Canada, is a critical staging location on southbound migration for eastern and central breeding Semipalmated Sandpipers (Hicklin, 1987; Gratto-Trevor et al., 2012a). Recent work has found adult sandpipers using the Bay of Fundy have high within and between-year fidelity, returning to the same areas of the Bay each year (Neima et al., 2020). Additionally, the behavior, movement and diet of adult sandpipers in this habitat are well understood (e.g., MacDonald et al., 2012; Quinn and Hamilton, 2012; Neima et al., 2022). Less is known about the use of these habitats by juvenile Semipalmated Sandpipers, which may need additional time or resources to gain sufficient weight for a successful southbound migration. Further, sites outside the Bay of Fundy, which are also used by Semipalmated Sandpipers and host a diverse assemblage of other staging shorebird taxa, have received little attention.

Juvenile Semipalmated Sandpipers have lower survivorship than adults, which may be contributing to population declines (Hitchcock and Gratto-Trevor, 1997). Anderson et al. (2019)

found that juvenile shorebirds had lower fuel loads and were less likely than adults to be detected south of James Bay, possibly suggesting higher mortality on southbound migration. Reduced survivorship among juveniles may be due to inefficient foraging, or insufficient fat stores to complete migration. Juvenile Semipalmated Sandpipers use a broader variety of sites than adults while staging in Atlantic Canada (Linhart et al., in press). This could lead to differences in prey consumption and slower fattening rates as they may burn more energy while traveling between sites. In some songbird species juveniles are forced to forage in less profitable areas, resulting in increased stopover duration to gain sufficient weight (Woodrey, 2000; Moore et al., 2003). Recent work in the region has found juveniles stay ~3 days longer than adults, adjusted for timing of migration (Mann et al., 2017; Linhart et al., in press), though the reason for this longer staging period needs more investigation. Additionally, juvenile sandpipers migrate through the region later than adults (Gratto et al., 1984; Hicklin, 1987; Dunn et al., 1988), which may reduce or change prey available to them.

Staging strategies of Semipalmated Sandpipers appear to vary depending on the sites they use. Recent work in Atlantic Canada found sandpipers tagged in the Bay of Fundy remained there, while birds tagged at a site outside the Bay would either choose to move into the Bay, or to remain outside the Bay for the duration of their stay in the area (Neima et al., 2020; Linhart et al., in press). Birds using sites outside the Bay had a significantly shorter length of stay than those using the Bay of Fundy, staying on average ~7 days less (Linhart et al., in press). This may be due to differences in migratory strategy, or it could be because birds using sites outside the Bay are able to gain weight more efficiently than those using the Bay of Fundy, possibly because they use a different prey base.

To assess these possibilities, and to better understand staging by birds in Atlantic Canada, we examined resource availability and use and metabolic state of adult and juvenile Semipalmated Sandpipers in the Bay of Fundy and on the Northumberland Strait, a coastal body of water separated from the Bay of Fundy by approximately 50 km. We hypothesized that diets would vary between adult and juvenile birds, and between our two study regions (Bay and Strait). Given that the Bay of Fundy is known to host an abundant invertebrate community consisting of high quality prey (Quinn and Hamilton, 2012; Gerwing et al., 2015; Quinn et al., 2017) and the majority of Semipalmated Sandpipers in Atlantic Canada use the Bay during migration, we predicted that sandpipers there would have higher plasma triglyceride values (signifying fattening rate) than those using small staging sites on the Northumberland Strait. In that event, the increased length of stay observed in the Bay (Linhart et al., in press) may be related to higher site quality (*sensu* Herbert et al., 2022). We also predicted that birds choosing to transfer from the Northumberland Strait into the Bay of Fundy would be those that needed to move to higher quality habitat to gain sufficient weight. Finally, we predicted that juvenile birds, which use a wider range of habitat (Linhart et al., in press) and are generally inexperienced may exhibit lower plasma triglyceride levels but higher β-OH-butyrate levels as a result of increased movement within the region. This study provides an opportunity to assess habitat quality through a lens of physiological response and helps us to understand the conservation value and utility of small staging areas in this region. Further, investigation of metabolic markers in adult and juvenile Semipalmated Sandpipers in Atlantic Canada may help us to better understand the implications of observed age-related differences in movements and resource use.

2 Materials and methods

2.1 Study area

We collected data at two coastal marine sites in the Northumberland Strait and Bay of Fundy (**Figure 1**). On the Northumberland Strait, we captured birds and collected invertebrate samples at Petit Cap (46.1791°N, −64.1398°W) in 2018 and 2019. We also collected invertebrate samples at another site, Cape Jourimain (46.1544°N, −63.8397°W), in 2019 (**Figure 1**). Petit Cap is a 1.25 km dynamic barrier beach with coarse sandy sediment and ~0.5 km of sand and mudflats at low tide, while Cape Jourimain is a 1.3 km beach with a gradual slope bordering an extensive salt marsh complex, and ~0.4 km of beach exposed at low tide. In the Bay of Fundy, we captured birds at Johnson's Mills (adjacent to the Grande Anse mudflat) and collected invertebrate samples at both Grande Anse (45.8339°N, −64.5119°W) and Pecks Cove (45.7567°N, −64.4891°W) in both years (**Figure 1**). The Grande Anse mudflat extends ~2 km from shore and is largely uniform with a high sediment water content and sediment penetrability (MacDonald et al., 2012; Gerwing et al., 2015). Pecks Cove is smaller, the sediment is firmer and has a lower water content than Grand Anse (Gerwing et al., 2015). The tidal flat extends ~850 m from shore, and there are deep ravines across the flats.

2.2 Bird capture and radio-telemetry

We captured birds at Johnson's Mills and Petit Cap during southbound migration from late July through mid-September in 2018 and 2019 (**Table 1**). On the Northumberland Strait we used mist nets deployed during low tides in the evening and at night. In the Bay of Fundy we used a Fundy pull trap (Hicklin et al., 1989) to capture birds roosting during high tide, as the high density of birds and speed of tidal movements made mist netting inappropriate in most circumstances. Upon capture, birds received individually numbered metal leg bands on the upper left leg and white alpha-numeric flags on the upper right leg. We recorded morphometric data including mass (±0.1 g),

FIGURE 1
Map of study sites in both regions: the Northumberland Strait (orange), and the Bay of Fundy (green). Semipalmated Sandpiper captures occurred at Johnson's Mills (adjacent to Grand Anse) (green circle) and Petit Cap (orange diamond). Habitat transects were completed at all four sites in 2019. In 2018 Cape Jourimain was not sampled.

flattened straightened wing chord (±1 mm), bill (culmen to tip), and tarsus length (±0.1 mm) for each bird. Birds were aged as hatch year (HY), second year (SY), or after second year (ASY) following Gratto-Trevor (2004) and Pyle (2008). We attached digitally encoded 0.67-g Lotek VHF nanotags (NTQB-3-2, Lotek Wireless Inc., Newmarket, ON, Canada) to a subset of light (<30 g) HY (hereafter referred to as juvenile) and AHY (hereafter referred to as adult) birds at both sites. Details of tagging are provided in Linhart et al. (in press) and are similar to Neima et al. (2020).

We collected blood from the brachial vein of birds using 27-gauge needles and heparinized capillary tubes. A maximum of 140 μl of blood was collected from each bird. Blood was transferred from the capillary tubes to Eppendorf tubes in the field and kept on ice until it could be centrifuged in the lab, a maximum of 6 h after it was drawn. Samples were centrifuged at 10,000 RPM for 1 min (mySPIN12 Mini Centrifuge, Thermo Scientific) to separate plasma and red blood cells. We pipetted off the plasma into separate tubes and stored samples at −20°C until used for analyses. We also collected a drop of blood from tagged birds on Whatman FTA cards (Whatman®, Marlborough, MA, USA) for molecular sexing. Blood used for plasma metabolite assays was collected within 20 min of capture to minimize the impact of handling stress (Guglielmo et al., 2002). Our average bleed time (time after capture) was 9.5 min (±4.5 min) for these birds. Blood was also collected from heavy birds (>32 g) for stable isotope analyses to estimate diet. Stable isotopes in blood plasma reflect the diet of birds for approximately the previous 6 days (Hobson and Clark, 1993). We chose heavy birds to ensure samples reflected the local diet of a bird that had likely been present in the region for at least 1 week (Quinn and Hamilton, 2012), as there is a positive relationship between fuel loads and length of stay in the region (Linhart et al., in press), and Semipalmated Sandpipers are known to arrive in the region light and roughly double their weight during their stay (Hicklin and Smith, 1984). All bird sampling was conducted under federal banding permits and was approved by the Mount Allison University Animal Care Committee under guidelines from the Canadian Council on Animal Care.

Tagged birds were tracked throughout their stay in Atlantic Canada using the Motus Wildlife Tracking Network (Taylor et al., 2017). Raw data were filtered by removing any detections with <3 consecutive hits, and by examining individual antenna signal plots for each tag (see Linhart et al., in press) following guidelines provided in the Motus R Book (Crewe et al., 2020). Birds were classified into three movement strategies depending on their tagging location. Sandpipers tagged within the Bay of Fundy remained within the Bay, while those tagged at Petit Cap either remained outside the Bay or moved into the Bay and remained there for the duration of their staging period in Atlantic Canada (see Linhart et al., in press for details). We calculated a minimum length of stay (as in Neima et al., 2022) for each bird by subtracting the deployment timestamp from the last known detection in Atlantic Canada. Detailed analyses of movement strategies, length of stay, and differences in site use between ages and tagging locations can be found in Linhart et al. (in press).

TABLE 1 Details of capture locations, dates, and sample collection for Semipalmated Sandpipers.

Year	Site	Age	Birds captured (*N*)	Transmitters deployed (*N*)	Blood taken (*N*)	TRIG (*N*)	BOHB (*N*)	ISO (*N*)
2018								
	Johnson's Mills (45.834°N, −64.512°W)	AHY	647	41	66	25	–	31
		HY	124	30	30	15	–	14
	Petit Cap (46.177°N, −64.177°W)	AHY	58	26	33	16	–	21
		HY	49	30	25	20	–	8
2019								
	Johnson's Mills (45.834°N, −64.512°W)	AHY	278	30	42	23	17	28
		HY	130	29	45	25	13	25
	Petit Cap (46.177°N, −64.177°W)	AHY	40	23	40	36	16	14
		HY	183	41	38	32	18	15

Blood samples collected for different purposes are as follows: TRIG, plasma triglyceride; BOHB, β-OH-butyrate; ISO, stable isotope analysis.

2.3 Prey availability

We collected sediment samples in 2018 and 2019 at our study sites to estimate prey availability. In 2018 we sampled in late July before bird migration. In 2019 we sampled twice, once in late July (pre-migration) and once in mid-September (late/post-migration). Samples were collected in a stratified random manner in habitat where shorebirds were known to forage, with transects running perpendicular to shore, differing in length depending on habitat available. In the Bay of Fundy in both years we completed two transects at each mudflat. Each transect was 500 m long and stratified into 100 m sections with two samples taken at random points in each stratum, for a total of 20 samples per mudflat per sampling period. Transects were ~500 m apart at each mudflat. In 2018 at Petit Cap on the Northumberland Strait, we had five 125-m transects stratified into 25 m sections, with one sample taken at a random point in each stratum, for a total of 25 samples. To cover more habitat at Petit Cap in 2019, we again had five transects, but made them 300 m long and stratified into 100 m segments, with two samples per segment, for a total of 30 samples. In both years three of the transects at Petit Cap were on the ocean side of the barrier beach, and two were on the inner, marsh/mudflat side of the beach. At Cape Jourimain in 2019 we ran three transects, each 300 m long and stratified into 100 m segments, with two samples per segment, for a total of 18 samples. At each sampling point, we collected samples using a 5.5 cm core pushed into the sediment until there was resistance from the consolidated anaerobic layer. These were then passed through a mesh sieve (Bay of Fundy 250 μm; Northumberland Strait 500 μm to account for coarser sediment found during preliminary sampling) and retained invertebrates were stored in 95% ethanol until they were sorted by size and taxon. The prey base differs between the Bay and Strait, with many of the smaller taxa that would be lost in a 500 μm sieve in the Bay not present in the Strait, so availability of prey relevant to shorebirds remains comparable. We only counted invertebrates that were clearly alive at the time of sampling. Sorted invertebrates were measured and dried in a drying oven (40GC Gravity Convection Oven, Quincy Lab Inc., Chicago, IL, USA) at 90°C for at least 24 h. Dry weight was recorded in g (±0.00001 g). All shelled invertebrates were subsequently ashed in a muffle oven (Isotemp Programmable Muffle Furnace 650-750 Series, Fisher-Scientific, Waltham, MA, USA) at 550°C for 2 h to combust organic material. Remaining shells were re-weighed, and shell weight was subtracted from the original dry weight to estimate consumable biomass. Kober and Bairlein (2006) suggested sandpipers consumed shelled items <8 mm, but to ensure that possible prey were not improperly excluded, we included all bivalves with a shell length <10 mm.

To determine whether shorebirds were actively selecting areas within the habitat with high prey availability, we conducted behavioral observations (Linhart, 2021) and then immediately collected sediment cores from locations where birds were foraging. Samples were processed as described above and prey densities compared to samples obtained from transects which reflect overall prey abundance at each site.

2.4 Stable isotope and plasma metabolite sample processing

We measured levels of stable isotopes of ^{13}C and ^{15}N in blood plasma of adult and juvenile birds at both capture locations. To prepare for stable isotope analyses, samples were dried in a drying oven (40GC Gravity Convection Oven, Quincy Lab Inc., Chicago, IL, USA) at 70°C for 24 h. In 2018 samples were analyzed for $\delta^{13}C$ and $\delta^{15}N$ at the Stable Isotope in Nature

Lab (SIN Lab, University of New Brunswick), using a Finnigan Delta Plus mass spectrometer (Thermo-Finnigan; Bremen, Germany) interfaced with a Costech 4010 elemental analyzer *via* the Conflo II. In 2019 we analyzed samples at the Environmental Analytics and Stable Isotope Lab (EASIL, Mount Allison University) using an Elementar PyroCube Elemental Analyzer (Elementar Analysensysteme GmbH, Hanau, Germany) and an Isoprime Precision Isotope Ratio Mass Spectrometer (Elementar UK Ltd., Cheadle, UK). Though samples were processed in different labs, the procedures were very similar, results were standardized to the same references, and the same operator worked in both labs, so results are comparable. Stable isotope values were given relative to standard references in $\delta(^{i}X)$ format as follows, where X is either ^{13}C or ^{15}N, and *R* is the corresponding $^{13}C/^{12}C$ or $^{15}N/^{14}N$ isotope ratio.

$$\delta(^{i}\mathrm{X}) = \left[\frac{R_{sample}}{R_{reference}} - 1\right] \times 10{,}000$$

All metabolites were quantified using commercially available assay kits. Plasma triglyceride (TRIG) concentration was quantified using Sigma Aldrich Triglyceride Determination Kit (Sigma-Aldrich, TR0100-1KT, Oakville, ON, Canada) using undiluted plasma. For β-OH-butyrate (BOHB) concentration, we used Cayman Chemical β-OH-butyrate (Ketone Body) Colorimetric Assay Kit (Cayman Chemical, 700190, Ann Arbor, MI, USA). Plasma samples were diluted for the BOHB assay; depending on the amount of plasma available we did between a 3 and 12× dilution using the buffer that came in the kit. BOHB was only measured in 2019 and the sample size was limited. To increase our sample size and improve generalizability, we also obtained samples collected in 2020 at Petit Cap (using the same protocol) for this assay. For both assays, samples were analyzed in duplicate on a 96-well plate in a spectrophotometer (Allsheng, AMR-100, Hangzhou, China). If duplicate samples had >20% difference in results they were re-run (if possible), or the data were excluded from analyses. Duplicates with acceptable variation (<20%) were averaged, with the average value used as the metabolite measure for each bird.

2.5 Statistical analyses

All analyses were completed using R statistical software, version 4.0.3 (R Core Team, 2020) with an R Studio interface. We set alpha at 0.05 for main effects, and 0.1 for interactions to ensure that main effects were not inappropriately interpreted in the presence of a potential interaction (as in Hamilton et al., 2006). Assumptions were tested using a Shapiro test for normality with visual inspection of Q-Q plots, and either Levene's or Cochran's test for homogeneity of variance with visual inspection of residuals. To account for unbalanced designs, we used type II Sums of Squares (Langsrud, 2003).

2.5.1 Invertebrate availability

To examine differences in prey availability between sites, years, and sample types (transect vs. foraging area), we completed a permutational multivariate analysis of variance (PERMANOVA, 999 permutations, Bray–Curtis distance matrix) using the vegan package in R (Oksanen et al., 2020). For each sample, invertebrate biomass was summed across size classes by taxon. In 2019, we had early and late season prey samples. To compare availability between years, we used only the early transects, as they were most comparable to 2018. Invertebrate biomasses were the response variables, and year, region (Bay vs. Strait), and type (foraging vs. transect) were predictors. When we detected significant multivariate effects, we used similarity percentages (simper) to determine relative contribution to the overall results of the different response variables. We also assessed multivariate dispersion (permdisp) with the betadisper function (vegan; Oksanen et al., 2020) to compare dispersion among levels of factors. We identified significant region × sample type and region × year interactions, which were investigated by splitting the analyses by region and developing models examining year, site and sample type for each region.

We also examined variability in invertebrate prey abundance between sites within each region to assess temporal and spatial variation. Using 2019 transect data, we completed separate linear mixed effect models for each region, with time (July vs. September) set as a fixed factor and transect nested within site, both as random factors. Invertebrate biomasses were pooled by sample and used as the response variable for each model. To meet assumptions data were log-transformed for the Bay of Fundy and square-root transformed for the Northumberland Strait. We extracted variance components for the random factors in the models and completed a variance component analysis to assess sources of variability within the system. To compare variability between regions we completed a Levene's test using transect data from both regions, with log-transformed biomass as the response variable and region as the predictor.

2.5.2 Stable isotopes and dietary niche

We assessed differences in dietary niche breadth between adult and juvenile birds by comparing multivariate dispersion (permdisp analyses) of $\delta^{13}C$ and $\delta^{15}N$ signatures using the vegan package in R (betadisper function; Oksanen et al., 2020). We completed separate analyses for each region due to differences in the prey base. To visualize dietary niches, we used the SIBER package (Jackson et al., 2011) to generate plots.

2.5.3 Movement and metabolites

Linhart et al. (in press) identified three main staging strategies, with length of stay varying amongst them from approximately 2 to 3 weeks – birds captured in the Bay of Fundy remained there, whereas those captured on the Northumberland Strait either remained there or transferred into the Bay and remained there until they departed. We completed two sets of analyses to examine differences in plasma metabolites between birds using different staging strategies, one for tagged birds that had blood samples drawn, and one including a larger sample of birds bled from each site. For both analyses we calculated relative fuel loads to control for the fat content of each bird. Many studies have found weight affects metabolite levels in shorebirds (Guglielmo et al., 2002; Seaman et al., 2005; Lyons et al., 2008), and relative fuel loads allow us to control for fat content adjusted for body size, as juveniles can be smaller than adults. Gutiérrez et al. (2019) took a similar approach when comparing metabolic profiles of shorebirds of varying body sizes. Relative fuel loads at capture were calculated using the following equation from Anderson et al. (2019):

$$f = \frac{Mass\ at\ Capture\ (g) - Estimated\ Lean\ Mass\ (g)}{Estimated\ Lean\ Mass\ (g)}$$

Estimated lean mass was calculated using separate regression equations for adults and juveniles, generated by Anderson et al. (2019) using wing cord to account for variability between individuals.

For the analysis of all bled birds (tagged and untagged) we ran an additive generalized linear model (glm) to investigate differences in TRIG values between Petit Cap and Johnson's Mills. TRIG values were the response variable, with age, year, and site as predictors. We included time from capture to the bird being bled (bleed time) and relative fuel load as covariates. Bleed time is known to influence TRIG values, so although we constrained it to 20 min post capture to minimize this effect, we included it in the event the effect was still present. Further, there was a positive relationship between plasma triglyceride concentrations and relative fuel load for all age and site combinations (p = 0.003–0.04, R^2 = 0.11–0.17), so inclusion of it in the model controlled for this factor. To assess BOHB values we ran another additive glm. Log transformed BOHB values were the response variable, age and site were categorical predictors, and relative fuel loads and bleed time were covariates. BOHB values were generally higher for juveniles than adults but we had a small sample size and therefore limited statistical power. To clarify the result, we obtained additional data from birds sampled at Petit Cap in 2020. Using only Petit Cap birds, we ran an additive glm with year (2019 and 2020) and age as factors, and bleed time and fuel loads as covariates to better assess differences in BOHB concentrations between ages with a larger sample size. For each of the above metabolites, sex of birds was also tested as a predictor by subsetting the data to include only sexed birds (as determined in Linhart et al., in press). We found no effect of sex for any model, so it was removed and sexes were combined for all analyses.

For tagged birds we modeled rank-transformed length of stay on strategy, age (HY and AHY), year and TRIG concentrations using a glm. BOHB was not included in models of length of stay because we had a small sample size and only had results for 1 year. We also ran a glm with TRIG as the response and strategy, age, year, relative fuel loads, and bleed time as predictors. We ran a similar model with BOHB as the response and strategy, age, relative fuel loads, and bleed time as predictors using data from 2019. BOHB had to be log transformed to meet assumptions. To examine differences in TRIG levels between birds using different movement strategies at Petit Cap we ran a binomial glm and used AIC model selection (R package MuMin; Bartoń, 2022) with movement strategy as the response variable (positive being "moved" into the Bay of Fundy and negative being "did not move"), age, day of year, year, and TRIG as the predictors.

3 Results

3.1 Prey availability

Differences in prey biomass between sample types (transects vs. foraging areas) varied among regions (Region × Type: $F_{1,240}$ = 1.75, p = 0.09) and differences between regions varied by year (Region × Year: $F_{1,240}$ = 4.53, p = 0.001), so we split by region to investigate these interactions (**Table 2**). Invertebrate availability varied by year in both regions, and in the Bay of Fundy in 2018 by site as well (**Table 2** and **Figure 2**). In general, there was no evidence that Semipalmated Sandpipers foraged selectively in areas containing more prey biomass in the Bay of Fundy except for Pecks Cove in 2018 where samples collected in foraging areas had higher invertebrate abundance than those from transects. This appears to be driven mainly by amphipods (**Figure 2**). In contrast, sandpipers foraging in the Northumberland Strait did select foraging areas based on prey availability (**Figure 2**), driven mainly by selection of areas high in bivalves (simper: 50% dissimilarity, p = 0.02). Dispersion of prey community biomass measures in the Bay of Fundy varied between sites (permdisp: $F_{1,120}$ = 4.15, p = 0.04), with Johnson's Mills having higher dispersion than Pecks Cove. Dispersion was similar between sites on the Northumberland Strait ($F_{1,122}$ = 0.96, p = 0.33).

In the Northumberland Strait in 2019 more biomass was available at both study sites later in the season ($X^2{}_1$ = 7.15, p = 0.007, see **Supplementary Figure 1**). Conversely, prey availability was consistent throughout migration in the Bay of Fundy (BoF Time: $X^2{}_1$ = 0.86, p = 0.36). Using extracted variance components, we found that variation in both regions was largely at the level of sample (BoF: 79.8%, NuS: 77.3%), though sites in the Northumberland Strait appeared to have more variability than those in the Bay of Fundy (BoF: 7.2%, NuS: 11.1%). There was also a significant difference in variability between regions (Levene's test: $F_{1,167}$ = 18.89, p < 0.0001); the Northumberland Strait was more variable than the Bay of Fundy.

3.2 Estimated dietary niche

In 2018 the dietary niche based on blood plasma signatures for $\delta^{15}N$ and $\delta^{13}C$ of juvenile birds tended to be broader than adults, especially at Petit Cap (Figure 3), though a corresponding permdisp analysis found niches were similarly dispersed between adults and juveniles at both sites (Petit Cap: $F_{1,27} = 1.72$, $p = 0.20$; Johnson's Mills: $F_{1,43} = 1.06$, $p = 0.31$). The sample size of juveniles at Petit Cap in 2018 was small ($n = 8$), probably leading to low statistical power. In 2019 the juvenile niche at Petit Cap was more widely dispersed than adults (Figure 3, permdisp: $F_{1,26} = 3.90$, $p = 0.04$). At Johnson's Mills, juveniles appeared to have a narrower niche than adults, though the difference only approached significance (Figure 3, permdisp: $F_{1,48} = 3.51$, $p = 0.07$).

3.3 Plasma metabolites

Birds sampled at Petit Cap had higher TRIG values than those captured at Johnson's Mills, and there were no differences among ages or years (Table 3 and Figure 4). There was no relationship between TRIG values and bleed time, but there was a positive relationship between relative fuel loads and TRIG values (Table 3).

β-OH-butyrate levels varied by site and the amount of time between capture and bleeding, but not by age or relative fuel loads (Table 3). There was a positive relationship between time to bleeding and BOHB values. Sandpipers at Petit Cap had higher BOHB values than those sampled at Johnson's Mills, in 2019 (Table 3). Combining data from 2019 and 2020 (due to a small sample size for juveniles in 2019), we found that juveniles had significantly higher BOHB than adults, with no effect of

TABLE 2 Permutational multivariate analysis of variances (permutations = 999) of separate models analyzing prey biomass split by region.

Region	Predictor	df	Mean square	Pseudo *F*	*p*
Bay of Fundy					
Years combined	Year	1	1.43	8.05	0.001
	Site	1	3.69	20.82	0.001
	Type	1	0.24	1.34	0.25
	Year × site	**1**	**0.69**	**3.89**	**0.003**
	Year × type	**1**	**0.43**	**2.41**	**0.04**
	Site × type	**1**	**0.50**	**2.83**	**0.03**
	Residual	114	20.18		
Bay of Fundy					
2018	Site	1	2.96	19.00	0.001
	Type	1	0.44	2.80	0.03
	Site × type	**1**	**0.33**	**2.15**	**0.06**
	Residual	61	0.16		
Grand Anse					
2018	*Type*	*1*	*0.30*	*1.89*	*0.10*
	Residual	34	0.16		
Pecks Cove					
2018	**Type**	**1**	**0.47**	**3.10**	**0.03**
	Residual	27	0.15		
Bay of Fundy					
2019	**Site**	**1**	**1.41**	**6.98**	**0.001**
	Type	1	0.23	1.16	0.31
	Site × type	1	0.35	1.74	0.11
	Residual	53	0.20		
Northumberland Strait					
Years combined	**Year**	**1**	**0.64**	**2.16**	**0.04**
	Site	**1**	**1.45**	**4.88**	**0.001**
	Type	**1**	**0.66**	**2.21**	**0.03**
	Year × type	1	0.17	0.56	0.80
	Site × type	1	0.39	1.30	0.24
	Residual	118	0.30		

Biomasses of the different invertebrate taxa were the response variables. Factors are year (2018 vs. 2019), site (Bay of Fundy: Johnson's Mills vs. Pecks Cove; Northumberland Strait: Petit Cap vs. Cape Jourimain), and type (behavioral observation or transect). Significant and interpretable results are in bold ($\alpha < 0.05$ for main effects, <0.10 for interactions), and results approaching significance italicized.

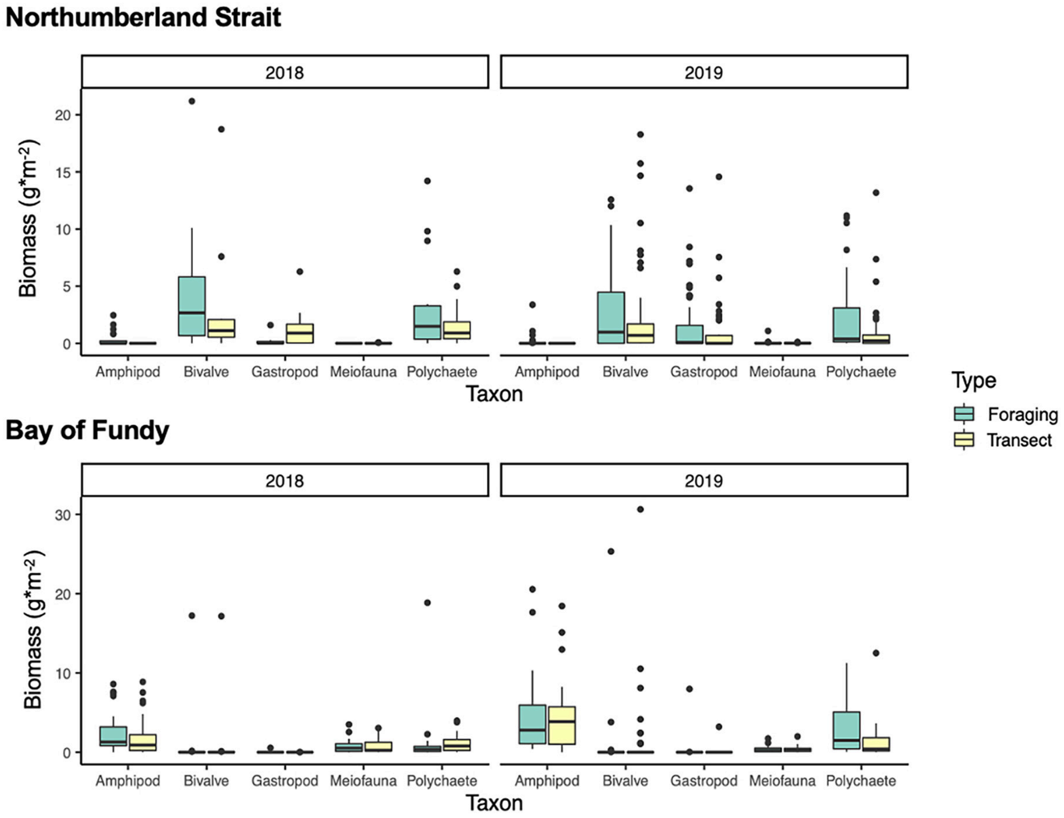

FIGURE 2
Dry biomass (g·m^{-2}) of invertebrates in 2018 **(left)** and 2019 **(right)** in the Northumberland Strait **(top)** and Bay of Fundy **(bottom)** in locations where birds were foraging (represented selected habitat) and on transects (representing available habitat). Center line represents the median, with first and third quartiles shown in boxes. Whiskers show interquartile range. Points show data beyond the 5th and 95th percentile. Note that the *y*-axis scale differs between regions.

year, bleed time, or fuel loads (Table 3 and Figure 5). Among birds for which sex was determined, we found that sex did not affect levels of either metabolite (TRIG model: $X^2{}_1 = 1.97$, $p = 0.16$, BOHB model: $X^2{}_1 = 0.64$, $p = 0.42$).

Among tagged birds, TRIG values did not predict length of stay in Atlantic Canada (Table 4). We found that TRIG concentrations had a positive relationship with relative fuel loads and varied by both strategy and year but not by age (Table 4). TRIG values were higher in 2018 than 2019 (Figure 6) and were higher for birds using only sites outside the Bay than those tagged in the Bay of Fundy (Table 4). However, birds tagged at Petit Cap that subsequently moved into the Bay were not different from Bay of Fundy birds. Further, we found that birds at Petit Cap with lower TRIG were significantly more likely to move into the Bay of Fundy than those with higher TRIG values, particularly among adults, and that the best model to predict movement included TRIG and age, though age only approached significance (Table 5 and Figure 7). BOHB values appeared to vary by strategy, with higher levels for birds tagged at Petit Cap remaining outside the Bay than birds tagged in the Bay of Fundy (Table 4). BOHB did not vary by bleed time, relative fuel loads, or age (Table 4), though values trended higher for juveniles.

4 Discussion

4.1 Dietary niche and habitat variability

We found that the breadth of dietary niche and invertebrate availability varied between our study sites, and between years in each region. This is consistent with previous work conducted in the Bay of Fundy, which found variation in stable isotope signatures and invertebrate availability between years (Quinn and Hamilton, 2012). Our results suggest that annual differences also occur at sites outside the Bay of Fundy. Shorebird diets reflect the invertebrate availability at a site, and they are highly flexible as they encounter many different prey items throughout their life cycle (Hicklin and Smith, 1979; Skagen and Oman, 1996; Tsipoura and Burger, 1999; MacDonald et al., 2012; Gerwing et al., 2016). Sites on the Northumberland Strait had more variable prey abundance than

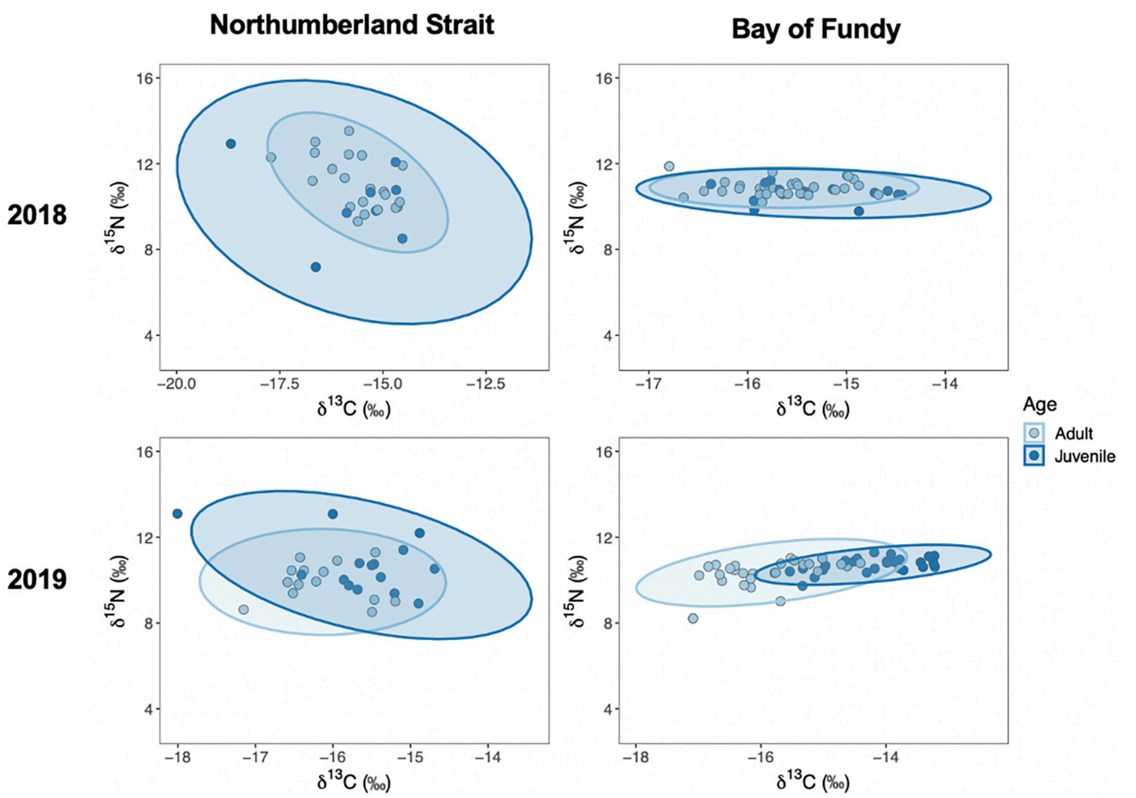

FIGURE 3

Isotopic dietary niches of Semipalmated Sandpiper adults (light blue) and juveniles (dark blue) captured at Petit Cap (**left**: 2018: N_{adult} = 21, N_{juvenile} = 8, 2019: N_{adult} = 14, N_{juvenile} = 14) and Johnson's Mills (**right**: 2018: N_{adult} = 31, N_{juvenile} = 14, 2019: N_{adult} = 28, N_{juvenile} = 24) in 2018 **(top)**, and in 2019 **(bottom)**. Ellipses represent maximum likelihood estimates and were developed using δ^{15}N and δ^{13}C isotope signatures of blood plasma in parts per thousand.

those in the Bay of Fundy, and overall exhibit a wider range of habitat types. This is reflected in the observed dietary niches of sandpipers; birds sampled at Petit Cap appeared to have broader niches than birds at Johnson's Mills (**Figure 3**). We also detected some differences in the breadth of dietary niches between adult and juvenile birds. Juveniles may have a broader niche than adults foraging on the Northumberland Strait. There are a number of possible explanations for this. First, juveniles use a broader range of sites along the Strait than adults (Doiron, 2021; Linhart et al., in press), so they may be exposed to a wider range of prey items, given the observed variability among sites in that region. Second, juveniles are inexperienced and unfamiliar with staging areas, which may cause them to sample the environment and forage more heavily on different food sources than would adults (Marchetti and Price, 1989), perhaps because they rely on prey that are readily available or easy to visualize (Wunderle, 1991). Juvenile sandpipers may also be forced to consume different prey items due to competition with adults, which has been seen in other bird species (Woodrey, 2000; Moore et al., 2003). However, passage of adults and juveniles is somewhat segregated in the region, with juveniles passing later (Gratto et al., 1984; Hicklin, 1987), so effects of such competition may be limited. Finally, they may be left with different choices due to changes in invertebrate availability through the season (**Supplementary Figure 1**).

4.2 Plasma metabolites and sandpiper movement

Sandpipers sampled at both of our study sites in Atlantic Canada exhibited high plasma triglyceride values relative to those seen in other parts of their range, including migratory (Lyons et al., 2008; Anderson et al., 2021) and non-migratory areas (Lyons et al., 2008; Linhart et al., 2022), consistent with the rapid weight gain they experience during staging on southbound migration. Sandpipers captured at Petit Cap (Northumberland Strait) had significantly higher TRIG and BOHB values than those captured at Johnson's Mills (Bay of Fundy) when controlling for relative fuel loads and bleed time. This was a surprising finding, as higher fattening rates were expected in the Bay of Fundy, which hosts a large proportion of the Semipalmated Sandpiper population (Hicklin, 1987) and is recognized as critical shorebird habitat by the Western

TABLE 3 Generalized linear models analyzing plasma metabolites of all sampled birds.

Variable	Estimate	SE	t	p
A. TRIG	**Residual deviance = 85.47, df = 166**			
Intercept	**1.32**	**0.24**	**5.58**	**<0.001**
Age (juvenile)	−0.12	0.11	−1.13	0.26
Year (2019)	−0.02	0.12	−0.16	0.87
Site (Petit Cap)	**0.26**	**0.12**	**2.10**	**0.04**
Relative fuel loads	**1.70**	**0.32**	**5.39**	**<0.001**
Bleed time	*−0.02*	*0.01*	*−1.71*	*0.09*
B. BOHB 2019	**Residual deviance = 1.23, df = 54**			
Intercept	−0.57	0.08	−6.90	<0.001
Site (Petit Cap)	**0.10**	**0.04**	**2.27**	**0.03**
Age (juvenile)	0.05	0.04	1.20	0.24
Bleed time	**0.01**	**0.004**	**2.14**	**0.04**
Relative fuel loads	0.17	0.10	1.67	0.10
C. BOHB at Petit Cap 2019 and 2020	**Residual deviance = 1.27, df = 51**			
Intercept	−0.35	0.07	−4.73	<0.001
Year (2020)	0.05	0.04	1.20	0.23
Age (juvenile)	**0.11**	**0.04**	**2.68**	**0.01**
Bleed time	−0.001	0.005	−0.26	0.80
Relative fuel loads	−0.01	0.09	−0.12	0.90

Response variables are plasma triglycerides (TRIG) and β-OH-butyrate (BOHB). Age, site, and year are categorical predictors, and relative fuel loads and bleed time are covariates. (A) TRIG; (B) BOHB using 2019 data from the Bay of Fundy and Northumberland Strait; and (C) BOHB using data from the Northumberland Strait in 2019 and 2020. Variable refers to the predictors and estimate to coefficients reflecting effect sizes. For categorical variables the category associated with the estimate (relative to the other level of the variable) is provided in parentheses. Significant and interpretable results are in bold (α < 0.05 for main effects, <0.10 for interactions), and results approaching significance are italicized.

Hemisphere Shorebird Reserve Network (WHSRN Sites, 2021). The Bay of Fundy is food-dense, with large quantities of *Corophium volutator,* a high-quality prey item rich in essential fatty acids (Maillet and Weber, 2006). Quinn et al. (2017) found diet items (*C. volutator,* polychaetes, and biofilm) in the Bay of Fundy are rich in n-3 polyunsaturated fatty acids which are essential for migratory flight and contribute to TRIG levels. Less is known about prey quality at sites outside the Bay, though our results suggest sandpipers were selective of bivalves and polychaete worms which are known to be quality food items elsewhere (Stillman et al., 2005; Quinn et al., 2017; Mogle, 2021).

There are a number of potential explanations for the higher values of both TRIG and BOHB at Petit Cap. It is possible birds using sites outside the Bay are gaining weight faster, reflected through higher TRIG values. Alternatively, a diet high in fat could also generate high TRIG levels. Macromolecular composition of prey items has been shown to impact plasma triglyceride levels in birds (Smith et al., 2007; Smith and McWilliams, 2009). Based on prey available in locations where sandpipers chose to forage on the Northumberland Strait, they appeared to be consuming many bivalves, which are high in lipids (Mogle, 2021) and could explain the elevated TRIG levels we detected. A similar trend of high-fat diets being associated with high TRIG levels has been seen in Western Sandpipers (*C. mauri*; Seaman et al., 2005). The apparent paradox of high BOHB, which is typically elevated when fasting (Jenni-Eiermann and Jenni, 1991, 1996), present with elevated TRIG in foraging sandpipers at Petit Cap may also be diet driven. A diet high in fat

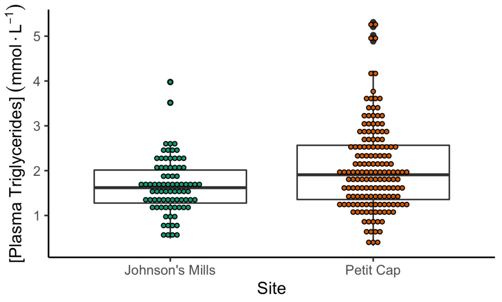

FIGURE 4
Concentration of plasma triglyceride values (mmol·L^{-1}) of Semipalmated Sandpipers captured at Johnson's Mills (Bay of Fundy) and Petit Cap (Northumberland Strait). Ages are pooled. Points show values from individual birds. Results of statistical comparisons are provided in Table 3. Note that values used for analyses were standardized by relative fuel loads.

TABLE 4 Generalized linear models analyzing plasma triglycerides (TRIG) in tagged birds.

Variable	Estimate	SE	*t*	*p*
A. Response variable: length of stay	**Residual deviance = 4,400.7, df = 95**			
Intercept	25.99	3.93	6.61	<0.001
Strategy (tagged on Strait and remained on Strait)	**−6.42**	**1.90**	**−3.38**	**0.001**
Strategy (tagged on Strait and moved into Bay of Fundy)	2.16	2.34	0.93	0.36
Age (juvenile)	1.22	1.44	0.85	0.40
Year (2019)	−2.44	1.53	−1.60	0.11
Relative fuel load	**−15.79**	**7.45**	**−2.12**	**0.04**
TRIG	−0.64	1.17	−0.55	0.58
Bleed time	0.13	0.18	0.72	0.48
B. Response variable: TRIG	**Residual deviance = 33.68, df = 96**			
Intercept	1.48	0.31	4.81	<0.001
Strategy (tagged on Strait and remained on Strait)	**0.43**	**0.16**	**2.69**	**0.008**
Strategy (tagged on Strait and moved into Bay of Fundy)	−0.01	0.20	−0.06	0.95
Age (juvenile)	0.006	0.12	0.05	0.96
Year (2019)	**−0.40**	**0.13**	**−3.19**	**0.002**
Relative fuel loads	**1.73**	**0.62**	**2.78**	**0.007**
Bleed time	−0.02	0.02	−1.62	0.11
C. Response variable: BOHB from 2019	**Residual deviance = 1.13, df = 23**			
Intercept	0.05	0.24	0.19	0.85
Strategy (tagged on Strait and remained on Strait)	**0.26**	**0.12**	**2.16**	**0.04**
Strategy (tagged on Strait and moved into Bay of Fundy)	*0.27*	*0.15*	*1.77*	*0.09*
Age (juvenile)	0.09	0.09	1.05	0.31
Relative fuel loads	0.37	0.50	0.74	0.46
Bleed time	0.02	0.01	1.63	0.12

Movement strategy, age, and year are categorical predictors and relative fuel loads and bleed time are covariates. TRIG is modeled as a predictor of length of stay (A) and as a response variable (B), and β-OH-butyrate is modeled as a response variable (C). Length of stay was obtained from Linhart et al. (in press). Variable refers to the predictors and estimate to coefficients reflecting effect sizes. For categorical variables the category associated with the estimate (relative to the other level of the variable) is provided in parentheses. Strategy comparisons are against sandpipers tagged in the Bay of Fundy that remained within the Bay. Significant and interpretable results are in bold ($\alpha < 0.05$ for main effects, <0.10 for interactions), and results approaching significance are italicized.

and low in carbohydrates could force sandpipers into ketosis and cause them to burn fat as fuel, which has been seen in poultry (Ohtsu et al., 2013). This could result in elevated BOHB values, even when birds were actively foraging, which was the case for birds captured at Petit Cap.

It is also possible that different capture methods and timing contributed to observed differences between birds sampled at Johnson's Mills and Petit Cap. Lower TRIG values at Johnson's Mills could be consistent with birds that were roosting, not foraging as they were at Petit Cap, because they had time to deposit free-flowing triglycerides as fat, lowering the amount measurable by our method. However, we found no evidence in adults and only limited evidence in juveniles of a decline in TRIG levels with increasing roosting time (**Supplementary Figure 2** and **Supplementary Table 1**). Therefore, it is unlikely that this would explain the difference between sites. BOHB was also unrelated to roosting time (**Supplementary Figure 3** and **Supplementary Table 2**), so methodological differences are likely not relevant to this result either. Further, in an effort to assess possible effects of time of day on results, we compared birds captured during evening vs. night at Petit Cap and again found only limited evidence of effects (**Supplementary Figure 4** and **Supplementary Table 3**). This is not surprising, as Semipalmated Sandpipers are known to feed actively during day and night in Atlantic Canada (Ouellette, 2021).

Regardless of the precise mechanism, the elevated TRIG values relative to other studies conducted outside the migration period (e.g., Lyons et al., 2008; Linhart et al., 2022) suggest that Semipalmated Sandpipers are able to gain weight efficiently at both Bay of Fundy and Northumberland Strait sites using a diverse range of prey items, reflective of the opportunistic foraging noted for the species elsewhere in Atlantic Canada (MacDonald et al., 2012). The potentially higher fattening rates observed on the Northumberland Strait may also contribute to shorter lengths of stay recorded for birds using sites outside the Bay (Linhart et al., in press).

Consistent with most other studies on Semipalmated Sandpipers (Lyons et al., 2005, 2008; Henkel and Taylor, 2015), we found no evidence of differences in TRIG levels among ages. However, in our study juveniles had BOHB concentrations 27–36% higher than adults. This result is also consistent with

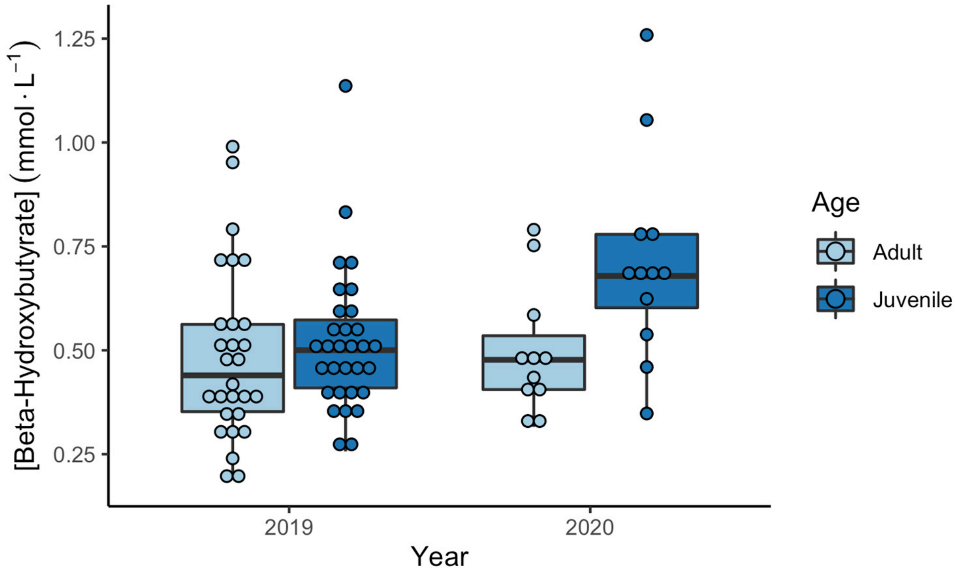

FIGURE 5

β-Hydroxybutyrate concentrations (mmol·L^{-1}) of adult (light blue) and juvenile (dark blue) Semipalmated Sandpipers in 2019 **(left)** and 2020 **(right)** sampled at Petit Cap. Center line represents the median, with 1st and 3rd quartiles shown in boxes. Whiskers show interquartile range, and points show individual measures. Results of statistical comparisons are provided in **Table 3**.

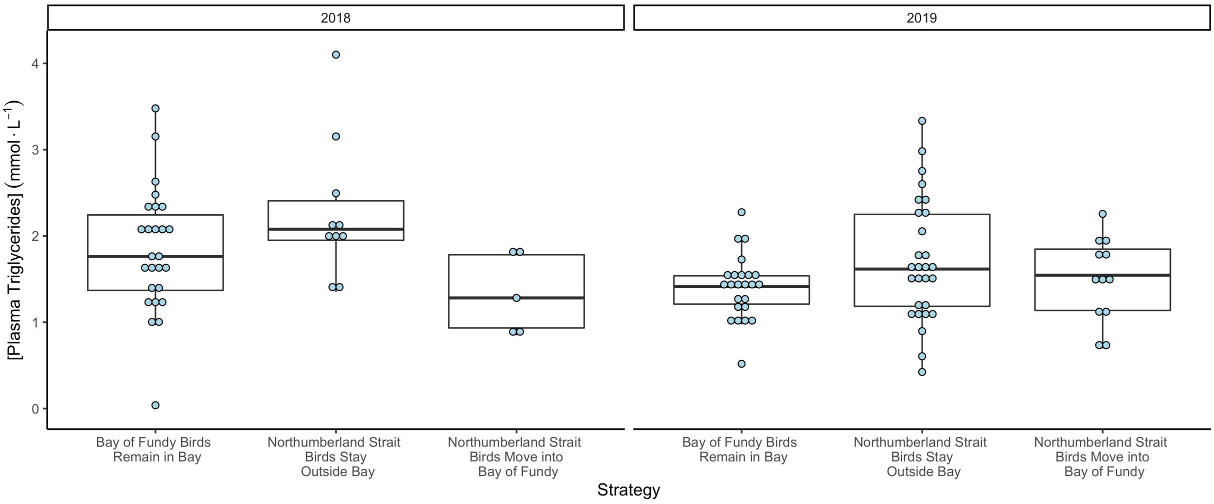

FIGURE 6

Plasma triglyceride concentrations (mmol·L^{-1}) of Semipalmated Sandpipers in 2018 and 2019 using different movement strategies. Sandpipers sampled in the Bay of Fundy remained in the Bay, and those tagged on the Northumberland Strait either chose to stay on the coast or moved into the Bay. Results of statistical comparisons are provided in **Table 4**.

other studies investigating plasma metabolites in adult and juvenile sandpipers (Guglielmo et al., 2002; Lyons et al., 2008; Thomas and Swanson, 2013), and could suggest juveniles may be prone to more fasting or higher energy expenditures than adults. Juvenile sandpipers tended to explore more staging sites than adults (Linhart et al., in press), which exhibit strong regional fidelity (Neima et al., 2020). These additional movements may cause them to burn fat throughout their staging period, generating elevated BOHB levels. It is also possible the additional movements and diet choices of juveniles have compounding effects, leading to the higher BOHB levels we detected. Finally, due to their later arrival in the region juveniles may also be exposed to higher predation risk from migrating raptors, as seen in other species (*Tringa glareola*;

TABLE 5 AICc model selection (A) and full model output (B) of a binomial generalized linear model using data from birds tagged at Petit Cap.

A. Model selection delta AIC < 3

Age	Day of year	TRIG	Year	Age × TRIG	df	AICc	Weight
+		−0.94			3	66.4	0.29
+		−1.48		+	4	67.4	0.18
		−0.98			2	67.9	0.14
+					2	68.0	0.13
+	0.02	−1.03			4	68.6	0.10
+		−0.99	+		4	68.6	0.10
	−0.03	−0.82			3	69.4	0.07

B. Full model, significant results bolded

Variable	Estimate	SE	*z*	*p*
Intercept	4.92	12.15	0.41	0.69
Age (juvenile)	*−3.28*	*1.94*	*−1.70*	*0.09*
TRIG	**−1.51**	**0.77**	**−1.97**	**0.05**
Year (2019)	−0.42	0.91	−0.46	0.65
Day of year	−0.01	0.05	−0.22	0.83
Age × TRIG	1.39	1.17	1.19	0.23

Movement decision was the response variable ("yes" = moved into Bay of Fundy, "no" = remained outside Bay of Fundy). Predictors were factors age and year and covariates day of year and plasma triglyceride (TRIG) values. Models with delta AICc < 3 are presented. Weight refers the likelihood that the model is the top model. (B) Full model including all factors. For categorical variables the category associated with the estimate (relative to the other level of the variable) is provided in parentheses. Significant and interpretable results are in bold ($\alpha < 0.05$ for main effects, <0.10 for interactions), and results approaching significance are italicized.

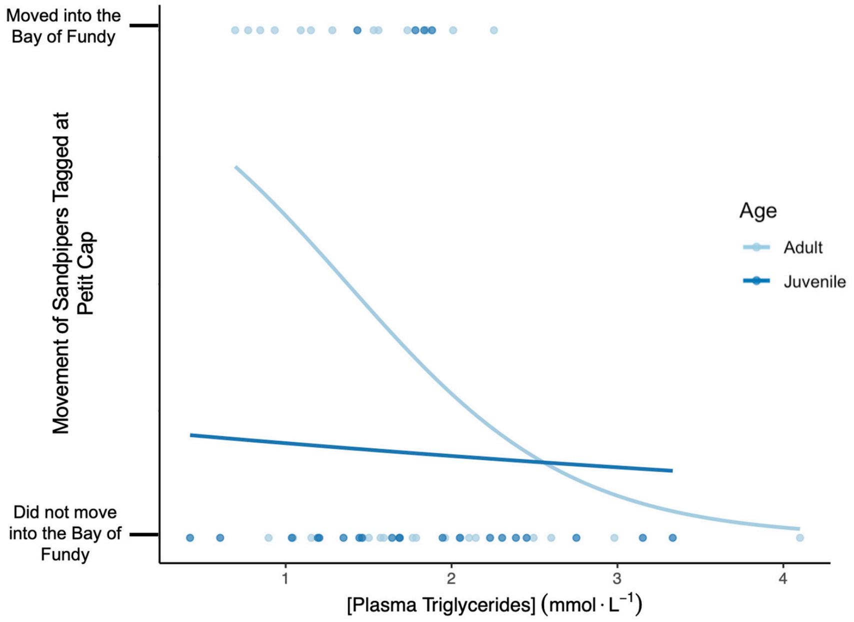

FIGURE 7
Movement decisions of tagged adult (light blue) and juvenile (dark blue) Semipalmated Sandpipers at Petit Cap (Northumberland Strait) relative to their corresponding plasma triglyceride concentration (mmol·L^{-1}). The lines show predicted probability of movement for sandpipers tagged at Petit Cap into the Bay of Fundy dependent on TRIG concentration. Statistical results are provided in Table 5.

Wichmann et al., 2004). Predator presence, largely attributable to the return of nesting Peregrine Falcons (*Falco peregrinus*) in the region, has been shown to affect sandpiper movement and habitat use (Sprague et al., 2008; Dekker et al., 2011), resulting in more energy expended in over ocean flocking during periods when they should be roosting (Dekker et al., 2011).

Among birds tagged at Petit Cap, those with lower TRIG levels were more likely to move into the Bay of Fundy, remaining there until they resumed their migration. Although there was no statistical interaction with age, this result was primarily driven by adults, with little evidence in juveniles, probably because juveniles in general were less likely to move into the Bay of Fundy (Linhart et al., in press). It is possible that sandpipers that were gaining weight less efficiently (as shown by lower TRIG levels) on the Northumberland Strait chose to move into the food-dense Bay of Fundy. Alternatively, this result could be an artifact of capture timing relative to migration strategy. Theoretically, some birds could have been captured during a brief stop on the Northumberland Strait while en route to the Bay of Fundy, and therefore may not have begun trying to refuel. However, if this was true we should have seen more tagged sandpipers moving into the Bay earlier in the season, when the bulk of arrivals would have happened. Linhart et al. (in press) found no evidence of this, and there was no effect of day of year in our analysis. Further, the Strait and Bay are only 40–50 km apart, making such intermediate stops unlikely. We therefore suggest that birds may be making decisions about whether to move based on success in refueling. Lyons et al. (2008) compared TRIG and BOHB values between sites at different migratory stages and found substantial differences in both metabolites, but they did not include movement between regions in their study. To our knowledge, our study is the first to detect a relationship between fattening rates, as measured by plasma triglycerides, and habitat selection decisions by individual shorebirds. Although this relationship needs additional study, it suggests that individual Semipalmated Sandpipers may vary in their ability to gain weight efficiently in particular habitats, and those that cannot refuel adequately may recognize this and adjust their habitat use.

5 Conclusion and conservation implications

The Bay of Fundy is one of the most important fall shorebird staging sites in the Atlantic Flyway and has been the focus of migratory shorebird conservation efforts for decades. Our work highlights the importance of conserving less recognized staging sites throughout Atlantic Canada. Not only are these sites outside the Bay used by a portion of the staging Semipalmated Sandpiper population (Linhart et al., in press), they offer a suitable prey base that may even allow birds using them to fatten more quickly than those staging in the Bay of Fundy. We also found that although juvenile sandpipers tended toward broader dietary niches, there were no differences in TRIG values, and by extension fattening rates, between the ages. This suggests juveniles that are using a more diverse prey base are still able to gain weight as effectively as adults. Additionally, the higher BOHB values we recorded in juvenile birds suggests they are possibly fasting more or expending more energy than adults, which aligns with the idea that juveniles are sampling more sites than adults while staging in Atlantic Canada (Linhart et al., in press) and as a result need to remain in the region slightly longer (Mann et al., 2017; Linhart et al., in press). Most notably, our plasma triglyceride and movement results suggest that individual sandpipers may make decisions about movement and habitat use based on their physiological state.

Over the past 40 years, shorebird habitat conservation in North America has focused on identifying and protecting important shorebird breeding, staging, and non-breeding sites where importance is typically defined by bird abundance. The Western Hemisphere Shorebird Reserve Network (WHSRN) has identified and nominated 112 sites in 18 countries throughout the Americas to date (WHSRN Sites, 2021) and has been extremely successful at raising awareness for shorebird conservation and protecting important habitat. However, to qualify at the lowest level, a site has to support a least 1% of the biogeographic population of a species or 20,000 shorebirds annually. Given resource limitations and the need to target sites with the biggest conservation payoff, thresholds like this are necessary. However, this means that the value of smaller sites may not be recognized, leaving them vulnerable to a variety of threats such as coastal development and human disturbance. Results from our study, coupled with those of Linhart et al. (in press), suggest that small sites in Atlantic Canada like those in the Northumberland Strait are indeed important to Semipalmated Sandpipers. This appears to be especially true for juvenile sandpipers, which appear to make use of a greater number of sites during staging (Linhart et al., in press) and potentially throughout migration (Van Brederode and Roersma, 2020). Our results point to the importance of conserving these sites. We suggest that in the future shorebird habitat conservation actions should consider the importance of smaller sites with multiple habitat types to support Semipalmated Sandpipers and other shorebird species during staging in Atlantic Canada and throughout the Western Hemisphere.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation. Movement data have been made available on Movebank (Movebank ID 2454115135).

Ethics statement

This animal study was reviewed and approved by the Mount Allison University Animal Care Committee under guidelines from the Canadian Council on Animal Care.

Author contributions

DH, JP, and RL conceived the study idea. RL wrote the manuscript and analyzed the data with substantial input from DH. DH and JP contributed to the resources and funding. All authors collected the data and assisted in editing the manuscript.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.1059005/full#supplementary-material

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Gender bias and inequity holds women back in their conservation careers

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The planet is facing climate and biodiversity loss crises that impact all of humanity and yet globally, women remain underrepresented in leading solutions to these urgent conservation challenges. As one of the world's largest conservation non-profit organizations, The Nature Conservancy (TNC) provided a large case-study for understanding inequity for women in the conservation sector. In 2018, all 1,789 conservation and science staff at TNC were surveyed to understand how they are able to develop their careers and contribute to conservation research and decision making. Of the 904 responses (490 men and 414 women), results show that men influence conservation and science decisions more than women; women face multiple barriers across their conservation careers due to gender bias; women experience sexual harassment and discrimination, as well as fear retaliation more than men; and men reported the sector as a more equitable and favorable place for women than women themselves experienced. Our data demonstrates that gender equality (equal representation of men and women) does not automatically mean that women no longer face systemic inequity and that intersectional issues such as race, location and caring responsibilities can all make it even more difficult for women to excel. Respondents drew from experiences across their conservation careers, to suggest how the conservation sector could address these issues. Based on our findings, we recommend practical ways the conservation sector can improve gender equity, including *via* workplace and cultural change measures, as well as changes to recruitment, pay transparency, and career development policies.

KEYWORDS

conservation, women, climate change, gender, leadership, science, bias, biodiversity loss

1 Introduction

Despite global emphasis on the benefits of, and need to, achieve gender equity across the sciences, progress remains slow. At current rates it will take generations, if ever, to fully address gender equity for women (Holman et al., 2018; Kuschel et al., 2020). Women are consistently paid less, promoted less often, cited less, as well as less likely to be invited to join editorial boards, research panels, and grant proposals (Ross et al., 2022). Demonstrating this inequality, less than 27% of authors nominated for the United Nations Intergovernmental Panel on Climate Change (IPCC) Special Report on 1.5°C were women (IPCC, 2018). Meanwhile globally, women remain poorly represented, and in some cases completely absent, from climate negotiations (Gonda, 2019). Women have identified multiple intersecting and systemic barriers limiting their participation in the sciences. These include disproportionate family and caring responsibilities and active discrimination against them based on gender, race, and/or nationality (Gay-Antaki and Liverman, 2018).

There are limited published data outlining how conservation organizations consider gender within their own institutions (Jones and Solomon, 2019), and a tendency across the conservation sector to view gender inequity as an issue only for locally based community conservation, primarily in low-income and emerging economies, rather than an issue conservation organizations themselves need to address (Westberg and Powell, 2015; James et al., 2021). Despite this, evidence shows women are under-represented and/or excluded from decision making within organizations focused on conservation, climate, and natural resource management, as well as in research and policy-setting contexts (Jones and Solomon, 2019).

Studies across sectors show that women and men perceive the degree to which their organization addresses gender equity differently. Despite evidence of gender gaps, men (and many women) consistently perceive gender inequity is less than women actually experience, and there is often a reluctance by men to acknowledge or reflect on gender bias in their workplaces (Handley et al., 2015; García-González et al., 2019). Without both men and women sharing awareness of the problem of gender bias, making improvements remains difficult (Handley et al., 2015).

This discrepancy between the perceptions of women and men is heightened by intersectional identities. For example, a 2022 study of over 25,000 professionals working in science, technology, engineering, or math (STEM), revealed that white able-bodied heterosexual men (WAHM) experienced better treatment and rewards in STEM when compared with members of all other intersectional categories relating to gender, race, sexual identity, and disability status (Cech, 2022). The study revealed that, as a group, WAHM were more likely to benefit from workplace inclusion, respect, and rewards. Furthermore, this privilege could not be attributed to any other reasons, such as greater work commitment or training (Cech, 2022).

There is evidence that in some STEM fields—such as conservation archaeology in the U.S.—men earn up to 30% more than women; a higher gender pay gap than the U.S. national average (Davis, 2019). Gender salary discrepancies are highest in settings conducive to individual negotiating (Finley et al., 2021), and women are particularly disadvantaged in terms of pay negotiations when there is limited transparency around pay (Bennedsen, 2019). Women also experience a wage penalty for motherhood, circumstances that continue throughout their careers (Gangl and Ziefle, 2009; Gough and Noonan, 2013). In contrast, men earn a wage premium for fatherhood, especially high-earning men (Glauber, 2018).

Studies in the conservation sector have shown that long hours and travel are often expected (especially if people wish to have influence and advance their career), and this is harder for women given their traditionally greater share of caring responsibilities (Campos-Arceiz et al., 2013; Jones et al., 2020). Other research also demonstrates that traditional gender roles are commonly reflected within conservation organizations (Mahour, 2016). For example, women often occupy administrative roles (with a focus on so-called "soft skills"), while men are over-represented in positions of leadership, risk-taking, or those that involve travel and fieldwork (Westberg and Powell, 2015; Jones and Solomon, 2019). This often leaves women with lower status, lower paid roles, and leads to them being sidelined as scientific experts and/or decision-makers (CohenMiller et al., 2020; Westberg and Powell, 2015).

Across all scientific disciplines and career stages, women are less likely to be recognized for their scientific publications. Their work is often not appreciated, not known, as well as being often ignored (Ross et al., 2022). Such structural disadvantage is evident across science and conservation institutions, including The Nature Conservancy (TNC)—the focus of this paper. An analysis of rates of scientific publishing at TNC found that only 30% of authors were women (James et al., 2022).

This paper builds upon existing literature about gender inequity in the conservation sector by examining perspectives from over 900 conservation professionals at The Nature Conservancy. The Nature Conservancy is one of the largest conservation non-government organizations (NGO) in the world, with an annual revenue of over $USD 1.2BN and approximately 4,000 staff (The Nature Conservancy, 2021a). We drew from this large pool of conservation employees to undertake a large-scale study into how women and men experience working in the conservation sector (see Box 1). Respondents drew from their experiences across their conservation careers, often referring to experiences in different organizations, locations, roles, and career stages. By identifying how women and men participate in decision-making and build their careers, we were able to identify significant areas that limit women across the conservation sector. Our recommendations are informed by these rich quantitative and qualitative data and are designed to support conservation and climate organizations to acknowledge the problem and take steps to address gender inequity (e.g., James et al., 2022).

BOX 1 | The case of The Nature Conservancy

The Nature Conservancy (TNC) was founded in the United States of America (U.S.) in 1951. It began as a land trust, originally with the intent of setting aside land for long-term protection and research (Adams, 2006). Its inception is interconnected with the broader U.S. conservation movement in the 1900s, which was led primarily by white men with a focus on buying and protecting land for biodiversity conservation and nature-based activities, including birdwatching, hiking, hunting, and fishing (Taylor, 2016). The conservation movement overall, is associated with processes of dispossession and social exclusion of both women and First Nations people across the U.S. (Zurba et al., 2019). Although still headquartered in the U.S., and with operations in all 50 states, TNC has extended its reach globally, to Latin America and the Caribbean in the 1980s, the Asia Pacific region in the 1990s, the African continent in 2007, and by 2014, the organization had also established in Europe. TNC now also focuses on global conservation issues across more than 70 countries, including climate change and biodiversity loss, with an increasing focus on people and social inclusion (The Nature Conservancy, 2021b). Despite the apparent globalization of the organization, conservation and science research and publications continue to be predominantly authored by men located in the U.S. (James et al., 2022). In 2019, an internal investigation revealed that women employees believed the organization's male-dominated culture made it difficult for women to thrive (Coleman, 2019). Over time, and with changing leadership, including appointment of TNC's first woman CEO in 2019, TNC has increasingly underscored the importance of gender equity both in the workplace and the conservation work (The Nature Conservancy, 2021b).

TABLE 1 Multinomial logistic regression analysis *p*-values indicating significant differences ($p < 0.05$; in bold) for the Likert question responses between women and men. "Agree" and "Strongly agree," and "Disagree" and "Strongly disagree," were aggregated to give "combined agree" and "combined disagree." Of the 32 Likert scale survey questions the difference in responses was significant for combined agree and/or combined disagree for 27 of the 33 questions.

Likert scale survey questions	Combined agree response	Combined disagree response
Q3 At TNC, the conservation/science staff in my business unit/program are at least 50% women	0.9848	0.5984
Q4 At TNC, I feel that I have an influential role in deciding the research/conservation priorities for my business unit/program	**0.0028**	0.1106
Q5 At TNC, I feel that overall women have an influential role in deciding the research/conservation priorities for my immediate business unit/program	**0.0015**	**0.0019**
Q6 At TNC, my supervisors regularly share ideas/seek my input when making strategic decisions for my business unit/program	0.1421	**0.0054**
Q7 At TNC, I have enough opportunity to influence science research/conservation priorities for my program/business unit	**0.0016**	0.1912
Q8 At TNC, I have made important contributions to shaping the Shared Conservation Agenda	**0.0166**	**0.0353**
Q9 At TNC, career/professional development opportunities are equally available to women and men in my team	**0.0001**	**0.0010**
Q10 At TNC, I am generally aware of opportunities for career enhancement and advancement	0.3154	**0.0054**
Q11 At TNC, I actively pursue opportunities for career enhancement and advancement	**0.0004**	0.4139
Q12 I believe my prospects for career enhancement/advancement at TNC are good	0.6973	0.1031
Q13 At TNC, my supervisor encourages me to apply for more senior roles/stretch projects	0.4145	0.1816
Q14 At TNC, I have a mentor (formal or informal) who helps me develop in my role	**0.0056**	**0.0047**
Q15 I am satisfied overall with my current role at TNC	0.0613	0.2603
Q16 I feel like I am realizing my full potential at TNC	**0.0220**	**0.0421**
Q17 At TNC, women have the same opportunities to advance as men	**0.0000**	**0.0002**
Q18 At TNC, if I took leave of absence for 6 months or more to handle a family matter, it would negatively impact my position at work	0.3694	0.1914
Q19 I am not achieving everything in my career because of balancing family commitments	0.2668	0.5748
Q20 TNC pay policies mean that women have the same opportunities to advance as men	**0.0000**	**0.0002**
Q21 TNC human resources policies and procedures mean that women have the same opportunities to advance as men	**0.0000**	**0.0014**
Q22 At TNC, my gender has not influenced me getting a raise, promotion, key assignment, or chance to get ahead	**0.0020**	**0.0000**
Q23 TNC is doing a good job to improve the role of women in conservation and science	**0.0000**	**0.0007**
Q24 TNC should be doing more to increase gender equity at all levels at TNC	**0.0000**	0.2174
Q25 I would recommend TNC as a great place to work for women pursuing a career in science and/or conservation	**0.0000**	0.2434
Q26 I think staff in science/conservation roles at TNC outside the U.S. have significant influence on setting our global conservation/science priorities for the organization	**0.0056**	0.4111
Q27 I think women in science/conservation roles at TNC outside the U.S. have significant influence on setting our global conservation/science priorities	**0.0098**	**0.0106**
Q28 I think women from outside the U.S. are well represented in science/conservation leadership roles in TNC	**0.0025**	**0.0017**
Q29 I would recommend TNC as a great place to work for women pursuing a leadership position in science and conservation	**0.0000**	**0.0125**
Q31 BEFORE I came to TNC, my gender played a role in me missing out on a raise, promotion, key assignment, or chance to get ahead	**0.0000**	0.0634
Q33 At TNC, I feel supported to raise issues of gender bias (intentional or unintentional) without fear of reprisal	**0.0335**	**0.0000**

(Continued on following page)

TABLE 1 (*Continued*) Multinomial logistic regression analysis *p*-values indicating significant differences ($p < 0.05$; in bold) for the Likert question responses between women and men. "Agree" and "Strongly agree," and "Disagree" and "Strongly disagree," were aggregated to give "combined agree" and "combined disagree." Of the 32 Likert scale survey questions the difference in responses was significant for combined agree and/or combined disagree for 27 of the 33 questions.

Likert scale survey questions	Combined agree response	Combined disagree response
Q34 At TNC, women are just as likely as men to be offered opportunities such as co-authoring a paper or speaking at a conference	**0.0079**	**0.0001**
Q35 At TNC, the overall culture supports women as much as men to advance their career in conservation/science	**0.0000**	**0.0000**
Q36 I have experienced sexual harassment at past conferences or important meetings I have attended	**0.0000**	**0.0437**
Q46 I care for a child/children/other family members which can impact on my ability to work fulltime, travel or work outside of hours at short notice	0.1491	**0.0132**

2 Materials and methods

2.1 Survey design and method

Using our experience across conservation, as well as the social and behavioral sciences, we developed an online survey to collect perspectives on each respondent's involvement in science and conservation decision making, as well as their career satisfaction and opportunities and barriers to career development. Research complied with TNC's Standard Operating Procedures for Research involving Human Subjects and was approved by the University of Queensland Institutional Human Research and Ethics Committee (Approval number: 2018001799).

The survey was designed to understand how respondents felt their gender influenced both their career and their influence in conservation. We focused only on staff working in conservation and/or science positions (excluding staff in other functions such as human resources, marketing, and information technology) as part of specifically understanding trends across the conservation sector. A total of 33 questions were asked to elicit personal reflections and experiences using a five-point Likert scale (refer to Table 1 for the questions). In addition, open-ended questions asked respondents to provide context about their experiences. While the survey was only sent out in English, before being circulated, the survey was tested three times with respondents from different locations, genders, and primary languages, and was revised where any confusion around the meaning of the questions was encountered (see also Letherby, 2011; Patton, 2015).

TNC Human Resources team generated an email list of all 1,789 staff within TNC who held conservation and/or science positions. All staff on the list self-identified as either male or female as listed in TNC's human resources data (there were no other options available at that time). Although this study lacked available data to shift beyond a binary definition of gender or sex (woman/man, male/female), we acknowledge this does not reflect the lived experience of all staff at The Nature Conservancy, or in conservation more broadly and sexuality or gender identity can greatly impact people's experiences within the workplace (Cech, 2022). Further, we use the term "gender" (grounded in identity) rather than "sex" (grounded in biology) since staff self-report their gender to human resources upon hiring; however, we recognize that only providing two options makes it likely that staff likely reported biological sex even if their gender identity was different.

In October 2018, the online survey was sent through Survey Monkey to the staff email list. To maximize the response rate, it was sent out by the TNC Chief Scientist (the most senior science position within the organization) who encouraged all conservation and science staff to complete it. Gender was not specifically mentioned in the cover letter to minimize the risk of respondents interpreting the survey as "for women" or "for women only," given the common (and often incorrect) assumptions that "gender" is synonymous with "women" (Lau, 2020).

Once survey responses were received, they were sent to a representative in the Chief Diversity Officer's office of TNC who combined them with extra demographic data, including location and gender. All data were kept confidential, and responses were anonymized to prevent anyone being identified.

2.2 Analysis

Data analysis began with descriptive quantitative analysis of the online survey responses, including summaries of the sample and the measures, along with basic graphic analysis.

To identify significant differences between women's and men's answers to the Likert scale questions (Qs 3–29, 31–36, and 46), we aggregated "strongly (dis)agree" and "(dis)agree" into combined "agree" and "disagree" responses, respectively. We then ran multinomial logistic regressions with agree/disagree as the response variable, and gender as predictor for each question (Venables and Ripley, 2002). All analyses were run using R (R Core Team, 2021). Significance was given by *p*-values.

Respondents were invited to provide open-ended free text responses to questions relating to the following: "*Please share any personal reflections about how you have been treated in relation to your gender*" and "*Do you have any recommendations to ensure women are included in science and conservation strategy and practice at TNC*?" Answers from these open-ended questions were also analyzed to provide context to the quantitative data. The lead author read each response to gain an overall familiarization and understanding of the data. Each response was then assigned a broad theme and crosschecked by two other authors.

TABLE 2 Representative quotes associated with the four themes that emerged from our analysis. Quotes were drawn from two open-ended survey questions: Q40 Please share any personal reflections about how you have been treated in relation to your gender [N = 402: 225 (54%) women and 233 (36%) men] and Q37 Please list the top three issues/ideas your organization could address to ensure women are included in science and conservation strategy and practice at TNC [N = 485: 252 (61%) women and 233 (48%) men].

Respondents' experiences and recommendations to address gender inequity in conservation (representative quotes)
Theme 1: Men influence conservation and science outcomes more than women
Personal experiences
R315 (woman): There are many situations where it is assumed that women will go along with whatever men want to do, even if what men want to do is counter to plans that a team has originally discussed and decided upon. I have encountered a number of situations where men "close ranks" with one another to push through an agenda or idea, without a clear decision-making process, or without any regard to what women on the team would like to see happen
R485 (woman): . . .even as I've moved into a more senior management role in my business unit, I still notice that a disproportionate amount of the administrative/logistics/fixing problems work falls to me and many of my female colleagues and I just do not have the same time and space to stay current on trends in conservation science, think strategically, develop new projects and proposals, etc. as my male colleagues. It is exhausting. . ., especially when trying to balance strategic thinking for work with administration for work, with taking care of my family with taking care of myself
Recommendations
a) Greater integration of gender equity into conservation work
R256 (woman): Prioritize gender in our own conservation work and outcomes
R461 (woman): . . .ensure integration of gender equity lens into all strategy and practice implementation
b) Working with women from early career
R102 (woman). . .capture lessons learned from women that have been at TNC a long time to learn what works and does not work to pass on knowledge to more junior women
R076 (man): . . .Promote science/conservation as a career choice for women, highlighting the work of women at TNC. . .
c) Connecting women and providing them with what they need to succeed
R073 (woman): . . .It is not enough to invite women to the table to be included in science and conservation strategy, you have to rebuild the table to have new voices heard and respected
R518 (woman). . .Ask women in science and conservation what they need to be better supported to contribute to their full potential and then provide it
R076 (man): . . .provide networking opportunities for women new to TNC to find mentors in science/conservation
d) Ensuring women are represented
R124 (man): . . .Strive for equal gender representation on project teams
R199 (woman): Including an equal amount of women speakers and men speakers at conferences and web calls
R499 (woman): I believe that when I am in a meeting with all men, I'm automatically viewed as having the least "power" in the room to make decisions. Men in positions of power have sometimes rebranded my ideas as their own or taken credit for my work. . .
Theme 2: Women face gender bias and multiple barriers across their conservation careers compared with men
Personal Experiences
a) Gender bias is faced across career
R010 (woman): As a woman I have received more pressure to be outstanding, compared to my male colleagues (my supervisors usually expect/ask more from me than from men colleagues). In spite of this, my performance has not been recognized in the same way and it ends up being compared with the performance of my male colleagues, of whom less is demanded
R022 (man): I have always felt easily included in the engineering and science worlds as a male. No barriers were ever experienced due to gender
R149 (woman): . . . my observation is that women are generally 5–7 years behind men in career and salary advancement . . . because men have been cultivated to move into higher job grade roles at younger ages than women
R308 (woman): Senior leadership does not give credit where credit is due and tends to credit the male employee involved in a successful project, regardless that most of the work is done by a woman (behind the scenes)
R314 (woman): I feel like a man doing my job with my quality of work would have advanced more rapidly and been more valued and recognized for their contributions that I have been as a woman. . .
R314 (woman) . . .My supervisor is female. I think gender bias is a cultural issue, not just something men do to women. Female supervisors can hold female employees down too
b) Women face extra barriers as parents/carers
R627 (woman): There are bigger societal issues that TNC cannot alone break—the fact that I, and most other women I know, still do 90% of the childcare but are expected to travel for work just like men, or that lack of good childcare can really limit working/summer hours. Those are not TNC's fault or responsibility to change, but it is important to recognize that these things are still out there and pose obstacles to talented female scientists
R561 (woman): As a woman and as a mom, I do sometimes miss out on opportunities because my family is more important, and I cannot make every networking opportunity to boost my career building skills. . . As compared to fathers.. I think mothers have a difficult time being able to get away to embrace career building opportunities

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TABLE 2 (*Continued*) Representative quotes associated with the four themes that emerged from our analysis. Quotes were drawn from two open-ended survey questions: Q40 Please share any personal reflections about how you have been treated in relation to your gender [N = 402: 225 (54%) women and 233 (36%) men] and Q37 Please list the top three issues/ideas your organization could address to ensure women are included in science and conservation strategy and practice at TNC [N = 485: 252 (61%) women and 233 (48%) men].

Theme 2: Women face gender bias and multiple barriers across their conservation careers compared with men
R356 (woman): . . . No resources as a mom returning from parental leave. i. e., no Mom's room, meetings were scheduled without breaks and in locations without mom's rooms, requiring me to pump in public restrooms while the meeting rolled on. . .
R286 (woman): My supervisor has asked male colleagues to pursue field activities for activities that he never requested of me, which I presume was because I'm a mom and should stay home with my kids
R218 (woman): I am a new mom of 2 years and I feel the balancing act of family life has put the brakes on any ideas for real advancement on my career, which makes me terribly sad, even as I write this the tears are welling up in my eyes. I love my family and I love my work...
R719 (woman): While not at TNC but during my career I have been directly told that I had been passed over for opportunities because, "Well, you're a mother." As though producing offspring prevented me from being capable or interested in any longer participating in my career, which was fully incorrect. . .
c) Barriers are intersectional
R500 (woman): I think women scientists of color face greater challenges in getting recognition. When I think of it, this has added another dimension of difficulty in being a scientist more so than being a woman, particularly in North America...
R228 (woman): I will tell you now as a middle-aged woman what I experience is being invisible. And I've spoken with lots of accomplished women of my age and instead of them feeling like they are on the top of their game, as they should be given their accomplishments and career, they feel invisible, marginalized and undervalued. Men at my age would be on the top of their game—getting awards, honors etc. Women on the other hand at a certain age are cast aside
R199 (woman): Often people think I am less capable than others since I am a small woman. . .
R392 (woman): I have struggled with the combination of gender and age as a young female. I find it challenging to garner the respect, support and inclusion I believe that I have earned through my work. Older men can create a unit of culture and language that seems very unique to them and hard to penetrate
Recommendations
a) Workplace culture and systems change
R168 (woman): . . . Be cognizant of our culture and work to ensure diversity of leadership styles as well - not working to "fit women in" to the gregarious, often male-dominated personality space
R706 (woman): TNC is really trying hard to create an inclusive environment, which I really appreciate. However, in some areas it is still an old-men's club, especially in science and conservation. At least once a month I still have to hear comments from men that I find sexist. For example, "this is a job for somebody that does not have a kid at home so has more time" (men also have children, but their time away from work is never questioned), or "given that you just had a kid, you are doing a great job" (am I being measured to a different standard?), or "here are my girls!" (from a male supervisor to a team of female researchers). I think men do not realize these comments are demeaning and can affect our self-confidence. Women normally do not report these because we think these are normal, or "I know he did not mean it the way it sounded"
R063 (woman): . . .Better institutionalize and value less hierarchical and more shared leadership and decision-making
R034 (woman): . . .Continue to build leadership opportunities for women - ensuring that women from outside the US can access these opportunities
R142 (woman): ...Keep highlighting women's conservation and science successes and leadership and promote more blogs and articles from women in conservation and science...
R275 (woman): . . .Get more women on the Executive Leadership teams and as Conservation and Science Directors
R612 (woman): . . .Do not just offer leadership training and develop your TOP female staff—there needs to be a much better program of mentorship, support, and development for entry- and mid-level female staff to keep them in the pipeline to become leaders
R632 (man)...Promote mentoring relationships among women scientists and conservation staff; creating a network of women and men to help advance women in science and conservation with-in the organization
R083 (woman): TNC has been very good to me, particularly in that it has allowed me to balance work and family life with flexible hours. That has been extremely important as I juggle kids, school, elderly parents, etc. . .
b) Addressing parenting/caring barriers
R620 (woman): As long as women continue to make less than men in the U.S., more women than men will be default primary caregivers for children. Many of us invest more time in the career that makes more money for our family
R136 (woman): . . .Providing sufficient post-natal leave and subsidizing child care would go a long way towards keeping women with children in the workforce
R168 (woman): . . . set a high standard no matter what the country's laws are—for both maternity and paternity leave
R612 (woman): Change the culture of MORE IS MORE so that people who are balancing caregiving and work roles are not automatically at a disadvantage and punished for their choices or responsibilities. . .
R088 (woman) . . .I would like to see more women role models at TNC, particularly those who are combining family and career. . .What was not visible to me was the more senior women role models who were successfully combining family and career to know that it was possible

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TABLE 2 (*Continued*) Representative quotes associated with the four themes that emerged from our analysis. Quotes were drawn from two open-ended survey questions: Q40 Please share any personal reflections about how you have been treated in relation to your gender [N = 402: 225 (54%) women and 233 (36%) men] and Q37 Please list the top three issues/ideas your organization could address to ensure women are included in science and conservation strategy and practice at TNC [N = 485: 252 (61%) women and 233 (48%) men].

Theme 2: Women face gender bias and multiple barriers across their conservation careers compared with men
c) Improving gender equity in an intersectional way
R461 (woman): . . . Recognize and call out the intersectionality of gender equity with race, class, able-ism, sexuality, education, etc. (provide learning opportunities, seek out guidance from other organizations doing it better, etc.)
R690 (woman): ...Provide trainings that reveal unintentional bias to all genders of staff-with regard to hiring, negotiation, salary expectations, promotion requests, career opportunity creation and expectations, presentation styles, and other aspects known to commonly suffer from unintentional gender bias. . .
R168 (woman): . . . Make sure we're taking into account women of color specifically in our hiring process—at all levels! Seek out applicants ("no woman/woman of color applied" is not good enough). . .
R703 (woman): . . .Always consider gender and racial make-up when putting together a panel, a working group, a committee. What does this snapshot say about our organization?
R155 (woman) . . .Make sure when international women are employed at TNC that their voices and perspectives are welcomed and encouraged rather than expecting assimilation
Theme 3: Women experience sexual harassment, discrimination, and fear retaliation
Personal Experiences
R742 (woman): With a past employer, in working with a conservation group, I was called Barbie and was not taken seriously in my role
R742 (woman): I have been told by a past employer that I should not pursue a PhD because I have children and they would not support me
R235 (woman): As a female scientist, I know the unconscious bias is against me when I challenge higher level directors. This has been established in the scientific literature. When women raise concerns and challenge superiors, they are punished in their careers, while men are promoted
R149 (woman): . . . I feel like there is no forum. . .where these problems can be safely discussed without being labeled negatively or risk further career advancement delays
R541 (woman): There are few enough of my white male colleagues that are skilled in the area of differences and bias that I often feel like a lone voice raising issues when I see them and can at times feel pretty alienated
R155 (woman): Our society teaches girls and women to "please, perform, perfect" so the vulnerability it requires to speak up, take a risk, etc. is much greater for women than for men
R035 (woman): Once you internalize the subtle, pervasive cultural messages about what you as a woman can/cannot do at work, you start to fall behind when you hesitate or flounder as male colleagues step forward
R345 (woman): It just feels like we are happy with how far we have come, but as women we still keep our mouths shut to avoid rocking the boat
Recommendations
R352 (woman):. . .TNC wants to encourage women to be empowered but I think the generic experiences we have all had in our life and careers affects individuals' self-esteem and holds us back from speaking up and getting involved. Also women have different psychological, emotional and health reasons that affect their work which we do not feel comfortable talking about with our senior male managers. It would be great to talk in a confidential and safe place about all the issues that are holding us back
R142 (woman): Promote communication/decision styles that encourage more listening and discourage dominating a conversation. Give people more ways to provide input—like this survey, facilitated group conversations or presentation polls—to ensure you are hearing from a more diverse group
R697 (woman): Ask us to participate. Encourage us to participate and support our participation. Be respectful of the opinions that we offer
Theme 4: Men overestimate gender equity for women in conservation
Personal experiences
R495 (man): I did not think this was an issue. Do we not have qualified female scientists on staff?
R085 (man): I have not seen a gender bias in science and conservation strategy and practice
R002 (man): I believe that the attention to gender issues at TNC is going beyond what is necessary. We are already doing well
R295 (man): It's all we hear about. I don't care about men versus women... it's about qualifications to do the work
R220 (man): . . .Having worked for other employers, I feel that TNC goes way above and beyond. Sometimes its overboard and actually does little to further the cause
R815 (man): I'm starting to feel like there is a conspiracy against me...
Recommendations
R068 (man): . . . design teams to be balanced in terms of gender
R461 (woman): . . .make some basic practices mandatory for all staff [e.g., no "manels" (all male panels)...or papers, meetings, teams, etc., external or internal. . .ensure integration of gender equity lens into all strategy and practice implementation

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TABLE 2 (*Continued*) Representative quotes associated with the four themes that emerged from our analysis. Quotes were drawn from two open-ended survey questions: Q40 Please share any personal reflections about how you have been treated in relation to your gender [N = 402: 225 (54%) women and 233 (36%) men] and Q37 Please list the top three issues/ideas your organization could address to ensure women are included in science and conservation strategy and practice at TNC [N = 485: 252 (61%) women and 233 (48%) men].

Theme 4: Men overestimate gender equity for women in conservation
R500 (woman): . . . having a supervisor who recognizes the unique opportunity and challenges that come with being a woman in science has been incredibly helpful in my career. These people have pushed me and put me up for opportunities without any hesitation and that has made all the difference
R073 (woman): . . . Stop focusing on just the % of women in the organization and instead work on how they are trusted, believed, and held up in the organization. . .
R618 (man): Continue to educate men to increase awareness and understanding of unearned privilege, including tips and practical tools for correcting unconscious bias. . .
R308 (woman): Moving away from women having to learn from men to be in leadership positions and focusing more on the men doing things differently to help change the entrenched culture bias
R217 (man): . . . adopt policies that make pay rates transparent to all. Research shows that when pay rates are transparent, employees are better empowered to assure they are receiving fair and equitable pay

2.3 Response rate

In 2018, there were 1,789 total Conservation and Science staff: 44% (781) women and 56% (1,008) men. We received a total of 904 responses to the survey: 414 (46%) women and 490 (54%) men), meaning a response rate of 53% for women and 49% for men. Respondents were also categorized by the region where they were physically located. Most respondents, 741 (82%), were in North America with the remainder 163 (18%) in Asia Pacific, Africa, Caribbean, Latin America, and Europe. In addition, a total of 402 respondents [225 (54%) of the women and 177 (36%) of the men] provided written responses to open-ended questions relating to their personal experiences of gender inequity throughout their conservation careers, and 485 respondents [252 (61%) of the women and 233 (48%) of the men] made suggestions for improving gender equity at TNC.

3 Results

We have highlighted the following four themes that emerged from the data, each of which we discuss in sections below:

1) Men influence conservation and science outcomes more than women.
2) Women face multiple barriers across their conservation careers due to gender bias.
3) Women experience sexual harassment and discrimination, as well as fear retaliation, more than men.
4) Men overestimate gender equity for women in conservation.

The results to all quantitative questions, including level of significance based on the binomial logistic regression output *p*-values, are provided in Table 1. In most cases, differences between women's and men's responses were significant or highly significant (Table 1; Supplementary Material S1). Representative quotes associated with the four themes that emerged from our qualitative data analysis are provided in Table 2. Throughout this paper we also include example quotes in italics (including their anonymized ID and gender) to provide further context for each theme.

3.1 Men influence conservation and science outcomes more than women

Overall, women felt less able to contribute to conservation and science than men. This ranged from large goal setting decisions for their organization to more specific conservation decisions for their management unit and immediate team. For example, only 49% of women compared with 65% of men agreed that they had enough influence in determining research and conservation priorities for their program (Q7; Table 1; Figure 1). These data were matched by written responses from women, who frequently described being sidelined, or overlooked, in relation to conservation science work (examples in Table 2).

Women were also less involved in conservation implementation and described the disproportionate administrative responsibilities they were expected to carry out related to project and staff management. For example, 54% of women, compared with just 38% of men, were responsible for providing support to other conservation and research staff (Q1; Figure 2). Such activities significantly restrict time available for conservation and science related work. For example: *. . .even as I've moved into a more senior management role in my business unit, I still notice that a disproportionate amount of the administrative/logistics/fixing problems work falls to me and many of my female colleagues and I just don't have the same time and space to stay current on trends in conservation science, think strategically, develop new projects and proposals, etc. as my male colleagues. It is exhausting. . ., especially when trying to balance strategic thinking for work with administration for work, with taking care of my family with taking care of myself* [*R485 (woman)*] (Table 2).

3.2 Women face multiple barriers across their conservation careers due to gender bias, compared with men

Women reported that their gender had played a key role in restricting their careers in conservation and science. For example, 29% of women reported that before they came to TNC their gender had played a role in them missing out on a raise, promotion, key assignment, or chance to get ahead whereas only 4% of men reported this (Q31; Table 1; Figure 3). This was backed by findings from qualitative data, where women gave examples of the long-term career and salary

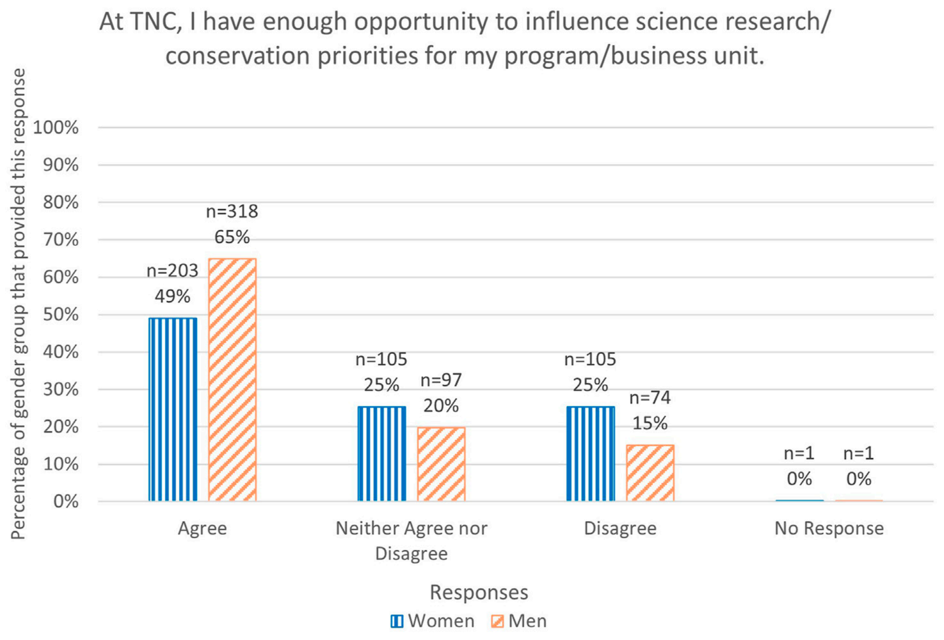

FIGURE 1
Graph of responses to Q7. At TNC I have enough opportunity to influence conservation and science priorities for my program as a percentage of the total number of respondents for each gender.

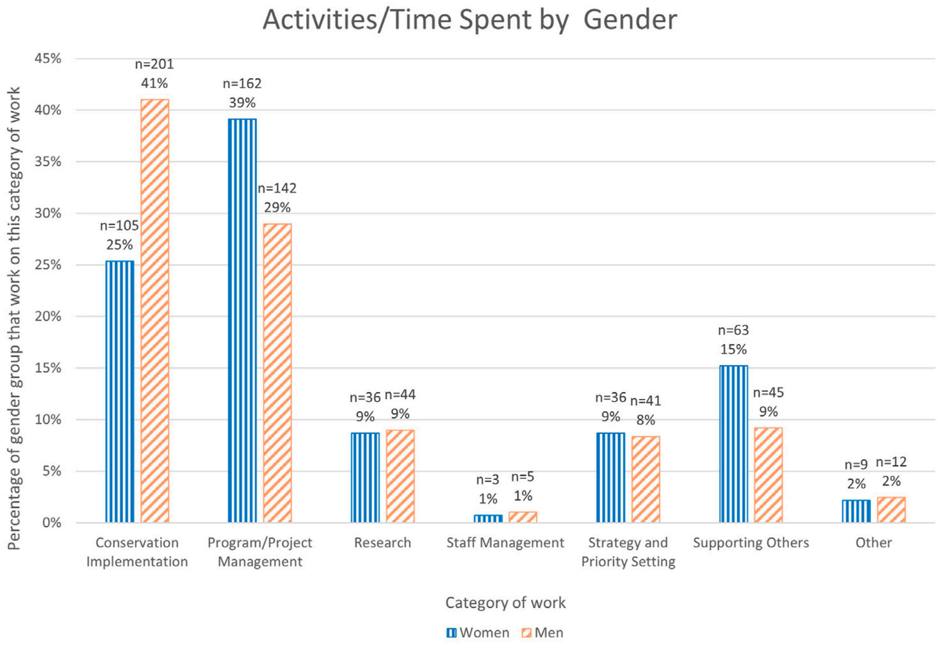

FIGURE 2
Graph of responses to Q1. Is your role predominantly? (Chosen from a drop down list). As a percentage of the total number of respondents for each gender.

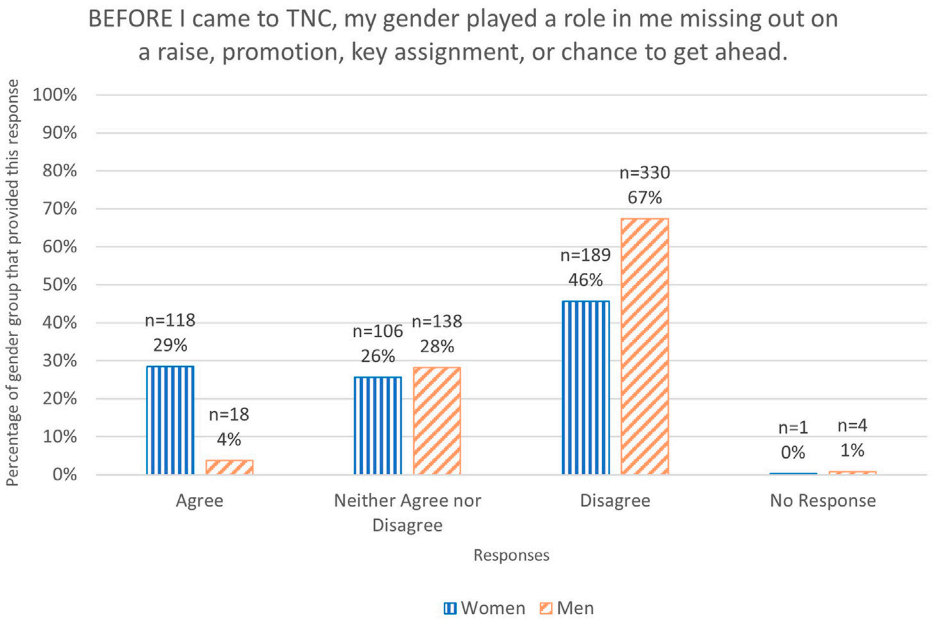

FIGURE 3
Graph of responses to Q31. BEFORE I came to TNC, my gender played a role in me missing out on a raise, promotion, key assignment, or chance to get ahead. As a percentage of the total number of respondents for each gender.

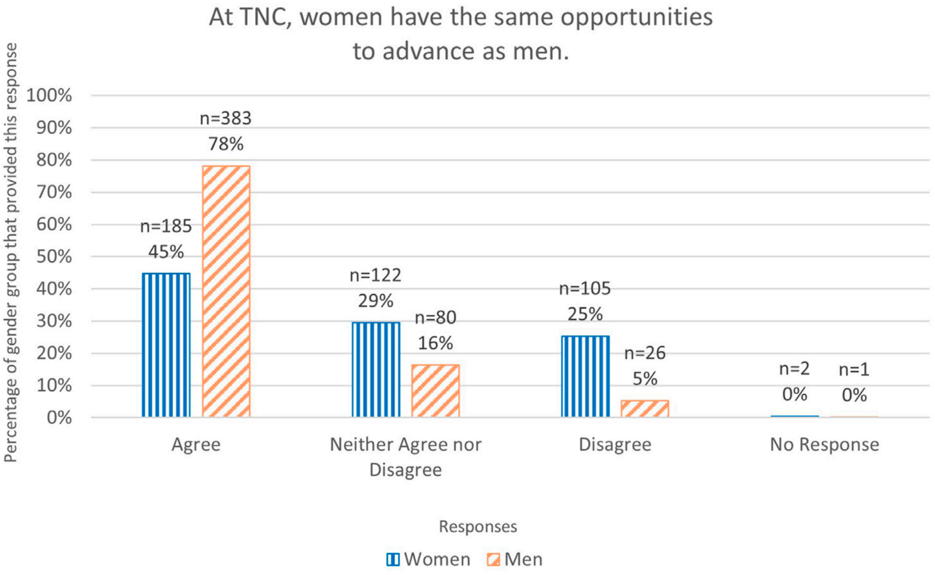

FIGURE 4
Graph of responses to Q17. At TNC, women have the same opportunities to advance as men. As a percentage of the total number of respondents for each gender.

outcomes of this trend. *I feel like a man doing my job with my quality of work would have advanced more rapidly and been more valued and recognized for their contributions than I have been as a woman…[R314 (woman)]* (Table 2).

Women also reported that they did not have the same opportunities in their careers as men (Figure 4) and that the expectations placed upon them were higher compared to their men counterparts. Various barriers were cited at all career stages from early career to senior leadership (representative quotes in Table 2). In stark contrast to the experiences of inequity cited by women, nearly all men commented that gender had not held them back or ever been an issue for them. *I have always felt easily included in the engineering and science worlds as a male. No barriers were ever experienced due to gender [R022 (man)]* (Table 2).

This disadvantage was not associated with a lack of effort by women in pursuing career advancement and leadership opportunities. For example, 65% of women noted they actively pursued opportunities for career enhancement and advancement, compared with 52% of men (Q11; Table 1). Despite this, women described career pathways and models of leadership as being largely defined by men and subject to entrenched gender bias. Respondents highlighted that cultural change was needed in conservation, including support for a diversity of leadership styles, as well as mentoring, sponsoring, and championing women across their careers. *Be cognizant of our culture and work to ensure diversity of leadership styles as well—not working to "fit women in" to the gregarious, often male-dominated personality space* [*R168 (woman)*] (Table 2).

Our data revealed that both men and women believed that family and care commitments could negatively impact their careers. Both genders (30% of women and 28% of men), for example, felt that they were not achieving everything in their career because of seeking to balance family commitments (Q19; Table 1). And 42% of men and 48% of women felt that if they took a leave of absence for 6 months or more to handle a family matter, it would negatively impact their position at work (Q18; Table 1). Furthermore, similar percentages (42% of women and 46% of men) agreed that care for a child/children, or other family members would impact their ability to work fulltime, travel, or work outside business hours at short notice (Q46; Table 1).

So, although both men and women felt that care commitments could impact their career, qualitative data highlighted some of the specific ways in which gender-defined roles including caring and parenting impact women disproportionately. These included, lack of financial support (parental leave), or a lack of structural support such as breastfeeding areas for women returning to work. Assumptions that women returning to work would not be capable or interested in traveling, attending meetings and workshops, or undertaking field work was cited as another challenge (Table 2). The weight of such inequalities bears down on women, with several women describing the stress of balancing the needs of a family with a strong desire to advance their careers. In responding to these challenges, respondents made suggestions that included setting high standards on caring leave policies across countries, making equitable pay for women a reality, tailoring specific support for mothers, flexible working hours, and the recognition that societal norms mean women have disproportionate caring responsibilities.

Respondents also noted that women experience barriers in their conservation careers due to multiple intersecting factors, including race, ethnicity, age, physical abilities, and geographic location. For example, only 8% of women and 14% of men felt women from outside the U.S. were well represented in science/conservation leadership roles in TNC (Q28). Women with intersectional identities described various experiences of unconscious bias and discrimination during their conservation careers. Respondents offered rich suggestions on how to improve gender equity in an intersectional way. These related to training for leaders in bias and privilege, recruitment programs and quotas, mentoring, and sponsorship.*. . .Always consider gender and racial make-up when putting together a panel, a working group, a committee. What does this snapshot say about our organization?* [*R703 (woman)*] (Table 2).

3.3 Women experience sexual harassment and discrimination, as well as fear retaliation, more than men

Women also reported higher rates of sexual harassment and discrimination across their careers in conservation, with 15% of women compared to just 2% of men, reporting that they had experienced sexual harassment at conservation related conferences or important meetings (Q36; Table 1).

There also continue to be barriers for women in speaking out about diverse forms of gender-based discrimination and harassment, with 18% of women compared to 6% of men, describing not feeling supported to raise issues of gender bias (intentional or unintentional) without fear of reprisal (Q33; Table 1). Women commented that they often felt that there was no safe mechanism to raise issues and that they did not feel supported to do so without fear of retaliation. They also felt that often managers were not skilled in understanding or addressing issues of discrimination. Some women reported workplace cultures that actively silenced such problems. Women also expressed that gender norms are pervasive across society, leading women to internalize and/or privatize these structural barriers as personal problems best managed individually (Table 2).

3.4 Men overestimate gender equity for women in conservation

By far the most significant differences between men and women across the survey related to how well respondents thought gender and inequity was being addressed in conservation, and how supportive they thought their workplace was for women. Across all issues, from women's influence and leadership in conservation to work culture, career advancement and pay, men perceived the conservation sector as significantly more equitable than how women actually experienced it. For example, only 48% of women compared with 74% of men, indicated that human resources policies and procedures supported equal opportunities for women (Q21; Table 1; Figure 5). When asked if they thought policies and procedures supported equitable pay, 63% of men compared with just 32% of women thought there was equity (Q20; Table 1). Furthermore, 79% of men and only 58% of women, felt that the overall culture of their organization supports women as much as men to advance their career in conservation/science (Q35; Table 1). Overall, 78% of men compared with just 44% of women, felt that women have the same opportunities to advance as men (Q17; Table 1; Figure 5). In addition, 82% of men compared with only 64% women, believed that women had an influential role in deciding the research/conservation priorities for their programs (Q5; Table 1) with one man stating: *I did not think this was an issue. Do we not have qualified female scientists on staff?* [*R495 (man)*] (Table 2). The trend continued, only 56% of women compared with 78% of men felt that their organization was doing a good job to improve the role of women in conservation and science (Q23; Table 1). This is reflected in the divergent experiences described by women and men. For example, some men felt that the focus on gender within their organization had gone too far, with adverse outcomes for the organization and themselves: *. . .Having worked for other employers, I feel that TNC goes way above and beyond. Sometimes it is overboard and actually does little to further the cause* [*R220 (man)*] (Table 2).

Regardless of these findings, most respondents, although still significantly more men than women (91% of men and 78% of women), would recommend their organization as a great place to work for women pursuing a career in science and/or conservation (Q25; Table 1). This figure dropped to 63% of women and 85% of men for a *leadership* position (Q29; Table 1). These findings were backed by other questions, with 73% of women compared with 50% of men,

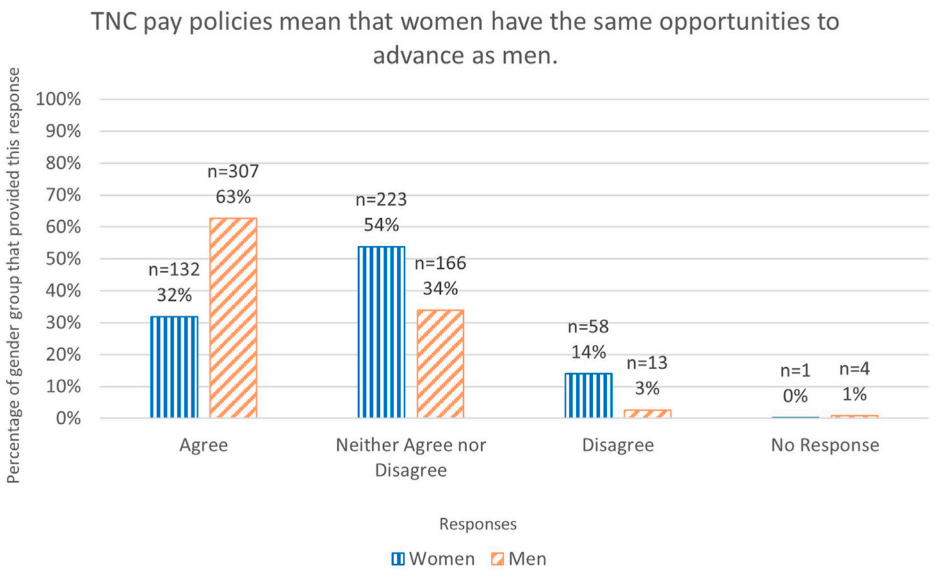

FIGURE 5
Graph of responses to Q20. TNC pay policies mean that women have the same opportunities to advance as men. As a percentage of the total number of respondents for each gender.

reporting that their organization should be doing more to increase gender equity at all levels (Q24; Table 1).

Several women respondents highlighted that society/sector wide inequity was pervasive and appreciated the efforts of their organization in addressing gender bias and inequity. Suggestions from respondents to further address gender bias included balancing gender on teams/panels/workgroups, trainings on gender bias (including unconscious bias), going beyond gender diversity to true gender inclusion, provision of support for early career women scientists, as well as the promotion of diverse leadership styles (so women do not have to fit into "male culture" to succeed) (Table 2).

4 Discussion

The conservation sector has passionate, ambitious, and committed individuals who want to make meaningful contributions (Pienkowski et al., 2022). But many people seem unaware of how gender inequity impacts both science and conservation efforts as well as individual's career progression. The fact that only 44% of women, but 78% of men think that women and men have the same opportunity to advance in their conservation careers, reveals a significant problem. Men's lack of awareness may be compounded by the reluctance of women to discuss discrimination they experience. Significantly, 18% of women reported fearing reprisal if they raised concerns about discrimination or harassment; other sectors have shown this fear is justified. There is evidence that situations often get worse for women when they speak out in the workplace (Rudman et al., 2012; Gianakos et al., 2022).

Our survey revealed that women felt less able to access and perform in leadership positions. Several women commented that they felt pressure to fit into culture that did not value a more collaborative style of leadership. Preventing women from progressing into leadership and then leading authentically is not only detrimental for individual women but can also hurt the organization. For example, the largest global study of women in the workplace, conducted across over 400 organizations collectively employing more than 12 million people, demonstrated that women are (a) more likely to be strong leaders that support staff and teams, (b) are more likely to advance diversity, equity, and inclusion efforts, and (c) do the work to speak out against discrimination in the workplace and mentor others (McKinsey, 2019).

Evidence across sectors shows that all people, regardless of their gender, consistently overestimate women's representation, and therefore, general progress towards gender equity. Focusing too much on how gender equity is good or has improved can, perhaps counter-intuitively, stall further progress (Ryan, 2022). In addition, men and women who overestimate progress towards gender equity in their workplaces are more likely to show gender bias in performance reviews: candidates randomly assigned a female name were more likely to be evaluated poorly, recommended to be paid less, and discouraged from seeking promotion (Begeny et al., 2020). Furthermore, studies of traditionally male dominated science fields (i.e., conservation) that have moved towards greatly increasing numbers of women represented, demonstrated that those who thought bias was no longer a problem were most likely to perpetuate gender bias (Begeny et al., 2020).

This is concerning when again, our results revealed that men consistently overestimated gender equity across questions relating to conservation decision making and leadership, and workplace culture and policies. Given that 78% of men thought there was already equal opportunity between the genders, it is likely to be challenging to work on improving it (only half of men thought their organization should do more to improve gender equity, whereas three quarters of women did). Accordingly, we see that raising awareness about existing inequities across conservation is crucial for everyone (not just women).

One way to both highlight inequities and address them is greater transparency for pay, benefits, and career advancement. Only 32% of women compared with around 63% of men felt that pay policies are equitable. There is clear evidence that disclosing salary range on recruitment and publishing pay data closes the gender pay gap. For example, in Denmark, a study of the gender pay gap before and after legislation mandating pay transparency noted that the pay gap closed by 13% (Bennedsen, 2019).

Interestingly, our results show no significant difference between men and women on how family and caring commitments impacted their careers. Given that evidence across sectors shows that women have far greater caring responsibilities both inside and outside the workplace, this may indicate that their organization's approach to flexible work is helpful. However, evidence from our qualitative data and from other sectors shows that women do still typically shoulder most of these caring responsibilities (Knudsen and Wærness, 2008). For example, women, and especially working mothers, do significantly more housework and childcare than working fathers; worldwide women spend 300% more time on unpaid care work than men (OECD Development Centre, 2015; McKinsey, 2019).

Intersectionality recognizes that people are subject to multiple layers of social division and power, including race, gender, age, class, and wealth, which all interact with each other to determine how people can benefit or be disadvantaged in the world (Hill-Collins and Bilge, 2016). This includes recognizing that gender diverse people (including non-binary, trans, and others) experience unique and compounding challenges, some (but not all) of which may align with those experienced by cisgender women, especially when they are perceived by others as women (regardless of their biological sex and gender identity) (Davis and Yeung, 2022). The qualitative answers from our respondents highlighted intersecting issues including race, nationality, location, age, and caring roles that intersected to further impact each woman's ability to influence conservation and build their careers.

For example, across international organizations, inequity can also show up as a lack of representation in leadership and decision making for women outside where the organization is headquartered, such as Europe and the U.S. There was recognition that a dedicated and sustained effort is needed for international organizations to fully include women located outside of the headquartered location. This could include diversity quotas for conservation leadership positions and career development opportunities. Support needs to be deliberate and include dedicated resources such as language translation and travel funds to ensure women can fully participate. These opportunities need to be designed so women are welcomed virtually where travel is unachievable. For example, this study would have been improved if resources had been available to translate our survey instrument into the primary language of all survey recipients. It is also important to note that conservation and science organizations work within countries that have different legal frameworks and minimum requirements for benefits such as paid parental leave. There is opportunity for international organizations to design policies that enable all women, regardless of which nationality they are or country they are located in, to benefit from equitable workplace standards, salary and benefit packages.

Many respondents identified the need for more training; some responses focused on women (leadership skills and mentoring, for example), and some responses focused on men or all staff (training about gender bias, diversity, equity, and inclusion). It is important to note that, focusing on training individual women (or men) rather than addressing inequitable systems and workplace cultures is helpful but insufficient when used as the primary approach to address gender equity issues in the workplace. It is much easier for an organization to focus on offering women extra coaching to take career risks, negotiate, overcome imposter syndrome, and boost leadership skills, rather than addressing the workplace systems and cultures that reward men for risk taking and limited care of their teams, whilst punishing women for the same behavior (McKinsey, 2021). Research suggests that women do not begin their careers with lower ambition or confidence, but that these are eroded by workplace cultures (Ryan, 2022). Therefore, any training to build skills for women must be accompanied by educating men on inequity and how to be better colleagues, as well as having women serve as mentors to men, and making changes to organizational policy and culture which go beyond individuals. The role of training should be to help women thrive within equitable organizations, not to ask them to make further changes and accommodations to survive within inequitable ones.

5 Recommendations

Based on the extensive literature on women and equity in the workplace, the quantitative survey, and over 1,800 suggestions in the open-ended section of the results, we propose a series of recommendations that individuals and organizations can apply to improve gender equity in conservation. These involve continual reviewing and adjusting policies, systems, and norms to create a culture that fully leverages the benefits of diversity, one in which women and all employees feel comfortable and able to reach their potential:

5.1 Show leadership

Ensure that diversity, equity, and inclusion are publicly stated and lived values of the organization and that they are actively resourced and demonstrated by leadership.

a. Conservation organizations and their leadership publicly pledge and then ensure intersectional gender diversity on panels, boards, and executive leadership teams.
b. Senior leaders fully and publicly support efforts to create more equitable workplaces—and are accountable for progress on ambitious diversity goals and metrics.
c. Actively recruit and value leaders with diverse and collaborative styles and approaches.
d. Build capacity and resource specialist leaders and teams to address gender inequity in conservation and the workplace.
e. Partner with organizations that specialize in addressing gender inequity and workplace culture across an organization rather than focusing on individual change. Fully resource best practice recommendations.

5.2 Transparency and accountability

Women do better where organizations are transparent, consistent, and accountable in their actions. Women also need to know that they are being promoted and paid equitably. Overall, women fall behind men when pay and progression is not transparent and relies on individual negotiation.

a. Set clear goals to improve intersectional gender representation in departments, roles, and especially in conservation leadership positions.

b. Track diversity metrics by gender, race/ethnicity, and the intersection of the two.
c. Collect and publish data on progress towards these goals.
d. Publish pay equity analyses and corrections, and internally share data on pay, promotions, and other rewards to ensure career development and progression is equitable. This needs to be disaggregated by gender and other variables including race and location.
e. Publish salaries for advertised positions.

5.3 Diversify teams and create career pathways and sponsorship for women

Women face challenges in science and conservation at all career stages.

a. Continue to reduce bias in hiring through bias awareness training for recruitment teams, diverse interview panels, and removing gendered language from job descriptions.
b. Track hiring and promotions to determine whether women, and especially women of color, and women in low to middle income countries, are being hired and promoted at similar rates to other employees. If there are gaps at certain levels or functions, adjust, including doubling down on best practices in those areas.
c. Provide dedicated sponsorship programs —that is, people who can provide new opportunities and connections—for women and especially women of color and women outside where international organizations are headquartered, especially the Global South.
d. Undertake anti-bias training for managers responsible for performance reviews and promotions. Monitor and adapt training programs.

5.4 Flexibility and wellbeing

Women have suffered higher rates of burnout during the pandemic and shoulder most caring responsibilities in and outside the workplace. The workplace culture across conservation consistently expects and rewards people who work and travel excessively. Women also shoulder higher office and family caring responsibilities and face career limitations when they become parents.

a. Establish work norms that promote flexibility in hours and location of work while also setting clear and fair boundaries so that people are not expected to always be working.
b. Establish equitable parental leave policies across countries, subsidized childcare, and flexible schedules.
c. Encourage virtual meetings and follow up for those who cannot easily travel or attend after-hours events.

5.5 Embed awareness, training, and mentoring

Training and mentoring is important for everyone to understand unconscious bias in individuals and systems and ways to address it. However, it cannot be the primary way to address gender bias, as advocacy and systems change is crucial. However, it is one important piece and can help move allies from awareness to action.

a. Provide quality and well-resourced training and awareness for all employees (not just women). This includes (but is not limited to) effective training in unconscious bias and effective hiring and retention strategies. Training and awareness must be ongoing and targeted at men as much as women. There must also be follow-up to understand how training was understood and applied.

5.6 Connecting women

a. Establish and resource employee resource groups and other official networks to allow women to discuss and address workplace issues that emerge.
b. Ask women across the organization what they need through anonymous surveys and through networks. Listen and be ready to respond and to resource their recommendations.
c. Establish programs for official mentoring, coaching, allyship, and sponsorship for early-mid career women to be connected to advocates across the organization.
d. Focus on intersectionality and allyship, which improves the work experience, particularly for women of color, parents, carers, and women from the Global South.

5.7 Address sexual discrimination and harassment

a. Create or revise reporting and support mechanisms to be current best practice and centered and informed by the rights and safety of the person raising an issue of sexual discrimination or harassment. Ensure there is access to dedicated professionals qualified in trauma informed responses and processes.
b. Regularly check workplace culture through anonymous surveys where gender disaggregated results are reported back to teams.
c. Continually reinforce workplace values which do not tolerate sexual discrimination and harassment.

5.8 Addressing intersectionality

a. Set goals and measures for representation that also explicitly cover intersectionality. Continual work is needed to understand how these recommendations address the challenges identified by women with various intersectional identities (e.g., race, disability, sexual orientation, country of origin, etc.).
b. It is also imperative that we move to considering gender in non-binary terms in conservation.

6 Conclusion

Comprehensive evidence shows that women do face bias across science, conservation, and research, from pay and benefits, promotions, publishing, funding, and hiring to decision making and setting strategic direction (Grogan 2019; Ross et al., 2022; Ryan, 2022). It is impossible and unrealistic for individuals to solve the problems they face, and it is also unacceptable to rely on individuals to forfeit their career goals and conservation influence because organizations are not designed for women to excel (Grogan, 2019).

Although most research papers conclude with suggestions for future research, we feel strongly that there is already sufficient robust evidence, some of it referenced in this paper, that supports action towards our recommendations. We strongly suggest that the next steps should be that conservation organizations commit to implementing actions towards gender equity and then report on their progress in a transparent and accessible way. Further research could then involve the success of various interventions, and the difference those interventions make for different women, and subsequently for the effectiveness of conservation and climate action. Conservation, and the climate and biodiversity crisis urgently need women to be fully involved.

Data availability statement

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

Ethics statement

The studies involving human participants were reviewed and approved by the University of Queensland Institutional Human Research and Ethics Committee. The patients/participants provided their written informed consent to participate in this study.

Author contributions

RJ developed the concept for the paper and designed the research with advice from JF, KL, and HP. RJ led the development and writing of the manuscript with guidance from JF, KL, and NB, and inputs from all co-authors. RJ with support from CC-G, BG, MB, and NB led data analysis. RJ and NB led the statistical analysis. All co-authors reviewed and approved the MS.

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Conflict of interest

Some authors are current or former employees of TNC, but all data was carefully anonymized before being analyzed. The results have been reported here without review or interference from the organization and under careful adherence of the Ethics Approval by the University of Queensland Institutional Human Research and Ethics Committee (Approval number: 2018001799) in which potential of conflict issues were comprehensively addressed.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2022.1056751/full#supplementary-material

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High sedimentation rates lead to rapid vegetation recovery in tidal brackish wetland restoration

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Introduction: Tidal wetland restoration in the Bay of Fundy involves restoring tidal hydrology to sites with tidal restrictions. Most have focused on salt marsh sites close to the mouth of estuaries, but there are also many tidally restricted wetlands closer to the freshwater end of tidal rivers. Recovery of salt marsh vegetation has been rapid in past projects, but little is known about sediment and vegetation dynamics post restoration in tidal brackish or freshwater environments.

Methods: We implemented tidal wetland restoration projects on two tidal rivers near the inland limit of saltwater. Hydrological restoration involved breaching (St. Croix) or realigning agricultural dykes (Belcher Street). We monitored hydrology, sediment accretion and vegetation at replicated plots on restoration sites and nearby reference tidal marshes; and conducted habitat mapping and elevation surveys using drones.

Results: After re-establishing tidal flow, sediment accretion was very rapid, leading to a deep layer of new sediments. Plant colonization at both sites resulted in a high diversity of halophytes in the first 2 years post restoration, but the St. Croix site transitioned to freshwater wetland species dominating by the fifth year post-restoration. The Belcher St. site has a mix of freshwater and brackish wetland species after the fourth-year post-restoration.

Discussion: High suspended sediment concentrations at both sites suggest that each site was positioned closed to the estuarine turbidity maximum within its river. Tidal wetland restoration at the head of estuaries may benefit from the large ecological disturbance associated with rapid sediment accretion, providing a productive substrate with little competition from prior vegetation. However ultimate vegetation patterns may take longer to develop as elevation gains alter tidal flooding frequency. Low salinities suggest that the physical disturbance of sediment burying prior vegetation is the main mechanism creating a clean slate for plant recolonization, rather than mortality of terrestrial vegetation due to salt water. The majority of elevation change was due to allochthonous sediment deposition, with belowground processes playing a minor role. The wetlands restored showed substantial net elevation gains in the first years following tidal hydrological restoration, but long-term monitoring is required to track their overall resilience in the face of sea level rise.

KEYWORDS

sediment accretion, sea level rise, blue carbon, dyke realignment, disturbance, wetland restoration, tidal freshwater wetland

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1. Introduction

Tidal wetlands play a crucial role in protecting coastlines from erosion as well as providing valuable habitat for many species. In the Bay of Fundy region, it is estimated that 357 ~ 395 km^2 of salt marsh existed before extensive dyking by European settlers in the 17th century, leaving just 52 ~ 65 km^2 salt marsh today (Thomas, 1983; Gordon and Cranford, 1994). In recent years, there has been considerable effort in eastern Canada to restore these dykelands back to tidal wetlands *via* tidal wetland restoration. This type of restoration prioritizes reestablishing tidal hydrology *via* breaching or realigning existing dykes. The reintroduction of tidal water to dykeland systems results in a sudden die-off of the pre-existing freshwater dominant vegetation (Bowron et al., 2011), but will also carry seeds or rhizomes of halophytic species from nearby existing salt marshes, therefore vegetation recovery generally begins with halophytic colonization (van Proosdij et al., 2010; Rabinowitz et al., 2022). While most tidal wetland restoration projects in the Bay of Fundy focus on salt marshes occurring along tidal rivers and are relatively close to the Bay (Bowron et al., 2012), there are also significant occurrences of brackish/freshwater tidal wetlands located upstream which provide unmet opportunities for restoration.

Tidal freshwater wetlands (TFW) feature tidal hydrology but are located in the upper extent of estuaries where coastal saline water meets freshwater flow resulting in lower salinities than salt marshes (Odum et al., 1984). TFW typically do not have salinities high enough to cause the death of terrestrial or freshwater wetland vegetation, but vegetation dynamics are largely unknown in the context of ecological restoration of these systems located in northeastern North America. Restoration efforts in tidal brackish or fresh systems elsewhere in North America often involve sediment augmentation using dredged or otherwise externally sourced material (Baldwin and Hammerschlag, 2019). In the Upper Bay of Fundy suspended sediment concentrations in tidal rivers can be high (>500 mg•L^{-1}; van Proosdij et al., 2006), but it is not clear if sediment supply will be adequate to restore marsh platform elevations. Dyked former wetlands are often low in elevation due to subsidence and lack of sediment addition (Byers and Chmura, 2007). However, after restoration this situation can lead to high rates of sediment accumulation–if tidal sediment supply is adequate–since lower elevations flood more frequently (Wollenberg et al., 2018). Tidal rivers are characterized by a salt wedge at the upper extent of saltwater penetration upstream. A turbidity maximum is often observed at the tip of the salt wedge, causing higher suspended sediment concentrations compared with regions up or downstream (Burchard and Baumert, 1998). While the phenomenon occurs worldwide, tidal rivers in relatively long estuaries and those with higher tidal ranges tend to have the highest maximum suspended sediment concentrations (Uncles et al., 2002). The ability for a restoring tidal wetland to accumulate sediment to keep pace with sea level rise is crucial for development of wetland vegetation (van Proosdij et al., 2006; Goodwin and Mudd, 2019). Therefore the ecomorphology in these systems is likely to be controlled primarily by proximity of the site to the estuarine turbidity maximum (Darke and Megonigal, 2003).

The reality of sea level rise and increased storm intensity has resulted in an upsurge in interest in tidal wetland restoration in eastern Canada, but current efforts are limited by a lack of examples that cover the full range of tidal conditions, including brackish and fresh tidal wetlands in the upper extreme of estuaries. This study presents a quantitative account of two TFW restoration projects located in the Upper Bay of Fundy with the goal of comparing the early trajectory of hydrological and ecomorphological changes post-restoration. A standardized monitoring program widely adopted in the region was used to quantify changes in hydrology, sediment dynamics, vegetation changes, and fish habitat use (Neckles et al., 2002; van Proosdij et al., 2010; Bowron et al., 2011).

2. Methods

2.1. Site descriptions

The Bay of Fundy is a large hyper-tidal embayment located mostly within Canadian Atlantic provinces at the northeastern end of the Gulf of Maine. Semi-diurnal tides in the upper portions of the Bay of Fundy reach an excess of 16 m on larger spring tides (Desplanque and Mossman, 2004; van Proosdij et al., 2006). Most Bay of Fundy watersheds are drained by large tidal rivers that discharge into the main tidal basin within intertidal zones completely exposed at low tide. A large tidal prism combined with high suspended sediment concentration contributes to high sedimentation rates recorded within the region (Chmura et al., 2001; Daborn et al., 2003; van Proosdij et al., 2006).

2.1.1. St. Croix River

The St. Croix River High Salt Marsh and Tidal Floodplain Wetland Restoration Project (SC) is located within the upper reaches of the Avon Estuary in Nova Scotia (Figure 1A). The site consists of a fallow dykeland tract adjacent to the Highway 101/St. Croix River that had not been flooded since the 1950s. The restoration site has an area of 10.03 ha and, prior to restoration, lay at a mean elevation[1] of 6.19 m, with the fringe (foreshore) marsh at a mean elevation of 6.58 m (Bowron et al., 2015; Table 1). Prior to restoration, the site was mainly pastureland (cattle) dominated by a variety of grasses, *Rosa virginiana*, and *Juncus effusus* (wet areas). Salinity in the St. Croix River adjacent to the study site ranged from 0.0 to 15.1 ppt and suspended sediment concentrations in the river water ranged on average from 40,296 (± 76,567) mg•L^{-1} (incoming tide average) to 32,157 (± 63,736) mg•L^{-1} (outgoing tide average) which was considered very high (Bowron et al., 2010).

Prior to restoration, SC contained a network of agricultural drainage ditches leading to one main aboiteau (Figure 1B), and two areas of higher elevation (islands) within the site but were not subject to any measurements (and remained post-restoration); these islands are covered by pasture grasses, shrubs, and trees. Cattle had access to the site up to the time of construction in 2009. A 0.46 ha section of marsh with a mean elevation of 6.83 m along the north branch of the St. Croix (Herbert River) was identified as a suitable reference site for this project (Figure 1D). This site exhibited similar hydrological and sedimentological conditions as

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[1] Mean elevations calculated from surveyed vegetation stations relative to the Canadian Geodetic Vertical Datum of 2013.

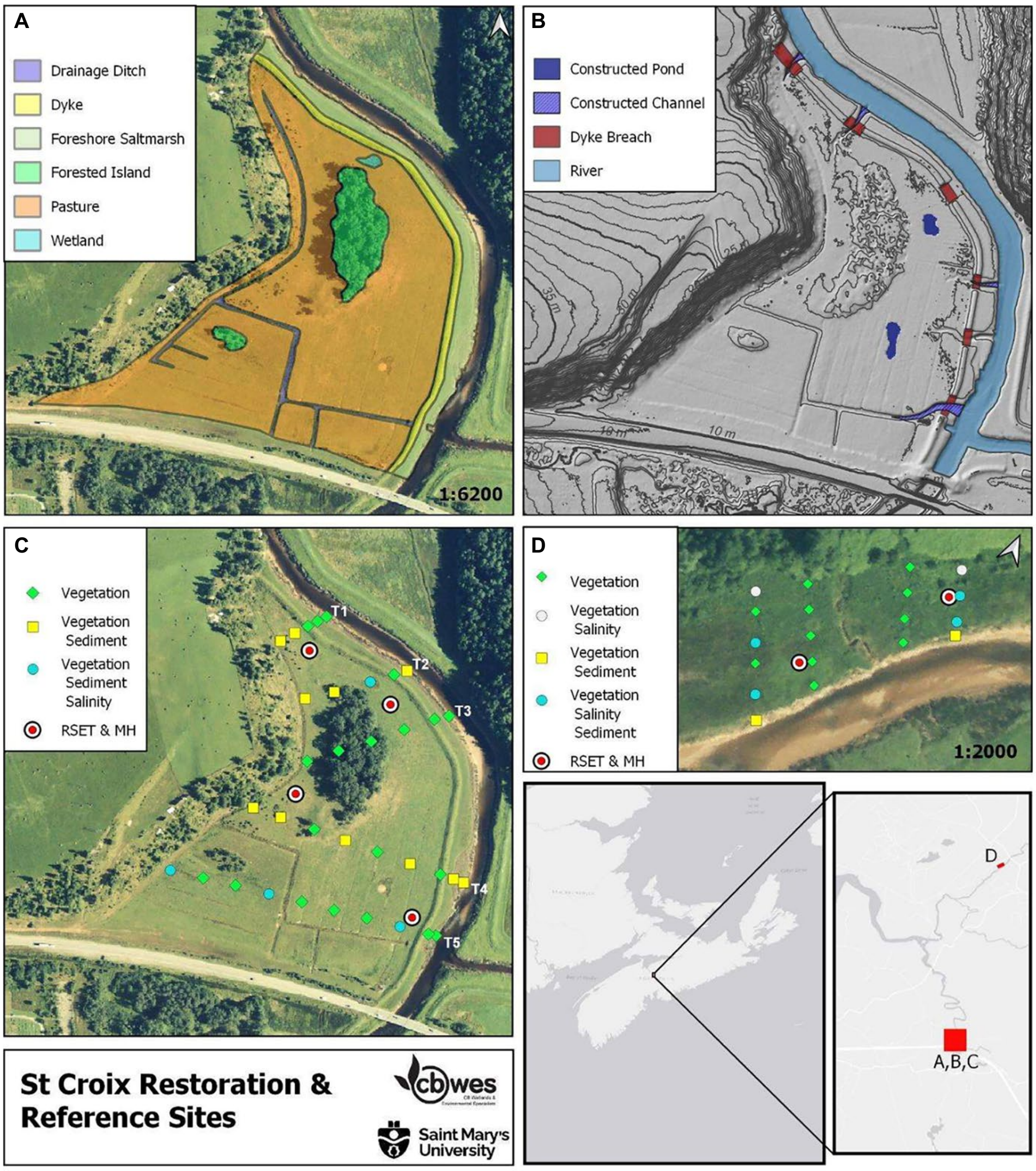

FIGURE 1
St. Croix site **(A)** Pre-restoration habitat map; **(B)** Restoration plan; **(C)** Sampling locations; **(D)** Reference site.

TABLE 1 **Mean elevation, IR, and IF for BEL and SC for baseline conditions (pre-restoration).**

Site	Area	Elevation (m CGVD2013)	IR	IF
BEL	Study (Baseline)	6.19	0.06	46
	Fringe	6.58	0.05	31
	Reference	6.83	0.03	30
SC	Study (Baseline)	6.24	0.03	26
	Fringe	6.7	0.007	8
	Reference	6.73	0.007	8

those present at the restoration site and is one of the few remaining undyked sections along the tidal component of the St. Croix River system that was also readily accessible for study. The SC reference site is characterized by brackish and freshwater marsh species (*Juncus balticus*, *Calystegia sepium*, *Sporobolus michauxianus*, *Galium palustre*, *Agrostis stolonifera*) as well as areas of pasture weeds (*Centaurea nigrum*, *Cirsium arvense*, *Filipendula ulmaria*, *Equisetum* and *Solidago* spp.).

The restoration project was designed to re-establish the tidal creek networks, re-connect the wetlands to the adjacent watercourse, redirect runoff flow, create two ponds, and overall create a productive floodplain wetland complex with fish passage and favorable bird habitat. Construction and dyke breaching took place in summer 2009. A total of 6 breaches were made, two ponds were excavated to a depth of 0.5 m. multiple tidal channels were excavated and an aboiteau was buried. Channels were constructed with an approximately 2 m wide bottom, a zero degree slope for 80% of the distance from the river edge grading up to meet the marsh surface over the remaining 20%. Channel sides had a 3:1 slope (Bowron et al., 2009).

2.1.2. Belcher street marsh

The Belcher Street Marsh (NS091; BEL) is located on the north side of the Jijikwtuk (Cornwallis) River, downstream (East) from the town of Kentville (Figure 2A). The site was a mix of active (forage and crop) and fallow (impounded freshwater wetland) agricultural lands prior to restoration (Figure 2A). Being part of the Bay of Fundy's Minas Basin, the Jijikwtuk River is a significant tidal river with the head of tide extending a short distance upstream from the project site. Salinities measured approximately 2 km upstream of BEL at Kentville range from 14.9 to 30.7 ppt (Brylinsky, 2014; Hatt et al., 2017). Suspended sediment concentrations in the river adjacent to the site are high, ranging from a maximum in June 2019 of 15,644 mg•L^{-1} to a minimum of 80 mg•L^{-1}. The dykes along the Jijikwtuk River are positioned close to the bank of the main river channel, resulting in a long sinuous dyke system which is costly and labor-intensive to maintain in the face of climate change, and was highly susceptible to (and experiencing) erosion at multiple locations.

The main dyke was 1.34 km in length and protected 22.6 ha of agricultural land (80% active, 20% fallow) with a mean elevation of 6.24 m (Table 1). The site had one single barrel 24″ diameter aboiteau, which was originally constructed in 1956 and last upgraded in 1997. The primary drainage ditch, particularly along the upland edge and in the fallow (western) portion of the site, has not been actively maintained and had become overgrown with floating mats of vegetation. While the dyke and active fields were dominated by agricultural grasses and crops, the fallow portion had degenerated into impounded freshwater wetland. Areas of higher elevations had

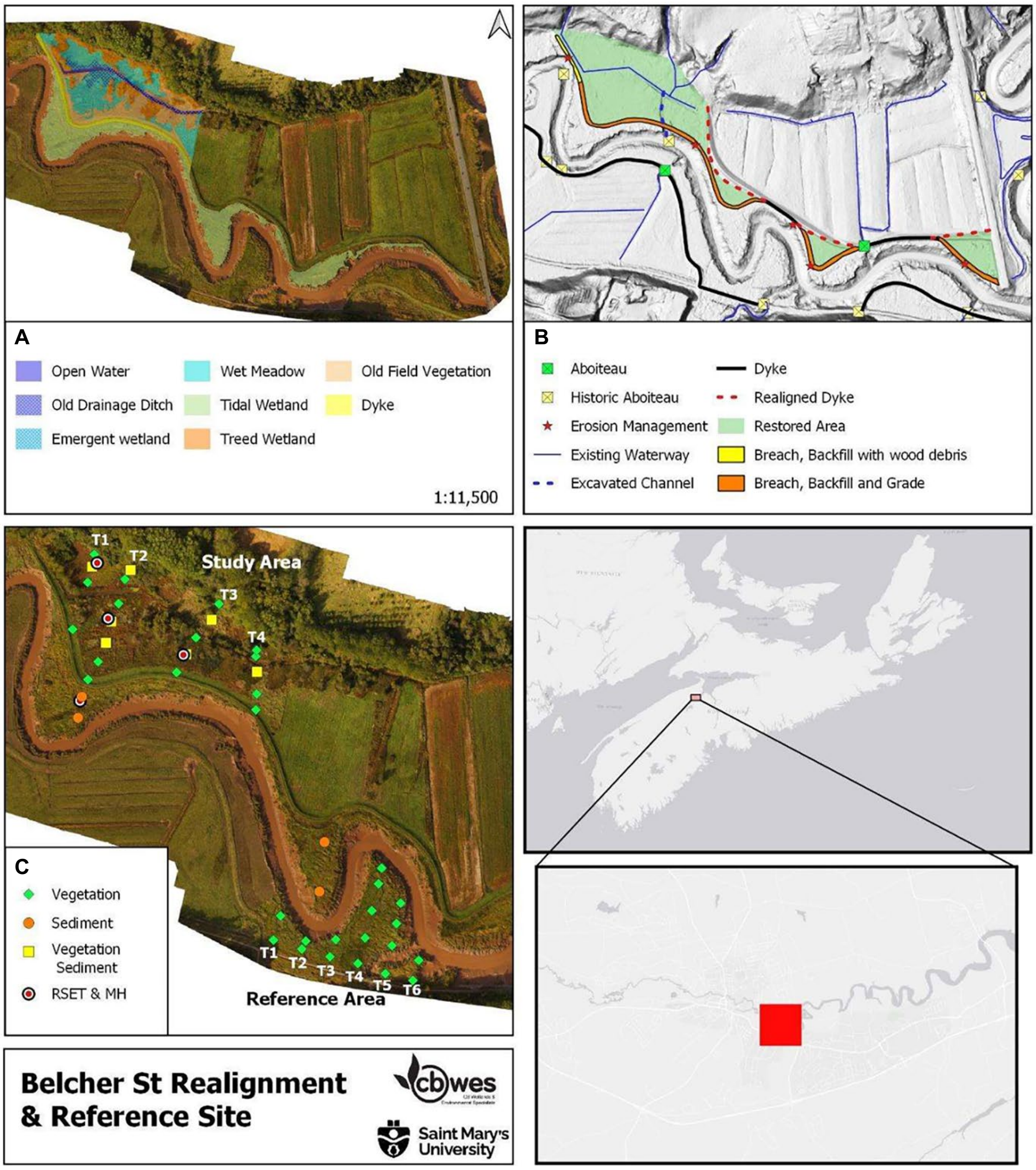

FIGURE 2
Belcher Street site **(A)** Pre-restoration habitat map; **(B)** Restoration plan; **(C)** Sampling locations.

largely been colonized by water tolerant trees and shrubs and old-field species.

The BEL reference site is across the river from the restoration site (Figure 2C). It contains approximately 1.5 ha of unrestricted tidal wetland with a mean elevation of 6.73 m. Because it is located near the head of tide, the site does not entirely follow the typical zonation pattern, hydrology and species composition expected of a salt marsh, but rather that of transitional tidal wetland between salt marsh and tidal fresh. The reference site has a well-defined low and high marsh, with low marsh dominated by *Sporobolus alterniflorus* limited to the river edges and high marsh dominated by brackish marsh species such as *Elymus repens*, *Solidago sempervirens* and *Sporobolus michauxianus*.

To reduce dyke length and address erosion concerns the dyke at BEL was straightened, eliminating sinuous sections of dyke which followed the riverbank, and realigned at its western end near the boundary of the utilized agricultural lands in June 2018 (Figure 2B). In addition, a drainage channel was created to allow tidal flooding and freshwater discharge across the width of the site and the old dyke was leveled to the foreshore elevation along all sections of realigned (newly constructed) dyke.

2.2. Data collection

Variables describing hydrology, topography, sediment and vegetation were sampled following regional guidelines (Neckles et al., 2002; Bowron et al., 2011, 2012). Most variables were sampled Year 1 ~ 2 pre-restoration, one, two, three and four (BEL) or five (SC) years after restoration (Table 2). Pre-restoration conditions were sampled in 2007 and 2008 at SC and 2017 at BEL.

Sampling was conducted using a series of permanent transects and sampling stations that were established in a non-biased, systematic sampling design as part of the baseline monitoring activities in 2007–8 (SC) and 2017 (BEL; Bowron et al., 2015, 2017). At SC, a permanent benchmark was installed and used to establish the first Line (transect; Figure 1C). Each sequential Line was then set using the location of the one previous. The five transects were permanently marked by a pair of wooden stakes (labeled as front stake and back stake) installed at the upland end of the transect; 35 sampling stations were established along 5 transects–25 stations were located at equal intervals on the landward side of the dyke (T1 20m; T2 ~ 5 40 m), and an additional 2 stations per transect located on the seaward side of the dyke in the high and low marsh. Four transects and 19 sampling stations were established at the SC reference site, with transects spaced 20 m apart with a 20 m buffer applied to the tidal creek bisecting the site, and stations placed 10 m apart (Figure 1D).

At BEL, four transects were established, 50 m apart (as measured along the upland edge of the north-west side), running roughly perpendicular to the Jijikwtuk River and marked along the upland edge with semi-permanent bamboo stakes (Figure 2C). Data collection was conducted at 21 sampling stations established at equal intervals (20 m) along each transect. Six transects with 17 sampling stations were established at the reference site. A Leica Geosystems G14 dual-frequency GNSS receiver was employed to relocate the transects and sampling stations. These stations are resampled each year as indicated in the monitoring schedule (Table 2).

2.3. Geospatial

Digital Elevation and Surface Models (DEM, DSM), orthophotography and ground surveys were carried out at each site. These are essential for characterizing morphological, surface cover and elevation changes.

For the SC restoration and reference sites a LiDAR DEM was used in the baseline analysis. The LiDAR was flown in April 2007, processed by the Applied Geomatics Research Group (Nova Scotia Community College, Centre of Geographic Sciences; (Bowron et al., 2008). In 2010, 2012 and 2014, the SC DEM was updated using ArcGIS's Topo to DEM tool with surveyed elevation points (Trimble G8 GNSS RTK) and contour data extracted from the LiDAR surface (major contours only) as inputs (Supplementary Appendix 1). Detailed elevation surveys of the SC and reference site marsh surfaces were completed annually.

By 2018, improved performance of and access to drone technology resulted in increased collection of geospatial data at BEL, particularly DSM and orthophotography. While baseline analysis relied on ground survey data and a LiDAR DEM provided by NSDA and flown in 2007 by AGRG, DSM collected in 2018 and 2019 contained large areas of bare ground. In 2020 LiDAR data was again collected by the province of Nova Scotia and was used for Year 4 analysis. Elevation surveys were conducted on multiple dates using a Leica Viva GS14 dual-frequency GNSS smart antenna[2] with nRTK positioning corrections (SmartNet NS; Supplementary Appendix 1). All elevations are reported relative to the Canadian Geodetic Vertical Datum of 2013 (CGVD2013; Natural Resources Canada, 2020).

For both SC and BEL Orthophotography was collected on multiple occasions. Several platforms were used including traditional plane-based imagery collection, remotely operated, tethered balloon and suspended camera system, quadcopter Remotely Piloted Aircraft Systems (RPAS) and fixed wing RPAS. Prior to conducting the RPAS flight, a Ground Control Point (GCP) network was designed to ensure optimal georeferencing results in the Structure-from-Motion (SfM) workflow for production of DSMs using the most up to date recommendations found in the scientific literature (James and Robson, 2014; Tonkin and Midgely, 2016; Raczynski, 2017).

2.4. Hydrology

At both sites automated water level loggers were deployed annually in still wells to record water levels and temperature at 5 minute intervals. Additional loggers were deployed in the upland to provide barometric compensation. At SC Solinist Leveloggers (Model 3,001) were deployed in 3 locations: the St Croix River, the primary tidal channel (old aboiteau channel), and at the reference site. At BEL, HOBO automated water level recorders (Model U20T) were deployed 400 m downstream of the restoration site and within the primary tidal channel. The positions of each of the units was surveyed using GPS RTK and water depth converted to geodetic elevation (m CGVD2013; Supplementary Appendix 2). Water levels

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[2] https://leica-geosystems.com/products/gnss-systems/smart-antennas/leica-viva-gs14

TABLE 2 Environmental sampling: Variables, including core and additional ecological indicators, methodologies, and frequency (sites: BEL: Belcher street; pre-restoration: 2017; post-restoration: year 1: 2010; year 5: 2014; SC: pre-restoration: 2007, 2008; post-restoration: year 1: 2018; year 4: 2021).

Category	Parameters	Sampling method	Annual sampling frequency	Monitoring year					
				Pre	Post-restoration				
					1	2	3	4	5
Geospatial	Landscape	UAS Orthomosaic; DSM (BEL); GNSS RTK surveying unit (BEL)	As required	BEL	BEL 2X	BEL 2X	BEL	BEL	SC
	Marsh surface elevation	Digital elevation model (DEM). RTK GPS; LiDAR (SC)	Annually/As required	BEL, SC	BEL, SC	BEL, SC	BEL, SC	BEL	SC
Hydrology	Tidal signal	Automated water level recorders (5 min intervals) (Solinst Levelogger Model 3,001)	Minimum 29 day period	BEL, SC	BEL, SC	BEL	BEL, SC	BEL	SC
	Suspended sediment concentration (in river; SSC)	Teledyne ISCO 6712 full size portable sampler	Over 2 days (SC); 3 days (BEL)	SC		BEL			
Soils and sediments	Sediment accretion	Rod surface elevation tables (RSET); marker horizons (MH)	Annually	Set-up	BEL, SC	BEL, SC	BEL, SC	BEL, SC	SC
	Sediment characteristics	Sediment cores: bulk density, organic matter content, sediment type, water content	Annually	BEL, SC	BEL, SC	BEL	BEL, SC	BEL	SC
Vegetation	Composition	Point intercept method (1 m^2 plots)	Annually	BEL, SC	BEL, SC	BEL, SC	BEL, SC	BEL, SC	SC
	Abundance								
	Height								
	Habitat map	Aerial photograph, DGPS/GIS, total station, LiDAR, low-altitude aerial photography	Annually	BEL, SC	BEL, SC	BEL	BEL, SC	BEL	SC
Winter walk	Winter conditions	Structured winter walk and photo-documentation	Annually between January and March	BEL, SC	BEL, SC	BEL, SC	BEL, SC	BEL, SC	SC

were graphed in Microsoft Excel with precipitation records obtained from the nearby climate stations (ECCC, 2022).

Hydrology was assessed using critical water elevations calculated from the loggers in conjunction with hypsometric curves and flood maps generated from DEMs previously described. Hypsometric curves show area flooded at a tide height, describing the way in which the marsh is expected to flood as the tide rises. Hydroperiod statistics such as inundation ratio (IR: time inundated during recording period) and inundation frequency (IF: number of tides resulting in flooding during recording period) were calculated using the tidal signal recorded from the level loggers and surveyed station elevations.

2.5. Sediments

Rod Surface Elevation Tables (RSET) and Marker Horizons (MH) (mm resolution) were used in combination to explain processes behind marsh elevation increases or decreases (i.e., sedimentation, subsidence; Neckles et al., 2002; Lynch et al., 2015). Marker Horizons provide a measure of sediment accretion (deposition) above a layer of white feldspar clay. A cryocorer using liquid nitrogen was used to extract a frozen 'bullet' of sediment. Sediment accretion since the first introduction of tidal waters was determined by measuring the distance from the surface to the feldspar layer. Net accretion between years was determined by subtracting the current year's measurement from the previous.

RSETs and MHs were installed at SC (four stations) and SC reference (two stations) in 2007 (Figure 1A). Three RSET and MH stations were installed at BEL in June 2018. A reference RSET and associated MH were installed at the existing fringe marsh to capture the reference condition (Figure 2A). All RSETs and MHs were sampled yearly (Table 2).

Sediment cores were collected at both sites and corresponding reference sites at the vegetation sampling stations. All cores were processed for bulk density, water and organic matter content and grain size. The samples were placed in a freezer and kept frozen until processing. The sediment cores were thawed before being extruded from their containers. The samples were photographed and split open to determine the color (Munsell Color, 1994), texture and composition of the core for a qualitative description. To determine bulk density and water content, soil samples were thawed and removed from the syringes, dried and weighed. Organic matter content was then determined using loss-on-ignition after 4 h at 550°C. Organic carbon density was derived using the equations in Craft et al. (1991). To determine particle size distribution, sediment cores were analyzed using a Coulter Multisizer 3$^{\text{tm}}$ which is based on electrical resistance and is more accurate for the analysis of fine sediments (McCave et al., 2006). The two aperture tubes that were used were the 200 μm tube and the 30 μm tube. The grain size distributions were analyzed using the GRADISTAT program and size classes determined using a modified Udden-Wentworth scale (Blott and Pye, 2001). Floc fraction, the proportion of deposited sediment deposited in flocculated form, was determined using the inverse floc model (Curran et al., 2004).

2.6. Vegetation and habitat mapping

Vegetation sampling locations were surveyed using permanent 1 m^2 plots positioned at intervals along each transect. Each 1 m^2 plot (quadrat) used was offset 1 m to the left of the transect (facing main tidal channel) and oriented toward the upland end of the transect. The quadrat was divided into a grid of 25 squares (20 cm × 20 cm) and the resulting 25 intercept points were used as sampling points. All plant species present in the quadrat were recorded and then a wooden dowel (3 mm in diameter) was held vertical to the first sampling point and lowered through the vegetation to the ground below. Any species that touched the rod were recorded and this was repeated for all 25 intercept points. Other categories, such as water, bare ground, rock or debris, were also recorded if hit by the dowel. Plant species richness, halophytic species richness and cover, and unvegetated area were compared among sites. Percent cover was estimated as the number of pins contacted by leaves/stems/flowers of that species out of a total of 25 pins. The species encountered at these sites that were classified as halophytes are: *Atriplex* spp., *Bolboschoenus maritimus*, *Juncus gerardii*, *Solidago sempervirens*, *Sporobolus alterniflorus*, *Sporobolus michauxianus*, *Spergularia salina,* and *Suaeda* spp. Change in vegetation cover and halophytic plant cover were estimated for each plot by subtracting Year 4 post-restoration values from Year 1 post-restoration values; ordinary least squares regression was carried out to determine whether the net change in elevation at each vegetation plot could predict vegetation cover change or halophytic cover change.

Habitat maps document vegetation community structure and other important habitat features at the landscape scale (e.g., channels, culverts, beaver dams). Habitat maps were developed for all sites by using vegetation analysis results to first identify larger community types (i.e., high marsh, low marsh, bog, etc.). Subsequently, plot-level data (training points) were used to manually digitize surface cover classes from available imagery. Where available, ancillary data such as DSM, image segmentations for bare ground areas, and site photos were used to aid in image interpretation (these products varied by both site and year). At SC habitat maps were generated pre-restoration (2007) from provincially available aerial photography and in Years 1, 2, 3, and 5 (2010 ~ 2014) from low-altitude imagery described previously. Baseline habitat maps at BEL were created as part of the pre-restoration surveys (2017) and updated in subsequent years (1 ~ 4).

3. Results

Overall, both sites experienced massive deposition of sediments in Year 1, burying pre-existing vegetation and soils (Figures 3, 4). At SC, the influence of the restored tidal flow was immediately evident by the retention of water in the constructed ponds at SC (Figure 4), large deposits of sediment leading to patches devoid of vegetation, and the re-activation of the hybrid tidal creek networks. At BEL, full hydrological restoration in Year 1 post restoration was indicated by equivalent tidal signal in the river and in the main drainage channel on the restoration site. Both sites experienced consolidation of sediments and rapid recolonization of vegetation in Year 2. Subsequent

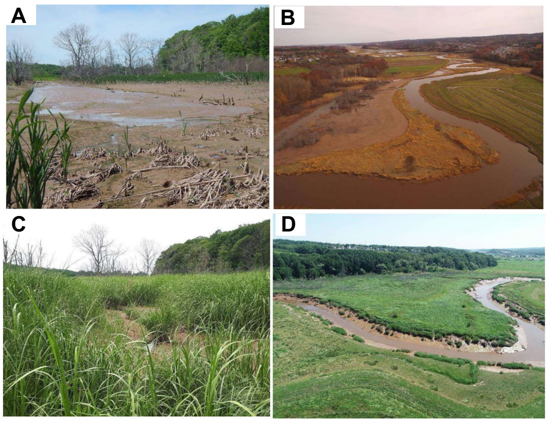

FIGURE 3
Belcher St. site **(A)** 2018 (Year 1 post); **(B)** 2018 (Year 1 post) aerial view after dyke realignment; **(C)** 2021 (Year 4 post); **(D)** 2021 (Year 4) aerial view.

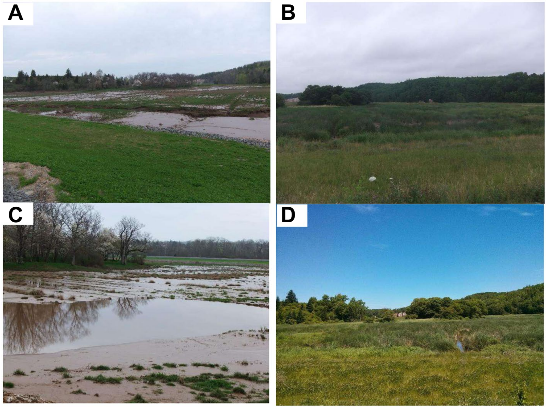

FIGURE 4
St. Croix restoration site **(A)** marsh landscape Year 1 (2010); **(B)** marsh landscape Year 3 (2012) post; **(C)** constructed pond Year 1 post (2010); **(D)** constructed pond Year 5 (2014) post facing north.

years showed continued but lower rates of accretion and elevation gain accompanied by almost complete coverage by vegetation.

3.1. Hydrology

Both sites fell within a similar tidal range, with the mean recorded high tide, maximum recorded high tide, and the historic High-Water Line (HWL[3]) slightly higher at SC than at BEL. HWL was 7.8 m at SC and 7.4 m at BEL, with recorded mean high tide at SC 6.1 m and 5.6 m at BEL. The lowest recorded high tides were 4.1 m (SC) and 4 m (BEL). However, lower mean elevations and slightly greater subsidence at SC prior to restoration (Baseline) resulted in higher IR and IF than were observed at BEL (Table 1).

Hypsometric curves for pre-and post-restoration conditions at both sites are shown in Figure 5. Prior to restoration, overbank flooding began at SC at approximately 5.5 m, a half meter below the mean recorded high tide, and flooded gradually to the upland edge (Figure 5A). Following restoration, overbank flooding begins at mean recorded high tide, but flood pattern remains the same. At the reference site, the presence of a tidal channel bisecting the site results in some early flooding, with the majority of the site flooding at ~6.8 m. At BEL, overbank flooding begins above the recorded mean high tide (5.6 m) both pre and post restoration (Figure 5B). Following restoration, the pattern of flooding became more similar to the reference site, with the site flooding more quickly and at higher elevations. When both tidal range and area flooded were converted to percent to allow direct comparisons, the similarity in flood patterns at all sites and greater subsidence of the SC site are evident.

3.2. Elevation and sediments

Both sites showed elevation gains of 8 ~ 18 cm at the RSET locations in the first year following hydrological restoration (Figure 6A), many times that at each respective reference site. Elevation changes at BEL were inconsistent among stations in Year 2 with two stations and the reference station showing a net decline in elevation. At SC in Year 2 elevations grew less than in Year 1 but were

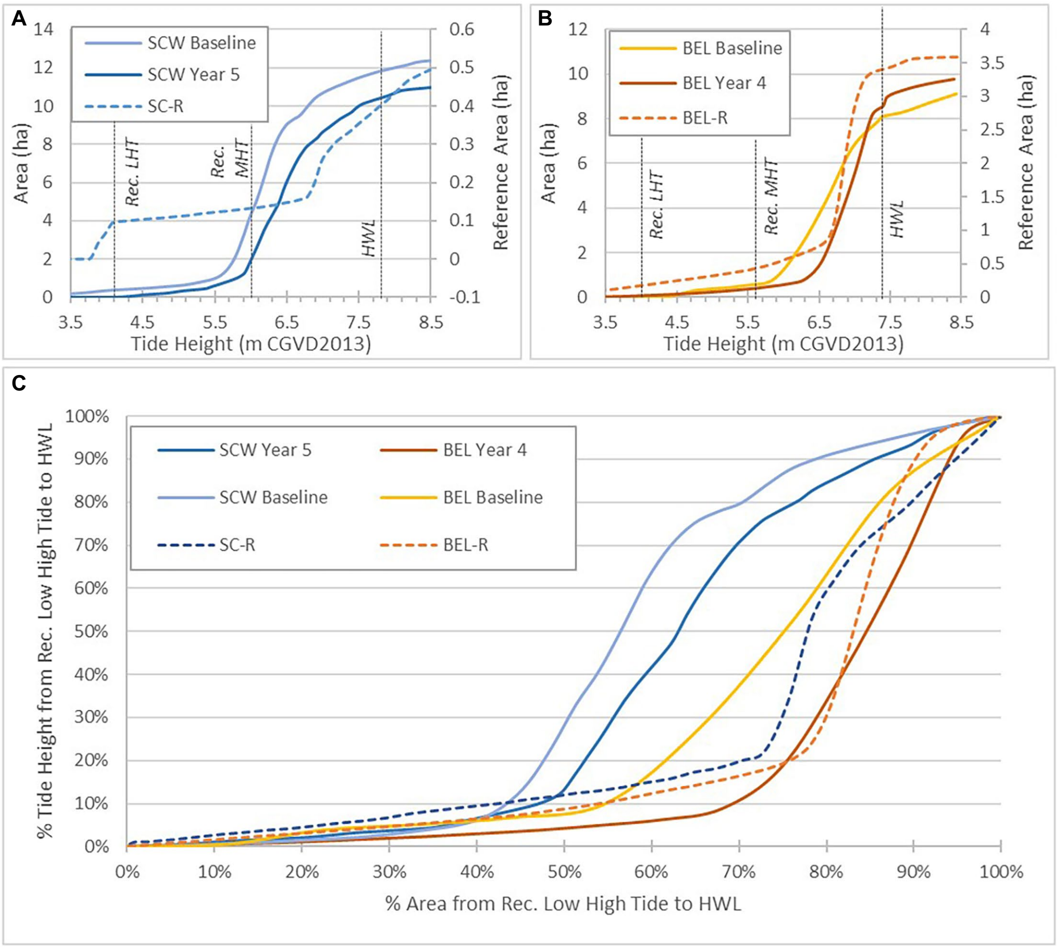

FIGURE 5
(A) SC hypsometric curves at reference site, pre, post restoration. **(B)** BEL hypsometric curves at reference site, pre, post restoration. **(C)** Area flooded (%) between recorded low high tide and HWL for SC and BEL.

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[3] HWL determined by Nova Scotia Department of Agriculture's Digital Marshlands Atlas.

still all positive. Year 3 elevation changes were positive at BEL (7 ~ 10 cm) and SC (1 ~ 7 cm). Net gain in elevation over the first 3 years post restoration at BEL ranged from 22.9 cm to 33.0 cm compared with only 0.2 cm at the reference site. Net elevation gain at SC over the first 3 years ranged from 16.0 cm to 32.4 cm compared with 0.3 cm at the reference site. SC elevation changes remained positive in Years 4 ~ 5 (Figure 6A), with total additional gains from 1.8 cm to 16.0 cm, compared with −0.7 cm change at the reference site. At SC, RSET stations closest to creeks and lowest elevations had the most elevation gain (SC SET-1, −2) overall.

Accretion was net positive for all stations that could be measured in the first year, and much greater than at each respective reference site (Figure 6). At BEL SET-02 in Year 2, the depth of accreted sediments exceeded the depth of the sampling containers, so this station was not sampled in that year. In Year 2, the two stations that could be measured had a negative value at SET-1, but a positive value at SET-3. Net accretion at BEL over the 3 years ranged from 9.3 cm to 27.6 cm while the BEL reference site showed only 4.2 cm of accreted sediments; at SC, patterns were similar with 13.7 cm to 33.0 cm compared with 7.3 cm at the reference site. Overall, high accretion and elevation gains in the first year were followed by lower gains in subsequent years.

Sediment bulk density increased consistently over time at BEL, from an average of 0.5 g•cm^{-3} pre-restoration to almost equivalent to the reference site average by Year 4 (Figure 7A). Sediment water content at BEL declined post restoration but stayed relatively consistent across years 2 to 4 and was slightly higher than the average reference site value. At SC, bulk density increased in Year 1 post-restoration but declined to pre-restoration levels in Years 3 and 5. SC bulk density values were consistently higher than the restoration site average throughout the study period. Sediment water content at SC showed no consistent pattern over the study period but was lower than the reference site average throughout the study (Figure 7B).

Sediment organic matter content and organic carbon density declined abruptly in the first year post-restoration at both sites (Figures 7C,D) but then remained relatively constant to the end of the study period. At both sites final sediment organic carbon density remained lower than corresponding reference site values.

Post restoration, particle grain size ranged from 8.43 μm to 18.05 μm at SC. These values fall into the medium silt range which is consistent with the expected grain size of suspended sediment in the area (Bowron et al., 2012). In Year 5, deposited sediments were finer, ranging from 5.23 to 9.49 μm (fine -med silt). This range was more similar to lower end of the range of particle sizes recorded at BEL post restoration (3.9 μm: very fine silt to 20.9 μm: medium silt). The largest grain sizes were recorded immediately adjacent to the tidal channel. All samples were poorly sorted over all years. BEL generally had a

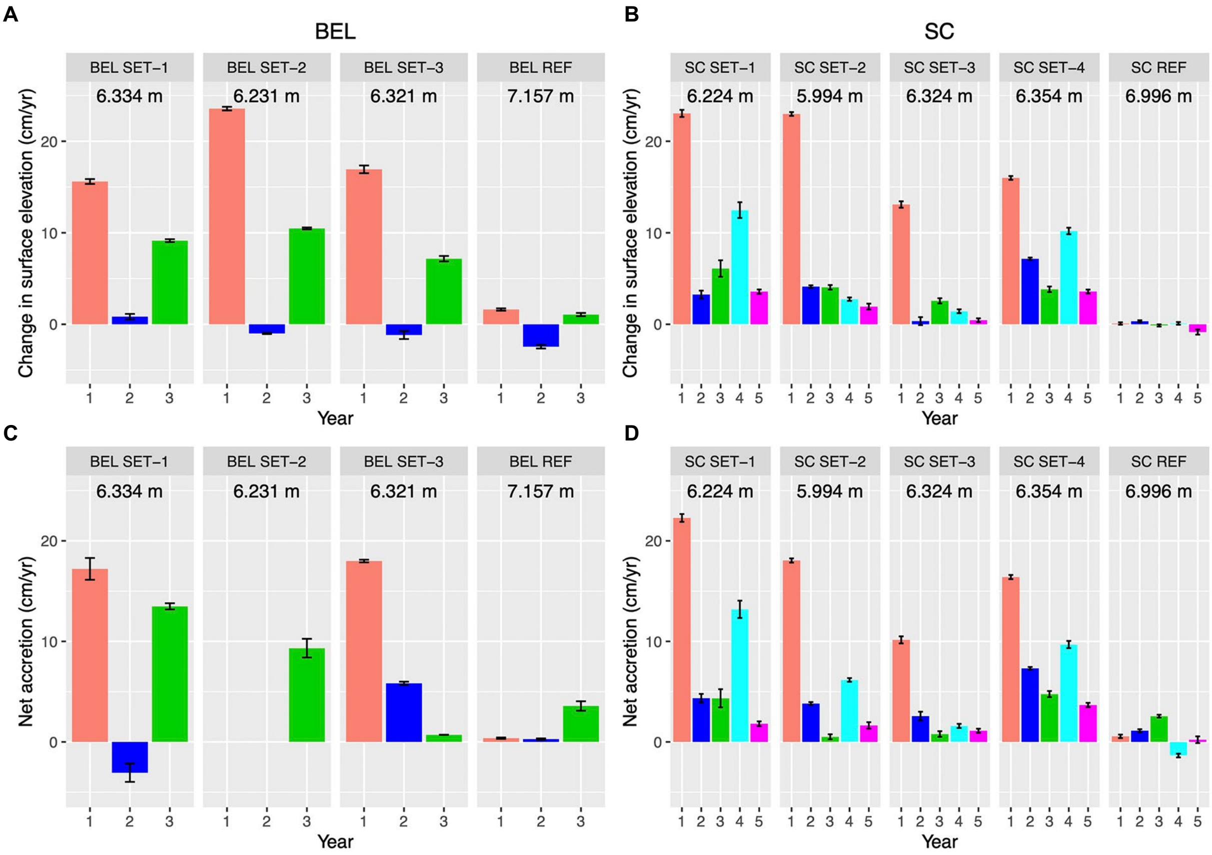

FIGURE 6
Surface elevation and sediment changes at BEL and SC restoration sites; error bars are standard errors; **(A,B)** Changes in surface elevation from RSET stations (Years post hydrological restoration); REF indicates reference site stations. Means are calculated across all pins on each station; **(C,D)** Accretion measured at RSET stations using marker horizons. Means calculated from three marker horizons per RSET location, REF indicates reference site stations.

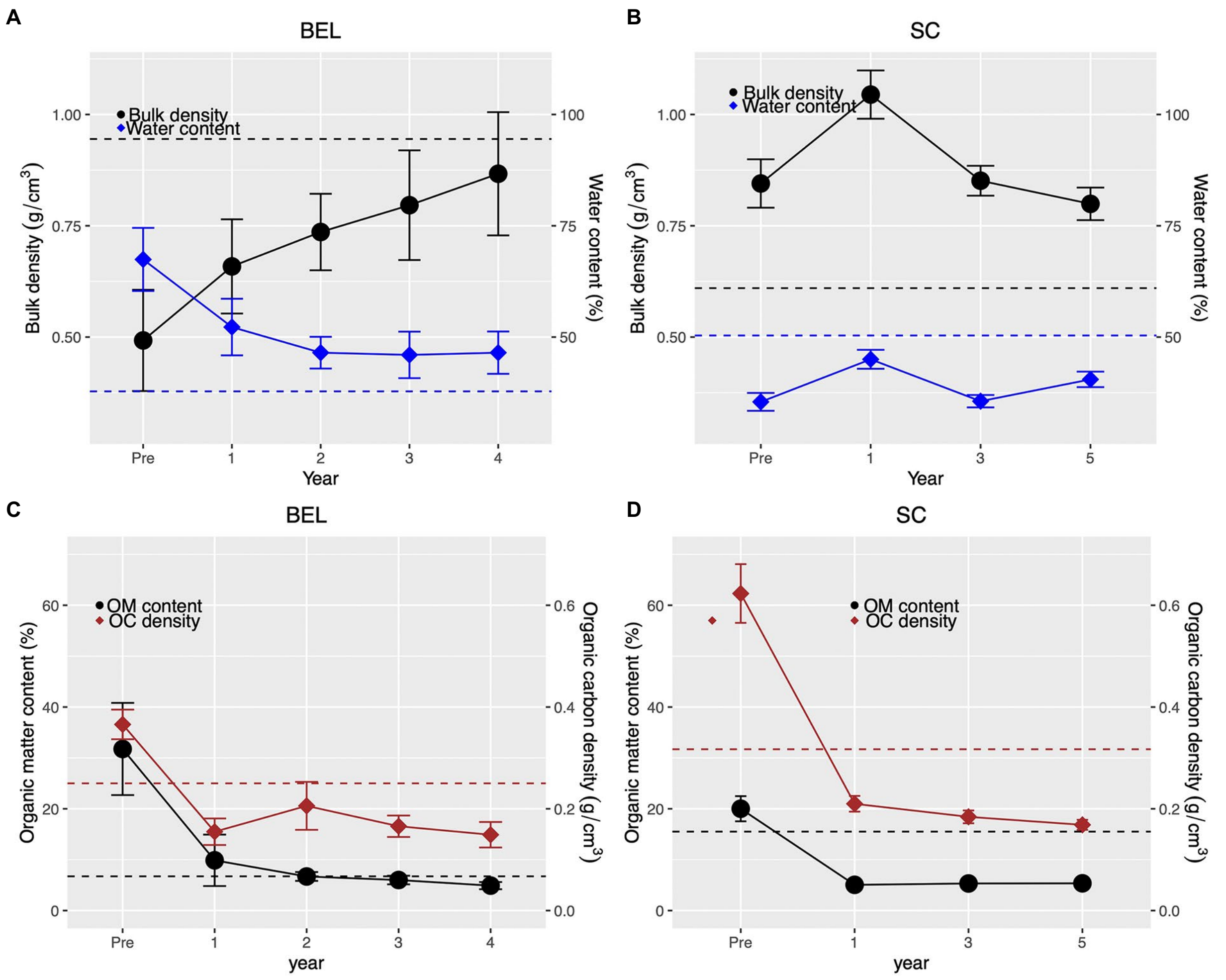

FIGURE 7
(A,B) Sediment core bulk density and water content at BEL and SC restoration sites. Dotted horizontal lines represent the average value for cores taken at the respective reference sites. **(C,D)** Sediment core organic matter content and organic carbon density changes at BEL and SC restoration sites. Dotted horizontal lines represent the average value for cores taken at the respective reference sites; error bars are standard errors.

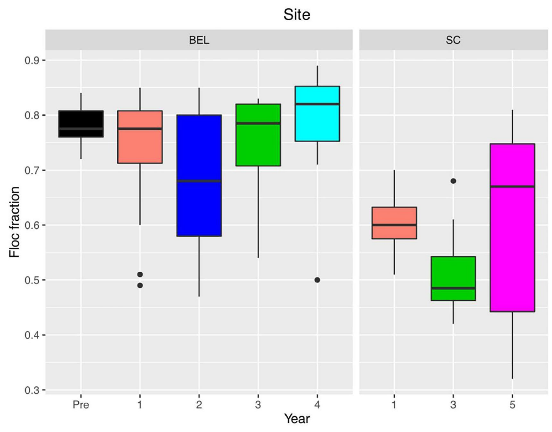

FIGURE 8
Floc fraction for sediment samples over time at BEL and SC restoration sites.

greater proportion of sediment deposited in flocculated form (0.7 ~ 0.8 on average) than SC (0.5 ~ 0.7). SC tended to have greater variability in floc fraction both within and between years (Figure 8).

3.3. Habitat and vegetation

Prior to restoration, both sites contained a mixture of wet pasture and fresh to brackish wetland patches (Supplementary Appendix 3; Figures 1, 2). In Year 1 at both sites there were substantial areas where pre-existing vegetation had been covered by a thick layer of sediment. Vegetated patches in Year one at SC were mainly dominated by sedge and rush communities, and a meadow with sparse cover of brackish tolerant plants, including *Alopecurus* spp., *Agrostis stolonifera* and *Elymus repens* (Figure 9; Supplementary Appendix 3). Both *Alopecurus* species increased post-restoration but declined to low abundance by year 5 (Supplementary Appendix 3). From Years 2–5 at SC, vegetation cover increased rapidly (96% cover by Year 3). By Year 5, the main cover at SC was patches of cattail marsh (mainly *Typha latifolia*) and tall, brackish meadow species (mainly *Sporobolus michauxianus*; Figure 9). SC also shares dominant species such as *Sporobolus michauxianus* with the reference site (Supplementary Appendix 3). However freshwater marsh species like *Typha* spp. were much more dominant at the restoration site (approximately 25% cover across all monitoring plots).

At BEL, patches of foreshore salt marsh comprised the main vegetation on the site in Year 1 (Figure 10). These patches had expanded from the pre-construction remnant fringe. *S. alterniflorus* and *S. michauxianus* were the dominant species in these areas, but the patches occurred mainly outside the monitoring plots in Year 1 (Supplementary Appendix 3). These species continued to expand on BEL such that they were dominant by Year 4 (Supplementary Appendix 3; Figure 10). There was also extensive colonization of bare ground by annual halophytic colonizers such as *Atriplex* spp. which occupied approximately 38% of the site by Year 2 and declined in Years 3–4 (Figure 10; Supplementary Appendix 3). Overall, vegetation at BEL has changed substantially since dyke re-alignment with a decline in wet meadow or pasture species and an increase in halophytes such as *S. michauxianus*, *Atriplex* spp. and *Solidago sempervirens* (Supplementary Appendix 3). There is now much closer overlap with the reference site vegetation (Supplementary Appendix 3). BEL also had

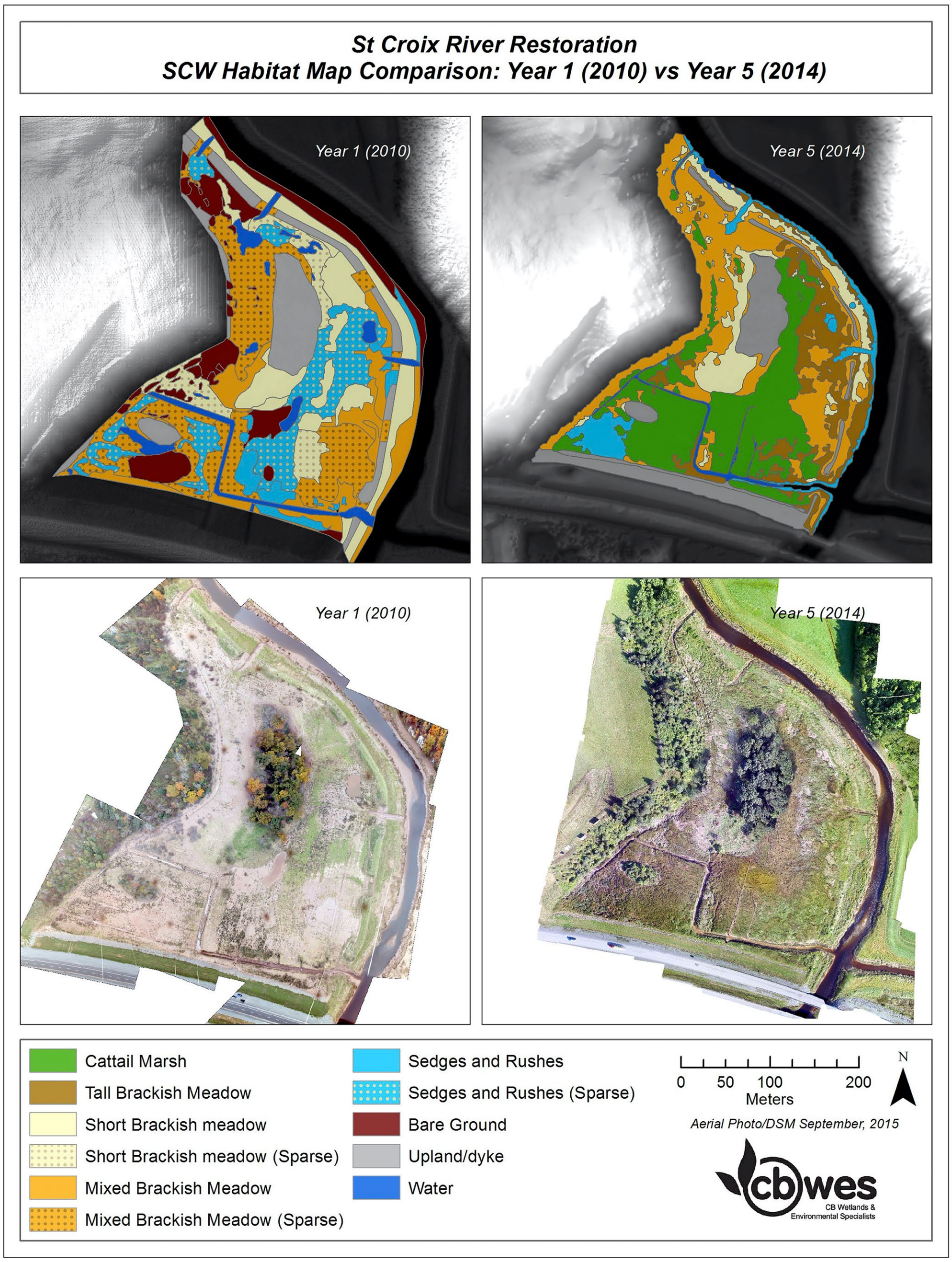

FIGURE 9
Habitat comparison at SC restoration site between Year 1 and Year 5 post restoration.

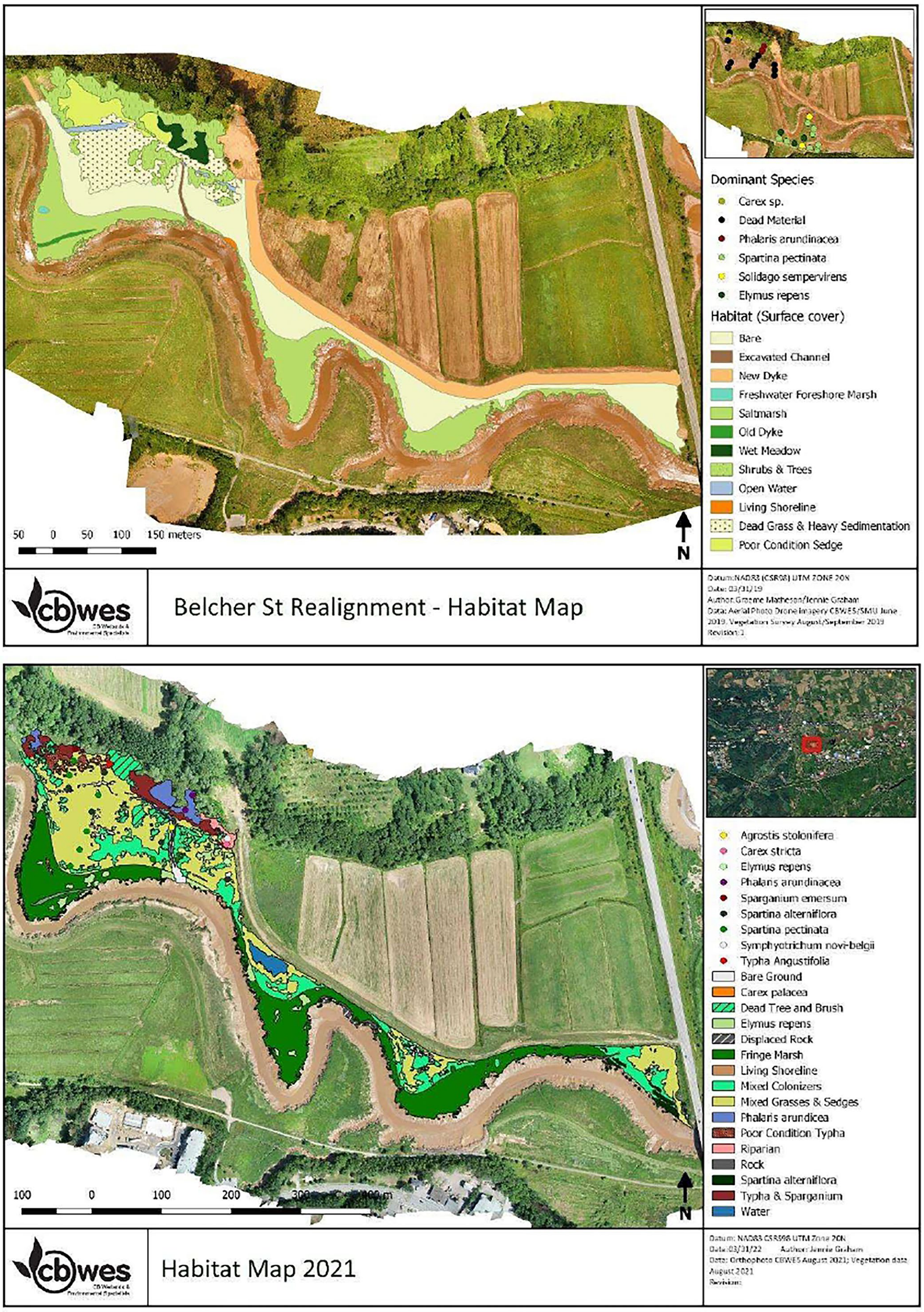

FIGURE 10
Habitat comparison at BEL restoration site: **(A)** Year 1 and **(B)** Year 4 post restoration.

some *Typha* spp. but it only covered an average of 4.8% of the monitoring plots, representing a decline from the pre-restoration condition.

By the end of the study period the dominant halophytes at SC by coverage were: *S. michauxianus* (24%), *Carex paleacea* (8%), *S. alterniflorus* (6%) and *Atriplex* spp. (2.5%). At the SC reference site the dominant species were: *S. michauxianus* 28 and 5.6% *C. paleacea* (Supplementary Appendix 3). In contrast, dominant halophytes at BEL by the end of the study period were: *S. michauxianus* (39%), *S. alterniflorus* (32%), *Atriplex* spp. (14%), *Bolboschoenus maritimus* (~9%), *Solidago sempervirens* (3%) and 1.5% *C. paleacea*. The BEL reference site has *S. michauxianus* (48%), *Solidago sempervirens* (16.5%), *Atriplex* spp. (16%), and *S. alterniflorus* (5.6%) as abundant halophytes (Supplementary Appendix 3).

Average plot plant species richness was similar at both sites pre-restoration (Figure 11A). At BEL richness dropped substantially in the first year post-restoration before returning to levels equivalent to pre-restoration and the reference site by Year 2. SC richness showed no such decline but peaked in Year 2. At SC by year 5 richness averaged five species per plot compared with over seven at the reference site (Figure 11A). Halophytic species richness was zero at SC pre-restoration, increasing to an average of one by year two, approximately double that at the reference site (Figure 11B). At BEL, there were some halophytes present on the site, and richness dropped in the first year post restoration. In Year two, there was a large increase in halophytic richness at BEL, and the site reached equivalence to the reference site by year three. Colonization of halophytes at SC began in Year 1 post but exceeded richness at the reference site by year two (Figure 11B). Halophytic species cover increased, following a similar pattern at both sites. At BEL equivalence with the reference site was achieved by Year three (~88% cover), and SC reached equivalency (~30% cover) by Year two (Figure 11C). Unvegetated areas at both sites increased dramatically in the first year post restoration followed by rapid recovery of vegetation (Figure 11D). Both the change and vegetation cover and the change in halophytic plant cover were weakly positively correlated with the net change in elevation at vegetation plots (Supplementary Appendix 6). This indicates that plots that gained more elevation post-restoration also had higher increases in coverage by any plants and halophytic species in particular.

4. Discussion

Both BEL and SC showed rapid change following the restoration of tidal hydrology. Rapid accretion of sediments buried the original surface and appears to have killed off most of the original vegetation over large areas of both sites. Net elevation changes reflect both aboveground processes of erosion and accretion as well as belowground processes of biomass growth and consolidation/dewatering. In these sites, the large amount of sediment deposited in the first few years drove marsh elevation increases, despite evidence of some losses due to consolidation and dewatering of sediments in Year 2. In contrast, elevation changes were very small at the

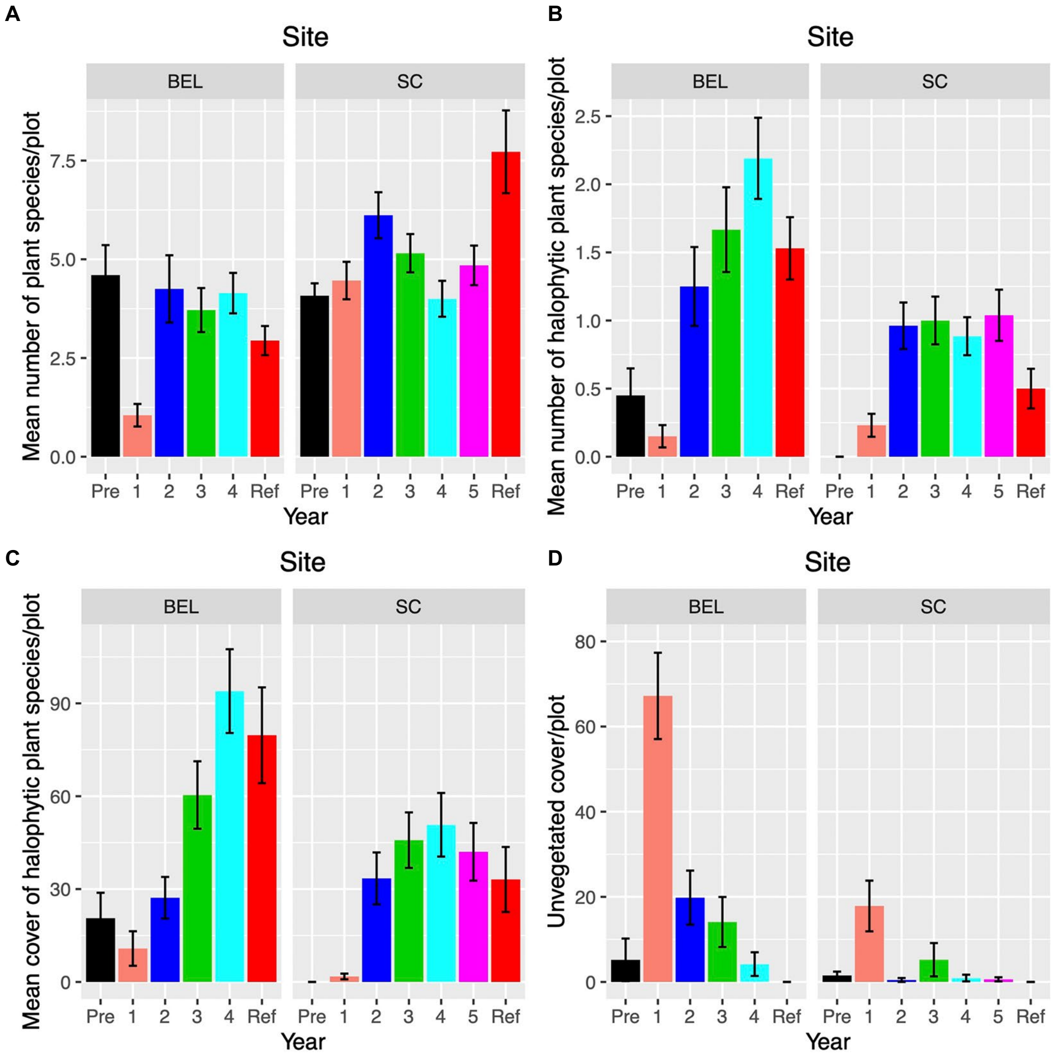

FIGURE 11
Vegetation plot (1m^2) changes over time at BEL and SC restoration sites. "Ref" indicates the reference site corresponding to each restoration site; **(A)** Average plant species richness. **(B)** Average halophytic species richness; **(C)** Average halophytic species cover; **(D)** Average unvegetated cover.

corresponding reference sites suggesting that later in the restoration trajectory belowground and aboveground processes may reach more of an equilibrium.

The rapid accretion of sediments and elevation gains following tidal restoration at BEL and SC contrast with some other sites in the region. Two other tidal marsh restorations completed at Walton and Cheverie Creeks, both within the Bay of Fundy, show much smaller vertical accretion and elevation gains in the first 2–3 years following tidal restoration (van Proosdij et al., 2010; Bowron et al., 2011). Both sites are much closer to the open bay and thus have less freshwater influence and correspondingly higher water salinities. Vegetation recovery was rapid in both Walton and Cheverie restoration, but this is likely due to mortality of pre-existing freshwater and upland vegetation due to exposure to salt water (van Proosdij et al., 2010; Bowron et al., 2011). In contrast, at BEL and SC the main driver of rapid vegetation change was burial of pre-existing vegetation by large amounts of deposited sediments. Plots at BEL and SC that gained more elevation also gained proportionally more coverage of all plant species and halophytic plant species. Plant species at Walton and Cheverie restoration sites also reflect greater saltwater influence with much higher abundance of low marsh plant species adapted to salinity and long inundation periods (e.g., *S. alterniflorus*; van Proosdij et al., 2010; Bowron et al., 2011).

Suspended sediment concentrations in the tidal waters at Walton and Cheverie are high and characteristic of the Upper Bay of Fundy, and similar to those at BEL and SC (van Proosdij et al., 2010; Bowron et al., 2011). The differences in accretion and elevation gain between BEL/SC sites and other restoration sites are likely due to the position of BEL and SC relatively far inland within their respective estuaries. Both BEL and SC are likely to be close to the location of the estuarine turbidity maxima in their tidal rivers. The interaction between the upper extent of tidal salt water and freshwater flow is associated with an increase in turbulent flow that can re-suspend sediments from the riverbed leading to high turbidities (Jay and Musiak, 1994; Burchard and Baumert, 1998). The flocculation of particles can increase deposition of sediment and may increase where salt and fresh waters meet (Manning et al., 2010). The high suspended sediment concentrations and high floc fractions likely led to extremely high deposition at SC and BEL during the first years following the restoration of tidal hydrology.

While the rapid accretion of sediments was important in driving vegetation dynamics at SC and BEL, both sites showed evidence of reductions in elevation gains toward the end of the study periods. This occurred as the marsh platforms became less frequently inundated, although overall totals suggest that both sites are keeping pace with the approximate 0.44 cm•yr.$^{-1}$ sea level rise measured at the Saint John NB tide gage (CHS station 65). Mean annual sea level data points were calculated as annual means from daily water levels downloaded from the Marine Environmental Data Section of Fisheries and Oceans.[4] Long-term monitoring will be required to determine the sustainability of these sites in the face of sea level rise.

Restoration of tidal hydrology at two sites following dyke realignment at Aulac, New Brunswick show rapid accretion in the early years but different vegetation trajectories than at SC or BEL (Boone et al., 2017; Wollenberg et al., 2018; Virgin et al., 2020). The restoration sites at Aulac were also dyked for approximately the same amount of time as SC and BEL, and are exposed to tidal waters with high suspended sediment concentrations (~200 to 1,400 mg•L^{-1}; Bowron et al., 2021). The Aulac sites differ from BEL and SC in that they are situated directly on the open bay, not within the floodplain of a tidal rivers (Virgin et al., 2020). The restoration trajectory at Aulac is characterized by high sediment deposition in the first year followed by consolidation and stabilization in years 2 ~ 5 post-restoration (Virgin et al., 2020). This matches well with the observations at SC and BEL over the same time frames where initial high deposition is followed by a period of low elevation gains as dewatering or other consolidation processes temper the initial elevation gains. The Aulac restoration sites were also lower in elevation than their corresponding reference sites (Virgin et al., 2020). This was also the case at SC and BEL (e.g., Figures 6A,B). Vegetation changes at Aulac included large areas of open, bare mud in Year 1 but followed by patchy revegetation in Years 2 ~ 5. The Aulac site took longer to dewater due to drainage issues possibly created by borrow pits in close proximity to the restoration site. In addition, the initial site elevations relative to the tidal frame were initially too low to support halophytic vegetation establishment (Millard et al., 2013). High sediment deposition rates paired with rapid dewatering and sheltered conditions inland on tidal estuaries seem to have led to rapid revegetation at BEL and SC. Plant communities at Aulac came to be dominated by *S. alterniflorus* rather than *S. michauxianus* or *Typha* spp. due to the position of the site immediately adjacent to the ocean, reflecting polyhaline conditions.

Organic matter content and carbon density decreased after hydrological restoration at both SC and BEL. This represents a switch from more organic soils in the pre-restoration condition to the dominance of minerogenic allochthonous sediments that have a lower overall carbon density than the soils they are replacing. Despite lower carbon density, the high bulk density of the deposited sediments still probably results in a net gain of organic carbon on the sites. We calculated a rough estimate of the amount of carbon added to the system through sediment accretion by multiplying the average vertical accretion rate for each RSET station by the average organic carbon density recorded from sediment cores during the same years, and then converting to a weight of carbon per unit area (Supplementary Appendix 5). The amount of carbon input strongly tracks sediment accretion rates, so the pattern at these sites indicates rapid accumulation of carbon in the sediments early in the restoration process. Equivalence with the reference site is reached after 4–5 years, at least in the case of SC where we have a full 5 years of data (Figure 12). The initial values of carbon inputs (~1,500–3,700 gC/m^2/yr) are comparable values found at other sites in the Bay of Fundy and these show similar declines after the first year (Wollenberg et al., 2018). The restoration site studied by Wollenberg et al. (2018) differed from ours in that it was much lower (closer to open bay) in the estuary compared to our sites and has much less influence of freshwater. These results suggest that tidal wetlands can trap substantial amounts of carbon early in restoration projects if there is heavy deposition of sediments from the tidal waters. The actual amount of carbon sequestered in newly restored salt marshes cannot be estimated with our available data as this would require

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[4] https://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/twl-mne/inventory-inventaire/index-eng.htm

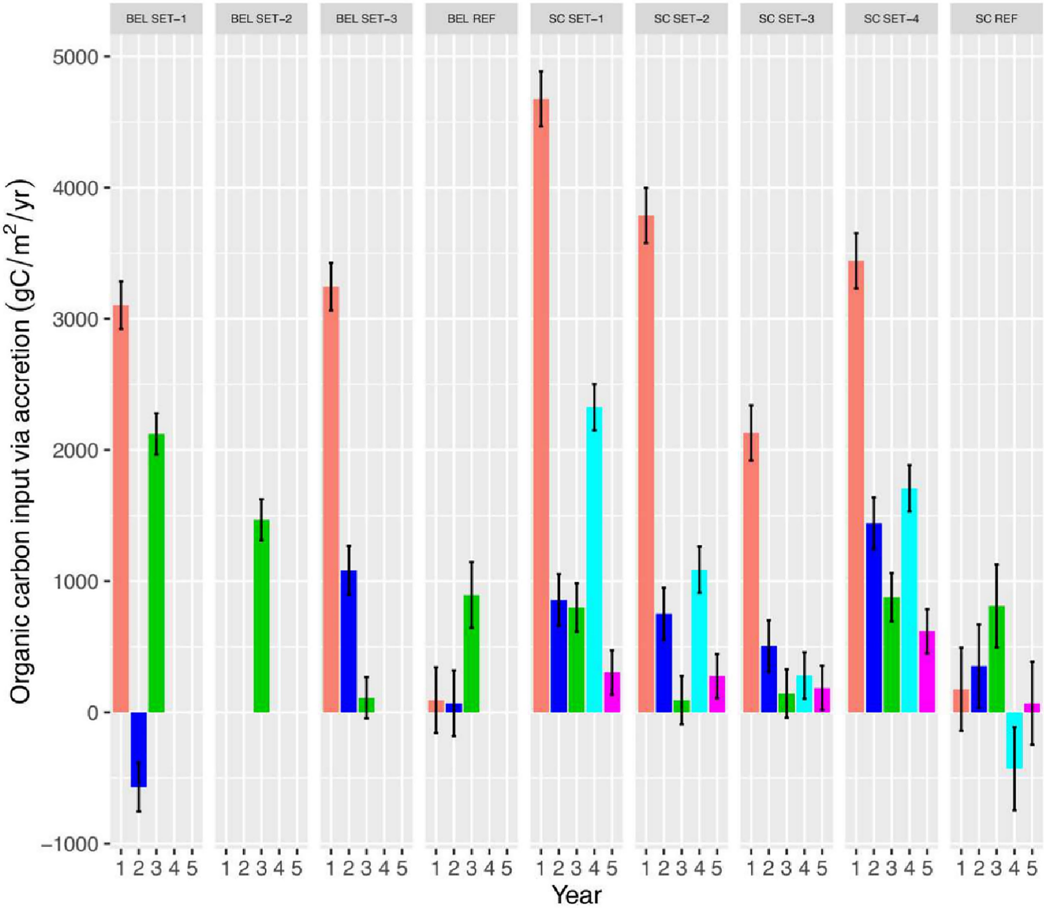

FIGURE 12
Estimated organic carbon input *via* sediment accretion over time at BEL and SC restoration sites.

additional information on belowground productivity and net flux of greenhouse gasses to produce a proper carbon account.

Rapid recovery of vegetation is a hallmark of tidal restoration projects in the Bay of Fundy (Bowron et al., 2012). Vegetation has a major influence of the stability of marsh surfaces and shapes ecomorphodynamics by reducing flow velocities and trapping sediments (Ashall et al., 2016). Rapid development of wetland vegetation occurred at both sites, likely because the accreted sediments created a 'clean slate' for colonization largely unaffected by previous soils and plants. Short ruderal species were common at both sites early post-restoration but tended to be displaced later by taller, more competitive species such as *S. michauxianus* and *Typha* spp. Tidal marsh restoration in sites close to an estuarine turbidity maximum may be expected to share a similar trajectory to BEL and SC provided that there is adequate sediment supply in the water.

While both BEL and SC showed similar overall trajectories post-restoration, vegetation composition differences were evident by Years 4 ~ 5. BEL restoration site is dominated by *Sporobolus* spp., typical of a brackish marsh (Odum et al., 1984) whereas SC is dominated by *Typha* spp., characteristic of freshwater tidal marsh vegetation (Tanner et al., 2002). This pattern likely indicates a greater saltwater influence at BEL compared with SC. Site visits in 2022 to SC indicate that the site is still overwhelmingly *Typha* dominated over 10 years post-restoration. Reference site vegetation conditions are consistent with the restoration site differences as well. Halophyte coverage at BEL reference site is approximately 80% compared with 30% at the SC reference site. Species richness is consistent as well, with the higher values at SC reference associated with more freshwater and upland floras (Odum et al., 1984).

It should be pointed out that neither reference site is a perfect match for its corresponding restoration site. The SC reference site is less frequently inundated than the restoration site, leading to more of an upland component in its vegetation. The BEL reference site has lower habitat diversity than the restoration site (e.g., no patches of *Typha*) but largely overlaps in terms of overall plant species composition. While tidal freshwater marshes share many species with non-tidal fresh marshes, there is very little understanding of the extent and compositions of tidal freshwater marshes in the region. Surveying and establishment of more potential reference sites in tidal brackish and fresh conditions are necessary to further understand the dynamics of vegetation recovery.

Site changes following restoration of tidal hydrology at both BEL and SC are characterized by the following trajectory: massive deposition of sediments in Year 1, burying pre-existing vegetation and soils, dewatering and consolidation of sediments and rapid vegetation spread in Year 2, continued but lower rates of accretion and elevation gain in Years 3–5 accompanied by almost complete coverage by vegetation. Final vegetation composition differs among the sites according to the amount of freshwater reaching the site, including through upland drainage. The proximity of the restoration sites to the estuarine turbidity maxima led to an abundance of flocculated particles which in turn promoted high sediment deposition rates. This helped create a clean slate of substrate for vegetation colonization and a rapid transition from early colonizing species to dominant highly competitive fresh or brackish marsh plants. Restoration of tidal wetland vegetation in similar contexts globally may yield similar trajectories.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

DP: conceptualization, supervision of graduate students and field technicians, analysis writing, and editing. JG: analysis, writing, editing, and preparation of figures. BL: analysis and MSc thesis. TB: editing. EP: analysis. JK: writing and editing. JL: analysis, writing, editing, and preparation of figures. All authors contributed to the article and approved the submitted version.

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Conflict of interest

Authors JG, TB, JK, and KE were employed by the company CB Wetlands and Environmental Specialists.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1112284/full#supplementary-material

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Integrating traditional ecological knowledge into US public land management: Knowledge gaps and research priorities

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Traditional Ecological Knowledge (TEK) is an understanding of natural systems acquired through long-term human interactions with particular landscapes. Traditional knowledge systems complement western scientific disciplines by providing a holistic assessment of ecosystem dynamics and extending the time horizon of ecological observations. Integration of TEK into land management is a key priority of numerous groups, including the United Nations and US public land management agencies; however, TEK principles have rarely been enshrined in national-level US policy or planning. We review over 20 years of TEK literature to describe key applications of TEK to ecological understanding, conservation, restoration and land management generally. By identifying knowledge gaps, we highlight research avenues to support the integration of TEK into US public land management, in order to enhance conservation approaches and participation of historically underrepresented groups, particularly American Indian Tribes, in the stewardship of ancestral lands critical to the practice of living cultural traditions.

KEYWORDS

TEK, Indigenous knowledge, federal land management, conservation, global change, restoration

1. Introduction

Traditional Ecological Knowledge (TEK) refers to an understanding of ecosystems acquired through long-term observations by people inhabiting a region. In contrast to western Scientific Ecological Knowledge (SEK), TEK is often encoded in rituals, beliefs, and cultural practices (Gadgil et al., 1993; Berkes et al., 1994; Berkes et al., 2000). Any group of people routinely interacting with the environment for extended time periods develop TEK, though the term often refers specifically to Indigenous Traditional Ecological Knowledge (ITEK). The term '*traditional ecological knowledge*' has been criticized, since the word '*traditional*' can be construed negatively to imply a regressive or static knowledge system. While TEK has been described using other terms, like '*Indigenous knowledge*' or '*local ecological knowledge*', these monikers are less broadly applied, in part because they do not fully capture the range of knowledge systems represented in contemporary, highly mobile, pluralistic societies and in part because '*traditional ecological knowledge*' quickly established after its use in several seminal publications. Some argue that no single term or definition can capture the plurality of local environmental knowledge, and instead suggest using the term 'TEK' as a working concept to drive inclusive collaborations aimed at achieving sustainable management of ecological systems (Whyte, 2013). In this spirit and given its widespread application, we continue to use TEK here, while acknowledging the drawbacks, limitations and history of the term.

While TEK has existed for millennia, formal description of the term in western scientific literature occurred in the late 1980s and early 1990s (Johannes, 1989; Berkes et al., 2000). Since that time, hundreds of papers have incorporated TEK, and described the value of including local knowledge in management and conservation planning (Gadgil et al., 1993; Berkes et al., 1994, 2000; Moller et al., 2004; Berkes and Turner, 2006). Limited, yet critical, inroads have been established to include TEK, and more broadly, ecocultural-related goals in US federal land management (Armatas et al., 2016; Ens et al., 2016). Simultaneously, frameworks for understanding human roles in ecosystems are evolving (Berkes and Turner, 2006; Liu et al., 2007), providing a springboard to incorporate TEK in management plans, improve protections for cultural natural resources, and identify novel methodology for evaluating the socio-ecological merits of management actions.

Building on this momentum, we review literature related to TEK, explain how and why TEK can inform management, enumerate challenges of incorporating TEK into land management, and address a core debate within this field that suggests that TEK and SEK are incompatible. Using this framework, we highlight best practices, knowledge gaps, and US policies that could be strengthened or expanded to enshrine protection of ecocultural resources in Federal land management. Finally, we support key concepts using a case study of the Emory oak Collaborative Tribal Restoration Initiative (EOCTRI), a collaboration between western Apache Tribal Nations, the US Forest Service, industry, and university researchers to conserve a cultural keystone species in the southwestern US. While numerous opinion pieces or case studies describe the benefits of TEK-integrated land management, to our knowledge, no review has examined the current body of literature to inform US federal land management and policy.

There is an urgent need for a clear strategy to manage ecocultural resources on US Federal land, and to co-develop management actions with local or Indigenous groups (Bach et al., 2019). Indigenous communities, relocated to reservations a fraction of the size of ancestral territories, rely on public lands to access sacred areas and harvest sites to supply natural products used in traditional foods, crafts, and ceremonies (Souther et al., 2021b). Mismanagement of public lands could trigger irrevocable cultural loss since language, traditions and spiritual practices are often tied to particular species and ecosystems (Ens et al., 2016). At the same time, global change has amplified risks of inappropriate management actions and necessitated large-scale restoration initiatives to prevent broad-scale habitat and diversity loss (Benito-Garzón et al., 2013). Rapid integration of TEK into US federal management plans could improve ecological outcomes of these restoration actions, support local communities and tribal sovereignty, and proactively prevent global change exacerbating historical injustices.

2. Methods

To identify literature related to TEK and land management, we conducted systematic searches in both the ISI Web of Science and the SCOPUS databases. We intentionally used broad search terms to retrieve a wide-range of manuscripts linked to this theme. Within both databases, we searched the terms “traditional ecological knowledge” OR “Indigenous knowledge” OR “local environmental knowledge” AND “land management” OR “natural resource management” for occurrence in the title, abstract, or keywords of manuscripts published from 1900 to 2022. This initial search yielded 432 primary research articles. Articles were then screened for relevance, excluding literature that described predominantly human-dominated systems, such as agricultural and urban areas, and literature focused on describing the knowledge system itself, without tangible ecological or management connections. Using this method, we culled the original body of literature by *ca.* 28%, resulting in a total of 284 articles with content that matched the theme of this review (Supplementary Data Sheet S1). We were unable to review a total of 27 publications, primarily because they were not published in English; however, publications excluded due to inaccessibility represented only 6% of the 432 articles from the original search. Finally, we used a snowball sampling technique, in which we followed citation chains associated with emergent themes, adding a further 37 citations. In total, we reviewed 321 manuscripts for this review.

We used an inductive-deductive approach, in which we iteratively developed and refined themes that emerged from the literature (Shamseer et al., 2015). In order to characterize the current TEK literature, we also categorized manuscripts according to manuscript type, which included the classifications, primary research (studies in which data were collected and reported by the authors), literature reviews, case studies and opinion pieces. The literature reviews, case studies, and opinion pieces reviewed here, by our definition, included no direct data collection or analysis. For primary research studies, we noted whether investigators collected social data, ecological data, or both data types. Finally, we classified primary research studies in terms of analytical data treatment. If data were collected, but simply summarized to characterize TEK or other response variables, we indicated that statistics were descriptive. Alternatively, if data were used in hypothesis-testing, studies were classified as employing inferential statistics.

3. Key informational gaps in TEK literature

Overall, the number of TEK-focused studies has increased since the term was initially introduced in the published literature (Figure 1A). Less than half of all studies we reviewed were primary research on TEK, while the remaining publications were classified as case studies, literature reviews, or opinion pieces (Figure 1B). For the majority of primary research publications, authors collected solely social data, with many fewer incorporating ecological data (Figure 1C). Twenty-five percent of primary research studies employed inferential statistics to analyze data, with most describing data patterns only (Figure 1C). Globally, Australia contributed the highest number of publications, followed by the United States, and Canada (Figure 2). Within the US, TEK-research was geographically skewed toward the west coast, with the highest number of publications occurring in California. Notable gaps in publication rates were observed in the central and eastern portion of the country (Figure 3).

Interpretation of the literature reviewed herein should be contextualized within geographic, topical, and quantitative gaps in this TEK literature. Lack of data precludes quantitative techniques, such as meta-analysis, to examine patterns among studies, reducing inferential strength and preventing description of the magnitude of social and ecological impacts of incorporating TEK into management. As an example, several studies stated that incorporating TEK into land management increased species diversity at these sites, but either did not provide quantities or did not compare with a reasonable control method. Like most literature, TEK-focused manuscripts suffer from positive publication bias – in other words, virtually all studies suggest that TEK

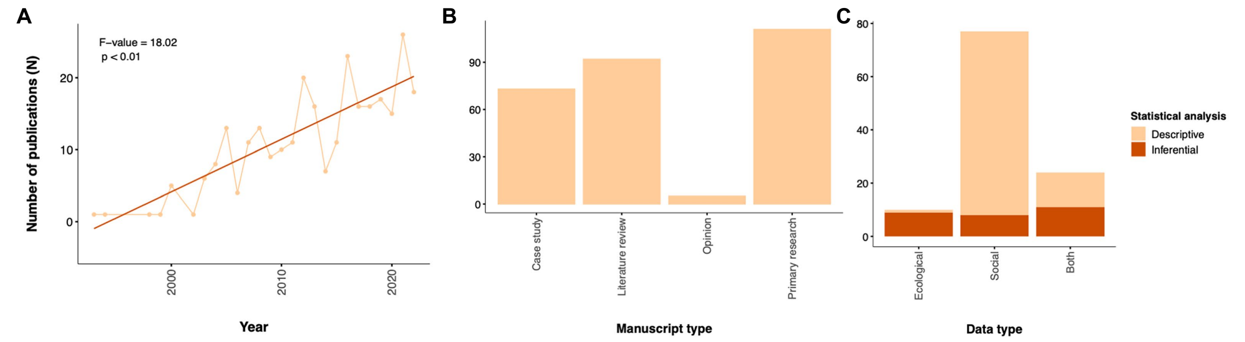

FIGURE 1
Summary information for literature reviewed within this manuscript. **(A)** Publication of TEK-themed manuscripts has increased through time since the year 2000. **(B)** Around half of the TEK-literature reviewed here was primary research and the remaining publications were divided among case studies, literature reviews, and opinion pieces. **(C)** Among the primary research papers, the majority collected social data only and applied only descriptive statistics.

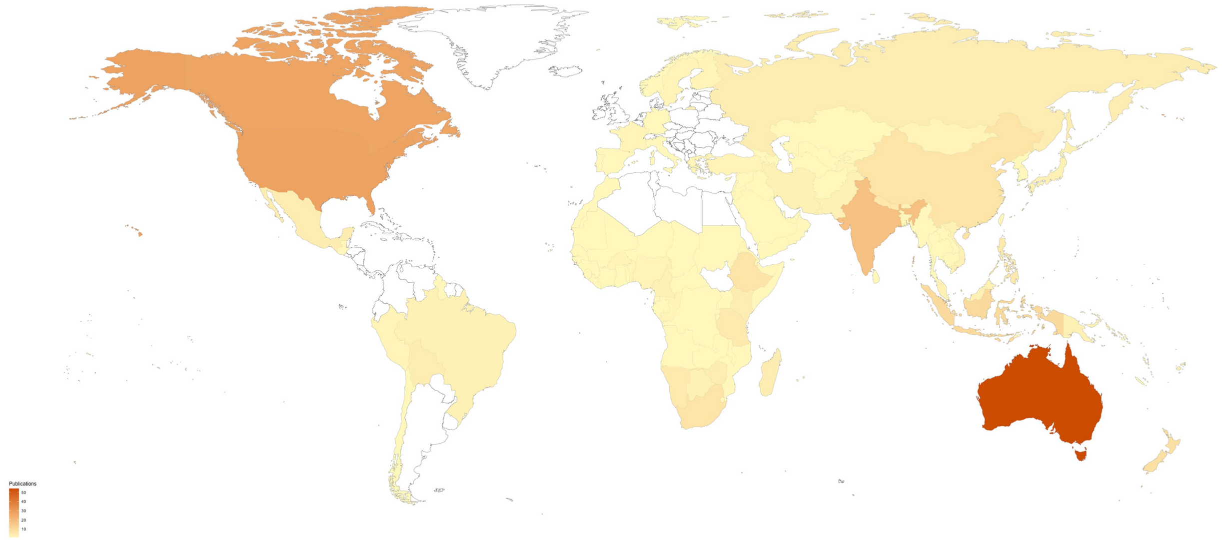

FIGURE 2
Global choropleth map of TEK-publications. The majority of studies have been conducted in the US, Canada, and Australia. South America, Africa, and much of Asia emerge as geographical gaps in TEK-focused studies.

has a positive effect on management outcomes. While we acknowledge these biases, this review revealed broad themes relevant to guide management actions as well as future research trajectories.

4. Traditional ecological knowledge (TEK) overview

4.1. TEK supports sustainable land management

Before modern supply chains introduced global commodities to local communities, human groups, particularly from non-agricultural societies, relied on nearby ecosystems for food, clothing, shelter, and other essentials. Irresponsible use of natural resources would therefore negatively impact reliant human communities. These feedback loops between ecological and social systems drove the development of cultural mechanisms that promoted sustainability (Gadgil et al., 1993; Berkes et al., 2000; Moller et al., 2004; Carpenter et al., 2009; Chapin et al., 2010; Camacho et al., 2012; Folke, 2015; Westley et al., 2021). For this reason, TEK emergent from coupled socio-ecological systems provides insight into sustainable land management practices. Viewing land management through a social-ecological lens can improve outcomes by identifying pathways and feedbacks structured by management decisions that shape ecosystem dynamics and dictates the nature of human-ecological interactions (Rai, 2007; Ruiz-Gutiérrez and Zipkin, 2011; Schultz et al., 2015; Cinner et al., 2016; Gill et al., 2017; Lyver and Tylianakis, 2017; Kobluk et al., 2021).

Traditional ecological knowledge improves understanding of contemporary ecosystems. While the past functional roles of Indigenous peoples have often been ignored or dismissed as insignificant, numerous studies demonstrate that the legacy of past social-ecological interactions manifests in current ecological systems. Humans, throughout time, have profoundly affected ecosystems, acting as ecosystem engineers that shape landscapes, (Smith, 2007), climate, and fire regimes (Kimmerer and Lake, 2001; Bond and Keeley, 2005; Raish et al., 2005; Bliege Bird

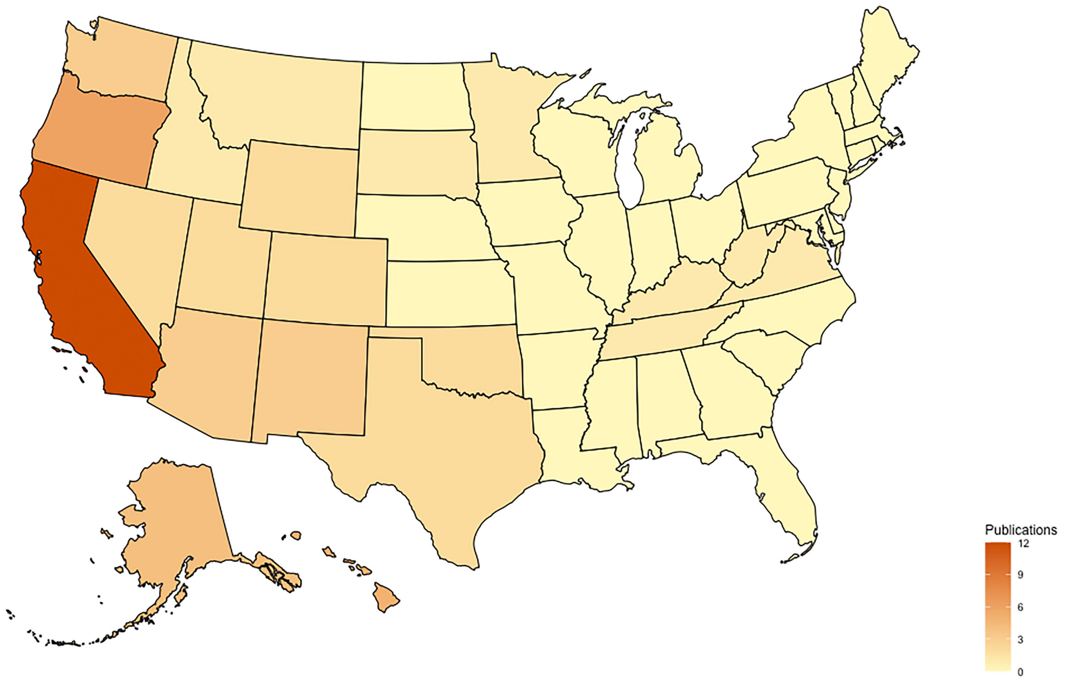

FIGURE 3
Distribution of TEK-focused publications within the US. The highest number of studies were conducted in California. Few studies were observed elsewhere in the US, with a notable gap in the central and eastern portions of the country.

et al., 2008, 2018; Rodenburg et al., 2012; Bird R. B. et al., 2013; Bird M. I. et al., 2013; McCune et al., 2013; Pellatt and Gedalof, 2014; Prober et al., 2016; Albuquerque et al., 2018; Bliege Bird and Nimmo, 2018; Power et al., 2018; Crabtree et al., 2019; Moura et al., 2019; Long et al., 2021; Halpern et al., 2022; O'gorman et al., 2022), as selective agents altering evolutionary trajectories (Rangan et al., 2015; Sullivan et al., 2017), as seed dispersers influencing gene flow patterns (Kondo et al., 2012; Auffret and Cousins, 2013), and as keystone species modifying trophic pathways (Lepofsky and Caldwell, 2013; Dunne et al., 2016; Suraci et al., 2016; Smith et al., 2017; Crabtree et al., 2019; Westley et al., 2021). For some ecosystems, removing traditional human communities has resulted in ecosystem degradation and loss of diversity (Bliege Bird and Nimmo, 2018; Knight et al., 2022).

In the US, new estimates suggest that human groups may have arrived from Asia to North America as much as 21 ka (Moreno-Mayar et al., 2018), indicating that human populations influenced ecosystems for thousands of years prior to the imposition of contemporary land management. The ecological impacts of these groups, particularly effects mediated through cultural burning practices, are thought to have been profound and persistant through time. (Devin and Doberstein, 2004; Kimmerer and Lake, 2001; Raish et al., 2005; Adlam et al., 2021; Halpern et al., 2022; Knight et al., 2022; O'gorman et al., 2022). Indigenous burning reinforced oak and chestnut dominance in the Appalachian forests of the eastern US, maintained the extent of the tallgrass prairie in the Midwest, and shaped the composition of western forests (Kimmerer and Lake, 2001). Cultural burning was widespread, implemented by numerous Indigenous groups, and practiced for myriad reasons; to clear home sites, to encourage the growth of desirable species such as food provisioning-species (i.e., oaks, chestnuts), to send long-distance signals, to foster habitat for important game species or to corral game, and to control pest populations (Kimmerer and Lake, 2001). Integrating TEK into prescribed burning to restore fire regimes has been largely successful (Bond and Keeley, 2005; Bliege Bird et al., 2008, 2018; Butz and Butz, 2009; Pellatt and Gedalof, 2014; Fache and Moizo, 2015; Clinchy et al., 2016; Bliege Bird and Nimmo, 2018; Adlam et al., 2021; Halpern et al., 2022). In addition to cultural burning, Indigenous communities likely shaped ecosystems through multiple pathways, including harvest, hunting, and transport of species, as has been shown for past human populations in other countries. Failure to acknowledge Indigenous functional roles within ecosystems on public lands will result in the omission of key ecological processes (Donlan, 2005; Alagona et al., 2012; Higgs et al., 2014). Engaging local and Indigenous communities for ecological insights may provide a more comprehensive understanding of these systems.

4.2. TEK developed over long time horizons

Traditional ecological knowledge develops *via* long-term interactions of human populations with ecosystems, and thus may contextualize contemporary ecological change, extending descriptions of baseline conditions to time periods preceding modern documentation (Homann et al., 2008; Gratani et al., 2011; Johnson et al., 2015; Armatas et al., 2016; Hopping et al., 2016; Bach et al., 2019). In response to changing climate, species are undergoing widespread changes in the timing of critical life events (i.e., phenology), traits, spatial distribution, and abundance (Thomas et al., 2004; Skelly et al., 2007; Kelly and Goulden, 2008; Lavergne et al., 2010; Walther, 2010; Parmesan and Hanley, 2015). System-level understanding of the timing of important ecological events can help identify phenological mismatches, disruptions of species interactions, and overall phenological shifts in response to climate change (Prober et al., 2011; Moura et al., 2013; Armatas et al., 2016;

Pyhälä et al., 2016; Wiseman and Bardsley, 2016). In North America, many tribes track cryptic seasonal events using the phenology of indicator species (Armatas et al., 2016). The Karuk, Hupa, and Yurok Tribes, for instance, track the migration of edible fish species by following the flowering schedule of dogwood trees (Armatas et al., 2016). Applying comprehensive phenological knowledge spotlights shifts in critical life events and mismatches among interacting species important for understanding ecological impacts of climate change that may not be identified by conventional short-term western scientific studies.

More broadly, long-term landscape perspectives may provide reference conditions for restoration targets and serve as an early warning of species extirpation, state transitions, or other changes from which recovery is challenging (Prober et al., 2011; Uprety et al., 2012; Vinyeta and Lynn, 2013; Johnson et al., 2015; Wiseman and Bardsley, 2016; Souther et al., 2021b). As an example, western Apache Tribes in Arizona, who consume Emory oak acorns as a traditional food, advised the US Forest Service that populations of this oak lacked smaller size trees and produced fewer acorns relative to populations in the past. Tribal members attributed decline in reproduction and recruitment to a variety of factors, including climate change, livestock grazing, and fire suppression (Coder et al., 2005). These observations initiated a landscape-scale Emory oak restoration project, the Emory oak Collaborative Tribal Restoration Initiative (EOCTRI), taking place on USFS and Tribal Lands in the Southwest (Figure 4; Souther et al., 2021a). Without this warning from western Apache people, land managers would likely not have identified Emory oak as a conservation concern, since the presence of long-lived adult trees masks risks to this species. Western Apache TEK drove implementation of conservation interventions for this species prior to irreversible decline (Souther et al., 2021a). Environmental change in response to anthropogenic disturbance of terrestrial and atmospheric systems is occurring at the local-level in complex and idiosyncratic ways (Pyhälä et al., 2016). By engaging local populations, land managers can broaden understanding of ecological change, and make management decisions in real-time as issues emerge (Pyhälä et al., 2016).

4.3. TEK is often holistic

In many cases, TEK is characterized by a comprehensive understanding of ecosystems, with humans situated within biotic communities, and landscapes representing not only ecological features, but also place-based sociocultural memories (Athayde and Silva-Lugo, 2018). Recognition of the complexities and interrelationships within biotic communities broadly supports scientific understanding of ecological systems. The model of coupled human and natural systems, or the concept of the eco-cultural landscape (i.e., the totality of ecological and cultural elements in a region) may improve management and conservation outcomes by appropriately recognizing human roles within ecosystems (Rai, 2007; Cullen-Unsworth et al., 2012; Johansson et al., 2019; Campbell, 2020; Pablo and Córdova, 2021).

Conservation failures due to lack of cultural understanding or engagement have increased recognition of the importance of collaborative planning in US and global resource management. A prime example is the establishment of biodiversity conservation reserves or carbon sequestration offset areas by wealthy countries in equatorial

Mr. Vincent Randall, Cultural Director for Yavapai-Apache Nation, advises Mr. Andrew Stevenson, USFS silviculturist.

Tribal monitors collecting data on soil stability at an Emory oak stand.

For several decades, Apache elders have voiced concern regarding the health of Emory oak ecosystems, specifically noting low levels of seedling recruitment and diminished acorn yields. In 2018, western Apache Tribes, the US Forest Service (USFS), industry groups, and researchers at Northern Arizona University convened to develop a conservation program centered on Emory oak restoration. The Emory Oak Collaborative Tribal Restoration Initiative (EOCTRI) serves as a regional model for co-produced science and conservation. Tribal members identified the management concern and steer research, restoration methodology, and communication activities. Tribal monitor field crews employed through the WestLand Resources, Inc. Tribal Monitor Program receive capacity in western scientific research methodology, and collect the majority of the ecological data that guides adaptive management of restoration activities. Restoration treatments focus on reducing biomass to reduce competition for dwindling water resources and to decrease the likelihood of stand replacing wildfires. Restoration sites will be used to host intergenerational events to support knowledge transfer and cultural activities related to acorn harvest. Novel ways of quantifying effects on human interactions with restored landscapes are being co-developed, in order to measure the socio-ecological objectives of this project. Student training merges SEK and TEK.

FIGURE 4
A model for co-produced science and management in the Southwest.

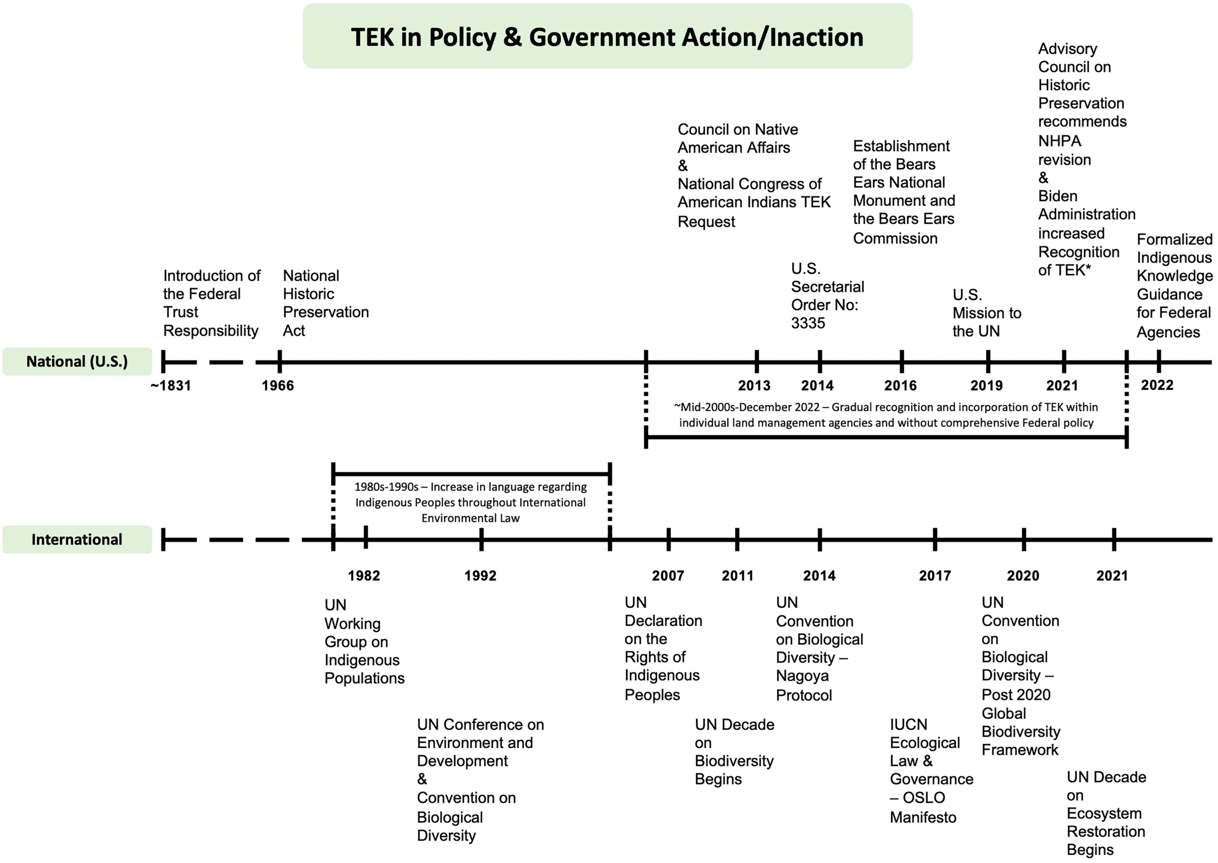

FIGURE 5
A timeline of TEK policy integration at both the national (upper timeline) and international (lower timeline) level. This timeline is not exhaustive but meant to highlight the overall progression of TEK acknowledgment within policy. *The Biden Administration's increased recognition of TEK is represented in policy such as: Memorandum for the Heads of Departments and Agencies, Indigenous Traditional Ecological Knowledge and Federal Decision Making, 2021, U.S. Joint Secretarial Order No. 3403: Fulfilling the Trust Responsibility to Indian Tribes in the Stewardship of Federal Lands and Waters, 2021, Executive Order #14072 Strengthening the Nation's Forests, Communities, and Local Economies, 2022, Executive Order #14049 White House Initiative on Advancing Educational Equity, Excellence, and Economic Opportunity for Native Americans and Strengthening Tribal Colleges and Universities, 2022, and Executive Order #13990 Protecting Public Health and the Environment and Restoring Science To Tackle the Climate Crisis.

regions where lack of consultation with local communities has resulted in ineffective programs (Michon et al., 2007; Dressler et al., 2012; Vaz and Agama, 2013; Albuquerque et al., 2019; Johansson et al., 2019). In Ethiopia, the creation of Reducing Emissions from Deforestation and forest Degradation (REDD) carbon conservation areas increased risk of large fires, reducing or potentially nullifying overall carbon sequestration gains (Johansson et al., 2019). More broadly, ignoring local traditions and use patterns has frequently resulted in conflict and non-compliance with imposed regulations; problems largely resolved by co-development of management plans with local communities (Rodriguez-Navarro, 2000; Anderson et al., 2005; Spak, 2005; Michon et al., 2007; Dressler et al., 2012; Uprety et al., 2012; Vaz and Agama, 2013; Indrawan et al., 2014; Albuquerque et al., 2019; Kiage, 2019; Nanlohy et al., 2019; Fabre et al., 2021). Inclusive land governance often results in increased engagement and stewardship behavior when local values and priorities are incorporated into land management practices, creating a shared vision for governance (Oettlé et al., 2004; McGetrick et al., 2015; Long and Lake, 2018; Pyke et al., 2018; Tsai, 2020; Skroblin et al., 2022). This is particularly important for reducing conflict when managing pooled or common resources (Kanwar et al., 2016). Applying a coupled human-natural system lens is critical to meet the multiuse missions of many US public land managers that must maintain ecological health, while supporting social uses of national forests, grasslands, and other areas.

4.4. Intrinsic value of TEK

Though this review focuses on improving ecological outcomes by integrating TEK into land management, we recognize the intrinsic value of ecocultural practices, traditions, and local ecological knowledge (Carino et al., 2009; Mackey and Claudie, 2015). For much of the 20th century, society broadly valued local knowledge of flora and fauna due to potential economic contributions of new foods, medicines or other products. While the benefit of TEK for identifying and managing these resources is still important (Turner et al., 2000; Chapman, 2008; McCallum and Carr, 2012; Rodenburg et al., 2012; Maroyi, 2017, 2022; Nalau et al., 2018; Strenchok et al., 2018; Guerrero-Gatica et al., 2020; Abbas et al., 2022), ecocultural resources have been more holistically valued within the framework of 'Cultural Ecosystem Services' (CESs). Cultural ecosystem services include intangible, yet invaluable, functions beyond supplying commodities, such as providing inspiration, aesthetically pleasing views, a sense of place, cultural vitality, and recreational, educational and fellowship opportunities

(Paudyal et al., 2016; Pascua et al., 2017). The CES categorization provides a strong foundation to better value human connections to ecosystems, yet may not fully capture the pivotal role of TEK in preserving culture, language and relationships. Cultural keystone species, a term coined by Nabhan and Carr (1994), describes species that feature so heavily in language, ceremonies, traditions and oral history to be necessary for cultural practices. The cultural keystone concept could be extended to describe ecosystems, places, and landscapes necessary to sustain culture.

Incorporating local and Indigenous perspectives into land management to support the continuation of cultural practices is increasingly valued, even when financial gains are not a primary driver (Kruger, 2005; Long and Lake, 2018; Lindsay et al., 2022; Skroblin et al., 2022), as exemplified by several recent court rulings requiring dam removal to support traditional fishing (Long and Lake, 2018). Support of bio-cultural sovereignty, the right of people to access landscapes and natural resources necessary for cultural practice, itself an important management goal (Cleary, 2005; Jackson et al., 2005; Spak, 2005; Alan et al., 2006; Jackson, 2006; Menzies, 2006; Christensen and Grant, 2007; Houde, 2007; Banjade et al., 2008; Grice et al., 2012; Uprety et al., 2012; Baldy, 2013; Brondízio et al., 2021; Fabre et al., 2021; Parsons et al., 2021; Lindsay et al., 2022). In addition to advancing favorable ecological outcomes, co-management of natural resources with local and Indigenous groups, protects cultural diversity, and power-sharing, a core value of democratic societies (Devin and Doberstein, 2004; Spak, 2005). As medical research increasingly demonstrates health benefits of interactions with nature (Driessnack, 2009; Hansen et al., 2017; Chaudhury and Banerjee, 2020), access to eco-cultural resources may be seen as a fundamental human right (Menzies, 2006). Given the reliance of local and Indigenous groups on nearby ecosystems for cultural practices and subsistence, mismanagement of natural resources disproportionally affects these often marginalized groups. Inclusive governance is particularly important to avoid exacerbating historical injustices and inequities as climate change drives shifts in ecosystems and natural resources (Pollino et al., 2007; Banjade et al., 2008; Blanch, 2008; Vinyeta and Lynn, 2013; Maldonado et al., 2014; McGetrick et al., 2015; Schick et al., 2018). Valuation of alternative knowledge systems is important in modern pluralistic societies and may drive novel insights of complex coupled human and ecological systems (Colchester, 2004; Houde, 2007; Bohensky and Maru, 2011). Integration of TEK and goals related to eco-cultural protections in to land management strategic planning is generally supported by local communities and should be prioritized by US land management agencies (Nanlohy et al., 2019; Fabre et al., 2021; Skroblin et al., 2022).

5. Applying TEK to improve land management

5.1. Harvest practices and single species conservation

Ecological constraints and human reliance on ecosystems reinforced norms associated with ecological sustainability, which can be broadly applied to single species management (Turner et al., 2000; Moller et al., 2004; Phuthego and Chanda, 2004; Menzies, 2006; Rai, 2007; Ulluwishewa et al., 2008; Mulyoutami et al., 2009; Newmaster et al., 2011; Nimachow et al., 2011; Baldy, 2013; Walsh et al., 2013; Childs and Choedup, 2014; Mackey and Claudie, 2015; Mavhura and Mushure, 2019; Shokirov and Backhaus, 2020; Alexander et al., 2021; Kobluk et al., 2021; Negi et al., 2021). Traditional harvest practices often integrate triggers to slow, pause or alter harvest based on on-the-ground observations, adjusting behavior to prevent resource degradation (Walsh et al., 2013; Mavhura and Mushure, 2019). In British Columbia, the Haítzaqv (Heiltsuk First Nation) harvest feather boa kelp for food, ceremonial use and as a trade item. Ecological analysis of traditional harvest revealed that the rate of removal of kelp fronds was similar to loss incurred through wave action during the growing season, revealing how traditional harvest mimicked natural ecological processes. Moreover, the Haítzaqv provided researchers with a variety of environmental conditions, like water temperature and wave exposure, that support recovery after harvest (Kobluk et al., 2021).

In some cases, traditional human harvest behavior may shape evolutionary, demographic or spatial characteristics of populations (Herrmann, 2005, 2006; Cosby et al., 2022). In Chile and Argentina, monkey puzzle trees (*Aruacaria araucana* (Molina) K. Koch), a threatened species of conifer, are an important food source for Mapuche people, supplying nutritious nuts, called *piñones*. The accepted Mapuche harvest technique of men climbing to harvest nuts, constrained which trees within a population were harvested, since harvest was limited to trees that could support the weight of an adult human (Herrmann, 2005, 2006). This not only promoted sustainable harvest, but may have shaped genetic diversity patterns, demographic structure of populations, and evolutionary trajectories, by allowing younger or smaller trees to disproportionally contribute to population growth, since seeds from smaller class trees avoided harvest. Species valued as food, fiber, or medicine may drive traditional management practices that influence ecosystems at the landscape-level. The Karuk and Yurok Tribes of California reduce acorn infestation of black oaks by filbertworms and filbertweevils through cultural burning (Halpern et al., 2022). Management for this important first food may have shaped fire regimes and community composition within Californian forests (Kimmerer and Lake, 2001; Adlam et al., 2021; Halpern et al., 2022). Understanding human interactions with such cultural keystone species may yield broad insights about landscape management and restoration.

As globalization and other forms of anthropogenic change increase pressure on natural resources, integrating TEK into regulations supports sustainable harvest and can reduce conflict over resources (He et al., 2011; Childs and Choedup, 2014). In China, land managers successfully employed TEK to establish harvest laws to regulate an emergent mushroom market (He et al., 2011). In response to the commercialized harvest of *Thelephora ganbajun*, or ganba fungus, a type of coral mushroom native to the Yunnan province of China, land managers co-produced regulations with local communities who had sustainably harvested this mushroom, in order to support the conservation of both the mushroom and the tradition of harvest practiced by Yunnan communities (He et al., 2011). Applying traditional harvest techniques may ensure sustainable harvest, and thus support continued cultural connections with harvested species, when global markets lead to increased demand on local resources.

5.2. Improving ecological assessments

Engaging local communities in the development of ecological monitoring and assessments has the potential to advance our ability to track ecological changes (Goodall, 2008; Kakinuma et al., 2008; Ens et al., 2010; Rasalato et al., 2010; van de Pol et al., 2010; Prober et al., 2011; Leonard and Parsons, 2013; Moura et al., 2013; Gratani et al., 2014; Behmanesh et al., 2016; Savo et al., 2017; von der Porten et al., 2019; Mugambiwa and Makhubele, 2021; Pyke et al., 2021; Souther et al., 2021b). First, incorporating TEK in ecological assessments can increase monitoring efficiency and coverage, which is particularly important, given that many land management agencies lack the resources to support comprehensive monitoring programs (Souther et al., 2021b; Teixidor-Toneu et al., 2022). Traditional ecological knowledge enhances efficiency by applying detailed understanding of landscapes to survey methodology (Ballard et al., 2008). As an example, one group tasked with monitoring lynx populations on public lands in California trained local community members to census lynx. Locals increased the completion speed of the surveys due to superior knowledge of the landscape and of lynx population locations (Ballard et al., 2008). Integrating TEK of local groups into monitoring is particularly important when species or phenomena of interest are not readily observed by the general public, federal staff, or researchers, such as when focal species are remote, rare or cryptic (Parlee and Manseau, 2005; Goldman, 2007; Marin et al., 2017; Deb, 2018; Pyke et al., 2018; Baker and Constant, 2020; Sloane et al., 2021; Teixidor-Toneu et al., 2022).

Local communities distil complexity of ecological systems using TEK, employing methods like identifying indicator species linked to more complex ecological phenomena, which can be used to simplify monitoring procedures (Armatas et al., 2016; Behmanesh et al., 2016). In Iran, for instance, the government modified rangeland degradation assessments to incorporate indicators (i.e., abundance or depletion of particular grasses) used by local pastoralists, supporting widespread and consistent documentation of key ecological processes (Behmanesh et al., 2016). Local communities may also have fine-scale knowledge of systems, critical for effective management (Pyke et al., 2018; Baker and Constant, 2020; Matshameko et al., 2022). Cree fishermen in Canada described more morphotypes of fish species, potentially representing important genetic variation in fish populations, and provided more detailed information on seasonal movement, spawning behavior, and reproductive timing compared to SEK research conducted in the same region (Marin et al., 2017). These observations allowed managers to attribute declining lake trout populations, an important game fish and food source, to climate change driven loss of trout prey base (Marin et al., 2017). Finally, the deep-time perspective of TEK may be leveraged to define baseline conditions, establish restoration targets (Uprety et al., 2012; Leonard and Parsons, 2013; Gratani et al., 2014), track global change impacts (Armatas et al., 2016), and serve as an early warning system of large-scale ecological state transitions (Souther et al., 2021a). Programs integrate TEK into monitoring in a variety of ways, like co-developing monitoring protocols with local and Indigenous groups and overlaying these procedures with western SEK techniques to extrapolate observations from monitoring plots using local insights (Ballard et al., 2008). Ecological studies and management actions employing Multiple Evidence-Based approaches, which include both western and traditional science methods, likely yield a more comprehensive ecological understanding and foster creative solutions to address environmental problems (Pyke et al., 2021).

5.3. Enhancing management actions

Indigenous and local communities interact with ecosystems in a variety of ways, ranging from species-specific interactions, like removing undesirable species to reduce competition with preferred plants, or acting as ecosystem engineers by modifying soils for cultural and food-generating purposes. TEK-guided management may especially improve ecological outcomes when ecosystems co-evolved with human populations long-term, and adoption of traditional behaviors represents a restoration of essential human functions within the landscape (Pellatt and Gedalof, 2014). In Australia, reintroduction of cultural burning practiced by Aboriginal people produced unexpected secondary ecological changes, increasing the diversity and abundance of mid-sized mammalian species, whose numbers were steadily declining (Gott, 1982; Kay, 1994; Bond and Keeley, 2005; Smith, 2007; Bliege Bird et al., 2008; Kondo et al., 2012; Bird M. I. et al., 2013; Bird R. B. et al., 2013; Rangan et al., 2015; Boivin et al., 2016; Clinchy et al., 2016; Suraci et al., 2016; Smith et al., 2017; Sullivan et al., 2017; Vigilante et al., 2017; Albuquerque et al., 2018; Bliege Bird and Nimmo, 2018; Power et al., 2018; Crabtree et al., 2019). Similar patterns are emerging in the US, where cultural burning supports land management agencies efforts to re-establish natural fire regimes following 20th century fire suppressions policies (Adlam et al., 2021; Long et al., 2021). Reintroduction of fire in fire-adapted systems reduces risk of catastrophic, stand altering wildfires and removes invading, non-fire adapted species, decreasing competition for resources of endemic species. In California, US, for instance, TEK-integrated forest restoration reduced burn severity and damage caused by wildfires relative to untreated areas (Slaton et al., 2019). Other forms of traditional land management, such as grazing strategies and alteration of vegetation for agroforestry or hunting, increases plant diversity, principally through increasing the heterogeneity of management strategies on the landscape (Pyke et al., 2018; Silva-Rivera et al., 2018; Uchida and Kamura, 2020; Fabre et al., 2021). Developing a understanding of ecological systems, which integrates human functional roles, provides a more comprehensive ecological perspective and is particularly important for developing appropriate restoration actions.

Co-development of management strategies generally improves land management outcomes (Michon et al., 2007; Vaz and Agama, 2013; Albuquerque et al., 2019; Forest et al., 2019). Engaging local populations in land management decisions has been found to increase buy-in on agreed upon practices, lead to stewardship behavior and reduce exploitation of shared natural resources (Sanchez, 2000; Spak, 2005; Mackey and Claudie, 2015; Sheil et al., 2015). Similarly, regulations developed specifically to enhance cultural connections to the landscape has been shown to increase engagement with public lands and reduce conflict (Rodriguez-Navarro, 2000; Indrawan et al., 2014; Matthews, 2016). On some tribal lands, management is shifting away from western scientific concepts of management, and explicitly making decisions that improve the viability of first foods (Quaempts et al., 2018). Reframing management of public lands to prioritize cultural ecosystem services may result in more equitable land management, increase long-term support for public lands, and reduce conflict with land management agencies.

Ecological restoration projects are growing in number and scale, particularly as anthropogenic change increases the frequency and severity of disturbances, like wildfire and drought (Copeland et al., 2018). Traditional ecological knowledge can contribute to restoration success in several key ways. Local or Indigenous groups may identify restoration plant materials that are not only adapted to regional climate and soils, but are also utilized by local populations, thus improving the intrinsic value of restored lands and encouraging stewardship behaviors (Gaur and Gaur, 2004; Tarbox et al., 2020). 'Traditional technologies' may represent low-cost, culturally appropriate methods of landscape restoration. Rock dams (commonly referred to as *trincheras* or, *gabions*, in the Southwest US) are used in arid and semi-arid regions to promote growth of vegetation (Bainbridge, 2012; Cassin et al., 2021; Norman et al., 2022). These rock dams slow water infiltration and stabilize soil during rain events driving revegetation in degraded areas. The Zuni people create waffle gardens to grow dryland crops (Bainbridge, 2012).

By creating indentations in the soil for planting, dryland farmers encourage water to accumulate at the base of the plant. Applying similar techniques prior to reseeding plant materials following disturbance in dryland areas could increase plant recruitment, which is notoriously low in these systems (Bainbridge, 2012).

5.4. Identification of protected areas

Many Indigenous groups identify sacred areas (Das et al., 2021), which often represent unique species assemblages, high numbers or performance of culturally important species, and/or areas with an abundance of a limiting resource (i.e., water; Watson et al., 2003; Rai, 2007, 2011; Boillat et al., 2013; Mackey and Claudie, 2015; Friday and Scasta, 2020; Utami and Oue, 2021). In India, sacred groves of trees have higher plant diversity relative to similar unprotected habitat (Rai, 2011). The Minangkabau people in Indonesia protect areas within forests and river habitat that serve as a source population for fish and other natural resources, ensuring the long-term provisioning of these resources (Utami and Oue, 2021). Higher diversity and function of these systems may be driven through cultural practices or because these regions are ecologically unique. Regardless, incorporating sacred areas into land management strategies can improve landscape-scale conservation and ecological resilience in the context of climate change by capitalizing on extant human connections to place (Watson et al., 2003; Herrmann, 2006; Rai, 2011; Kamal and Lim, 2019; Das et al., 2021; Utami and Oue, 2021). Many Indigenous and local groups connect lineages and family to particular places. Ensuring access to these areas is important for the health of human populations and culture, while also encouraging land stewardship (Mackey and Claudie, 2015). Prioritization of sacred areas for TEK-integrated management planning, conservation and restoration actions protects ecologically important areas, while simultaneously supporting cultural practices, and priorities of local and Indigenous groups (Rai, 2007).

5.5. Identifying and coping with novel threats posed by global change

Long-term perspectives allow the identification of novel threats posed by rapid global change, and can serve as an early warning system for catastrophic ecological events (Seely, 1998; Macharia, 2004; Pamo, 2004; Pollino et al., 2007; Goodall, 2008; Liwenga, 2008; Vaarzon-Morel and Edwards, 2012; Barber et al., 2013; Leonard and Parsons, 2013; Lepofsky and Caldwell, 2013; Ruiz-Mallén and Corbera, 2013; Armatas et al., 2016; Austin et al., 2017; Farimani et al., 2017; Kainamu-Murchie et al., 2018; Kaiser et al., 2019; Arias-Bustamante and Innes, 2021; Copes-Gerbitz et al., 2021; Sinta et al., 2022). Integrating TEK into management of ecosystems affected by global change may improve outcomes, since TEK guides management actions based on ecological indicators rather than arbitrary jurisdictional or bureaucratic dictates (Bach et al., 2019). As an example, Aboriginal Australian-led weed management activities, cataloged invasive weeds based on their effects and roles within ecosystems rather than government-generated categories, like native/non-native status or abundance, which may or may not reflect impacts to ecosystems (Bach et al., 2019). Traditional ecological knowledge may also provide technological advances to natural resource management of emergent threats. In Australia, Aboriginal Australians applied natural piscicides developed for fishing to reduce abundance of invasive tilapia (Gratani et al., 2011, 2014). Since TEK-management actions are tied to temporal ecological processes rather than Gregorian calendars or funding calendars, they are easily modified to account for global change. For instance, many local and Indigenous communities ignite fires based on observed fuel loading or the occurrence of seasonal rains, allowing flexibility to shift practices that result in desired conditions (Butz and Butz, 2009; Armatas et al., 2016). An understanding of social systems related to land management may support adaptive responses to changing environmental conditions by identifying beliefs, needs or behaviors that support or constrain mitigation (Leonard and Parsons, 2013). Impoverished communities in Peru prioritized meeting immediate existential needs, precluding long-term planning necessary for climate adaptation (Popovici et al., 2021). In this case, effective climate change-integrated management also addressed societal needs of Peruvian communities. In addition to improving climate adaptation strategies, local and Indigenous people should be involved in climate adaptation planning to prevent exacerbating historic injustices, since cultural practices depend on species and places that may be imperiled by climate change (Bardsley and Wiseman, 2012; Ruiz-Mallén and Corbera, 2013; Maldonado et al., 2014; Beamer et al., 2021; Souther et al., 2021a).

5.6. The role of western scientific knowledge in the TEK-management paradigm

Traditional ecological knowledge and SEK systems are frequently contrasted, and cited as a primary barrier that prevents incorporation of TEK into land management. While some contend that TEK and SEK are inherently incompatible (Bohensky and Maru, 2011), in practice these knowledge systems are largely complementary, providing distinct benefits and possessing inherent limitations (Moller et al., 2004; Cullen-Unsworth et al., 2012; Holmes and Jampijinpa, 2013; Johnson et al., 2015; Holtgren and Auer, 2016; Zahn et al., 2018; Keats and Evans, 2020). Traditional ecological knowledge provides a long-term and comprehensive view of ecological systems, which can provide key insights for scientific inquiry and advance ecological disciplines (Moller et al., 2004). Scientific disciplines have developed experimental, statistical, and instrumental methodology that allow researchers to attribute causality to particular phenomena, detangle effects of multiple variables, and quantify the magnitude and direction of ecosystem responses to various factors. The peer-review process and mandate to publish findings supports quality control and knowledge transmission. While advancing understanding of natural phenomena, the scientific process is limited by the accuracy of instrumentation and bounds on the complexity and realism of experiments, and in some cases may not have the capacity to test hypotheses posited by TEK-holders.

Some suggest that validation of TEK-generated hypotheses using the western scientific process is disrespectful and derivative (Bohensky and Maru, 2011; Gratani et al., 2014). Without exception, no research should take place without express support from local or Indigenous communities, and TEK must be properly attributed to knowledge-holders. However, issues of disrespect can be largely addressed by valuing TEK as a complementary and important form of knowledge, and by acknowledging the limits of scientific inquiry (McMillan and Prosper, 2016). In Canada, land managers and Indigenous Canadians, adopted the conceptual framework of ‘Two-Eyed Seeing’, with a focus on respecting both knowledge systems and working towards mutual understanding and integration of different viewpoints in land management decisions (McMillan and Prosper, 2016). With a respectful approach, SEK can codify lessons derived from TEK, which has several important benefits. First, Indigenous and local groups are not monolithic, but represent a diversity of opinions, observations, and beliefs, which means that there may be competing hypotheses generated within communities not easily translated into management recommendations without testing (Kiptot, 2007; Knapp and Fernandez-Gimenez, 2009; Fritz-Vietta et al., 2017; St Laurent et al., 2017; Albuquerque et al., 2019; Baker and Constant, 2020; Friday and Scasta, 2020; Varghese and Crawford, 2021). Secondly, while SEK is limited in scale and scope, strict adherence to the scientific process limits bias and erroneous conclusions. Devaluing scientific knowledge has significant risks and drawbacks, as exemplified recently during the COVID-19 pandemic in which a large portion of the US population ignored medical recommendations, prolonging and extending the reach of the pandemic with catastrophic loss of life, particularly in Indigenous communities (Hatcher et al., 2020; Wang, 2021).

Federal land-managers are often tasked with maintaining ecological integrity while supporting multi-use mandates for public lands. Certain social and cultural preferences are prioritized in land management, even when ecological sciences suggest negative impacts. A key example is the development of roadways for on and off-road vehicles to access public lands for recreational purposes. Development of roadways negatively impacts ecosystem connectivity and wildlife behavior (Trombulak and Frissell, 2000; Gelbard and Belnap, 2003), yet is broadly accommodated by land management agencies, since providing public access is an inter-agency value. Protection of traditional ecological knowledge and ecocultural resources should be similarly prioritized in federal land management for cultural benefits alone, regardless of consensus of TEK and SEK.

6. Challenges to integrating TEK into land management

6.1. Lack of financial support

Co-developing management strategies that integrate TEK with local and Indigenous communities is time-consuming and resource intensive, in ways that are difficult to justify under current budget, funding, and performance assessment structures. Months of engagement may result in a single document, management action or other deliverable; yet those months of collaborative planning are vital for ethical project management (Long and Lake, 2018). Many funding sources do not provide support for project co-development, leading projects to skip the critical step of building trust and consensus (Görg et al., 2014; Johnson et al., 2015; Woodward and Marrfurra McTaggart, 2016; Pristupa et al., 2018; Adlam et al., 2021). Funding constraints often prevent providing food and travel to participants, depressing participation of historically disadvantaged, impoverished, or rural groups. Similarly, funding may not support appropriately-priced honoraria to support TEK transfer (Adlam et al., 2021). As one member of the EOCTRI directory board explained, Indigenous elders are perceived in a similar way as PhD scientists, and deserve adequate compensation for expertise.

6.2. Institutional norms and barriers

Federal, and more generally, US workforce norms that promote transience preclude meaningful long-term engagement with communities. Upward mobility within many Federal agencies often requires detailing into and/or accepting positions in other regions across the country (Diver, 2016). Revolving doors of key project personnel limit the ability to build the trust and relationships to effectively engage with local or Indigenous communities. Top-down organizational systems also echo unjust power structures, while simultaneously limiting access of local and Indigenous community members to higher level managers to co-develop management plans (Robbins, 2000; Ferse et al., 2010; Ogbaharya and Tecle, 2010; Pickering Sherman et al., 2010; Raymond et al., 2010; Gallemore et al., 2014; Diver, 2016; Schick et al., 2018; Fache and Pauwels, 2020). At times, excellent co-developed projects spearheaded by lower-level federal employees are never realized due to lack of upper-level engagement and buy-in, exacerbating sentiments of mistrust (Gallemore et al., 2014). Disciplinary and organizational silos within federal agencies and academic institutions are often inherently incongruous with holistic concepts embodied in TEK. The structure of these systems adds to project inertia, since completing the necessary tasks and gathering decision-makers to move projects forward is time-consuming. Short-term funding cycles, which typically provide a maximum of 5 years of project support, do not permit sufficient time to develop the relationships and programmatic infrastructure necessary for successful project completion and delivery of meaningful products (Keppel et al., 2012). Extending timelines for project completion may result in disengagement of local communities (Ross and Pickering, 2002; Henn et al., 2010; Görg et al., 2014).

6.3. Informational sensitivity

Due to historic injustices, many local groups, particularly Indigenous communities, are hesitant to share cultural information with the broader public (Pinel and Pecos, 2009; Johnson et al., 2015; Lynch et al., 2017; Baker and Constant, 2020). Concerns around information security may make Indigenous communities less likely to engage with land management agencies to protect cultural resources or integrate TEK into practice. Co-produced management strategies must develop strong rules regarding the release, use and disclosure of information (Chapman, 2008; Singh, 2008; Pinel and Pecos, 2009; Holcombe and Gould, 2010; Johnson et al., 2015; Lynch et al., 2017; Baker and Constant, 2020). Formalized data management plans and information sharing agreements should be developed to protect both privacy and intellectual property of local and Indigenous groups. Informational advisory boards, like the EOCTRI *Chi'chil* advisory board, can review content prior to publication (Figure 4). Western scientific scholars are codifying methods to cite and attribute local and Indigenous knowledge (MacLeod, 2021). Incorporation of TEK into management must not be extractive, but beneficial to participating groups. Governing and academic institutions should support the professional development of local and Indigenous leaders to guide appropriate use and incorporation on TEK (Latulippe and Klenk, 2020).

6.4. Disparate data types

Traditional ecological knowledge is often passed through generations and communities in oral histories and information is generally qualitative, rather than quantitative (Prober et al., 2011; Long and Lake, 2018). For governing or land management institutions, analytical evidence generated through quantitative statistical approaches is often favored, and thus TEK is often translated to SEK frameworks (Ross and Pickering, 2002; Pickering Sherman et al., 2010; Lemieux et al., 2018; Lindsay et al., 2022). Translating TEK to SEK at times results in losses of meaning, because topics of faith or spirituality by definition cannot be tested *via* the scientific process and thus are dismissed as irrelevant to management (Prober et al., 2011; Long and Lake, 2018). Such cultural differences between land managers and local groups can lead to misunderstandings or generate unbalanced power dynamics that devalue TEK in favor of SEK (Salmon, 2000; Houde, 2007; Raymond et al., 2010; Quaempts et al., 2018; Friday and Scasta, 2020; Huambachano and Cooper, 2020). Reconciling different knowledge types is time-consuming, requires establishing a shared vocabulary, identifying metrics that can be evaluated, and creating a respectful environment for knowledge sharing (Keats and Evans, 2020). Because local and Indigenous communities are diverse, careful consideration must be given when conducting outreach to identify TEK-experts in order to create a holistic understanding of an ecosystem. In many cultures, for instance, women and men hold different knowledge of the landscape (Pfeiffer and Butz, 2005; Wirf et al., 2008; Pinel and Pecos, 2009; Elias et al., 2017; Pristupa et al., 2018; Rumbiak and Wambrauw, 2018; Nayak, 2019). Meeting times and locations should be created such that no group is systematically excluded from conversations. For many US Indigenous communities, respected knowledge holders are often elderly and may have mobility or other issues that must be addressed to ensure their participation (Kiptot, 2007; St Laurent et al., 2017; Williams et al., 2020).

6.5. Bridging the local-national scale

By nature, TEK is local, yet public land management occurs at a variety of scales, ranging from local to national-levels. Extrapolating information from one project area to another may be impossible, though broad themes and concepts will no doubt emerge and support programs nationally (Cox and Elmqvist, 1994; Robbins, 2000; Ballard et al., 2008; Raymond et al., 2010; Watson, 2013; Bocco and Winklerprins, 2015; Armatas et al., 2016; Fernández-Llamazares et al., 2016; Schick et al., 2018). Local communities must respond to emergent environmental issues, yet often, due to bureaucratic structures, decision-making power often resides with institutions or officials located far from management areas (Nooteboom and de Jong, 2010; Mistry et al., 2016). On the other hand, programs that are too large or complex, risk being so cumbersome and impersonal as to lose the consensus of participants necessary to effectivity function (Bocco and Winklerprins, 2015; Fernández-Llamazares et al., 2016).

7. Best practices and emerging tools to bridge TEK and SEK

Integration of TEK into land management and scientific inquiry must be ethical and inclusive. Several best practices for working with local and Indigenous knowledge emerged from this review, including the need for:

1. Rigorous safeguards to protect intellectual property around TEK;
2. Respectful knowledge sharing and co-creation of products, with formalized partnership agreements that outline roles and expectations at the onset of projects;
3. Prioritization of long-term consistent engagement of partners, with a focus on community and relationship-building; and
4. Proper acknowledgement and compensation for TEK.

These basic precepts could be expanded or adjusted to effectively protect and engage local or Indigenous communities depending on project needs. However, projects that explicitly integrate informational protections, specify collaborative best practices, particularly related to TEK attribution and compensation, and center relationships from the outset are more likely to lead to long-term meaningful outcomes (Chapman, 2008; Jones et al., 2008; Singh, 2008; Cullen-Unsworth et al., 2012; Woodward and Marrfurra McTaggart, 2016; Lynch et al., 2017; Albuquerque et al., 2019). Frameworks, such as ‘Two-Eyed Seeing’, offer conceptual structures to bridge TEK and SEK systems (Preuss and Dixon, 2012; McMillan and Prosper, 2016; Badry and Hickey, 2022). In essence, ‘two-eyed seeing’ is a collaborative strategy that aims to respectfully and equally represent both TEK and SEK perspectives during project development (McMillan and Prosper, 2016). Analytical methods to support project co-creation within the framework of ‘Two-Eyed Seeing’ and similar paradigms include Actor-Network Theory (ANT; Badry and Hickey, 2022). Actor-network theory is rooted in social-ecological theory, and provides a framework to investigate emergent properties of coupled human-environmental systems including critical system components, interactions and feedbacks (Badry and Hickey, 2022). In this vein, Bayesian Belief Networks (BBNs) allow users to explore system dynamics by using oral interviews and other forms of qualitative data to identify common vocabulary, structures, and processes (Liedloff et al., 2009). Another potentially powerful tool for incorporating TEK in land management Participatory Geographic Information Systems (PGIS), which is a form of participatory planning using maps. The use of maps to guide discussions provide a bridge among different knowledge systems (Puri and Sahay, 2003; Robbins, 2003; Sandström et al., 2003; McCall and Minang, 2005; Puri, 2007; Laumonier et al., 2008; Torres-Meza et al., 2009; Cullen-Unsworth et al., 2012; Hoverman and Ayre, 2012; McCallum and Carr, 2012; Cullen, 2015; Gadamus and Raymond-Yakoubian, 2015; McGetrick et al., 2015; Lynch et al., 2017; Albuquerque et al., 2019; Peart, 2019; Cho and Mutanga, 2021; Shaw et al., 2021). Other emergent methodologies, such as art-based ecological projects (Höivik and Luger, 2009; Foley, 2017), ecosystem accounting (Normyle et al., 2022), online collaborative tools (Pert et al., 2015), and other technologies (Touchette et al., 2021), could further support TEK-integration into land management. Land managers may benefit from training in group facilitation and frameworks for working with diverse human populations. Most critically, integrative projects, particularly when working with historically marginalized populations, must center respectful relationships by valuing different viewpoints and building trust (Jones et al., 2008; Cullen-Unsworth et al., 2012; Woodward and Marrfurra McTaggart, 2016; Lynch et al., 2017; Albuquerque et al., 2019; Badry and Hickey, 2022).

8. US policy pertaining to TEK

Within the US, there is a policy framework that could be expanded to enhance protection for ecocultural resources and prioritize TEK-integrated management actions on public lands (Figure 4). Policy relating to TEK began with the introduction of the Federal Trust Responsibility around 1831, which established a perceived responsibility of the Federal government to Native Nations *via* their government-to-government relationship (Berkey, 2006). While not specific to TEK, the Federal Trust Responsibility marks the initial recognition of the so-called trust relationship. The Federal Trust Responsibility has been loosely recognized by administrations throughout time and is characterized by ambiguity, providing little accountability or legal strength (Berkey, 2006). Into the 1900s, there was little to no activity surrounding TEK at a policy level. Later in the 1960s, a glimpse of recognition of traditional knowledge occurred through the verbiage in Section 106 of the National Historic Preservation Act, mentioning 'special expertise' when referring to the level of involvement by Indigenous peoples (Advisory Council on Historic Preservation, 2021).

More specific consideration of Indigenous peoples' knowledge systems and rights occurred first at the international level during the 1980s and 1990s with an increase in language within international environmental law (Colchester, 2004). The United Nations Economic and Social Council established the Working Group on Indigenous Populations in 1982, which shortly after began the two-decade-long process of drafting the Declaration on the Rights of Indigenous Peoples (Colchester, 2004; United Nations, 2007; Robinson et al., 2021). In 1992, the United Nations Conference on Environment and Development, also known as 'Earth Summit,' introduced a call to action to governments to integrate TEK in research, land management, and conservation but only at the 'appropriate level' (United Nations Sustainable Development, 1992). Simultaneously, the UN Convention on Biological Diversity recognized Indigenous peoples as knowledge holders with traditional ways of life relevant to conservation and biodiversity efforts (United Nations Sustainable Development, 1992; United Nations, 1992). By 2007, the UN finally formalized the Declaration on the Rights of Indigenous Peoples, which included rights to their traditional knowledge (Robinson et al., 2021). Upon formalization, 144 countries voted for the declaration and 4 countries voted against, one of which was the United States.

While some Federal agencies such as the Environmental Protection Agency (EPA) had mentioned cooperation with Indigenous peoples in their policies as early as the 1980s, the focus was often in consideration of the Federal Trust Responsibility and limited to reservation lands (Environmental Protection Agency, 1984). During the mid-2000s, there was a gradual recognition and incorporation of TEK within individual Federal agency statements and policies, such as the EPA, National Park Service, United States Fish and Wildlife Service, and the USFS. However, there was still no comprehensive Federal policy on TEK. In 2011, the United Nations Decade on Biodiversity began, which emphasized place-based knowledge and recommended the consultation of Indigenous and local communities to implement the strategic plan surrounding biodiversity conservation (United Nations Environmental Programme, 2011). Former President Barack Obama issued an executive order in 2013 establishing the White House Council on Native American Affairs, reaffirming the Federal Trust Responsibility and communicating support for honoring Indigenous sovereignty and self-determination (The White House Office of the Press Secretary, 2013). In the same year, the National Congress of American Indians passed resolution #REN-13–035 titled: Request for Federal Government to Develop Guidance on Recognizing Tribal Sovereign Jurisdiction over Traditional Knowledge (National Congress of American Indians, 2013). The following year US Secretarial Order No: 3335, Reaffirmation of the Federal Trust Responsibility to Federally Recognized Indian Tribes and Individual Indian Beneficiaries – recognized the failings of the Department of the Interior in fulfilling the Trust Responsibility and called for collaboration and partnership on mutually beneficial projects in a 'New Era of Trust,' but without specific mention of TEK (US Secretary of the Interior, 2014).

The 2010 Nagoya Protocol on Access and Benefit Sharing was an important international agreement that helped to implement protections for traditional knowledge holders regarding genetic resources. The Protocol, enforced in 2014, underscores the rights of Indigenous communities to grant access to genetic resources, the necessity of prior informed consent, and equitable benefit sharing to ensure recognition and compensation to the knowledge holders (United Nations Environmental Programme, 2011). The presidential proclamation that designated the Bears Ears National Monument also established the Bears Ears Commission, which communicated TEK as a 'resource' to be protected and heard rather than knowledge formation which should be built upon (The White House Office of the Press Secretary, 2016). Additional international policy continued to incorporate key perspectives from TEK, such as viewing ourselves as a part of nature rather than separate from, as referenced in the 2017 OSLO manifesto (Ecological and Governance Association, 2016).

Further mentions supporting TEK integration in international policy are included in the UN Post 2020 Global Biodiversity Framework draft and the 2021 UN Decade on Ecosystem Restoration (United Nations Environment Program, 2021a,b). Only in the last few years has the United States begun to formally recognize TEK as a knowledge system as valuable as western science and one to be considered in Federal decision-making. The United States delivered its mission to the UN in 2019, citing the intention to form a legal framework to incorporate traditional knowledge into US government decision-making. (Hauser, 2019). The Advisory Council on Historic Preservation (2021) released a recommendation to revise Section 106 of the National Historic Preservation Act to specifically define and incorporate traditional knowledge. The Biden Administration's commitment to 'strengthening Nation-to-Nation relationships' has increased more concrete recognition of TEK in US policy. In November 2021, the Administration released a memorandum for the heads of departments and agencies on Indigenous Ecological Knowledge and Federal Decision-Making. The memorandum officially formalized TEK as a valued knowledge system and recognized the 2013 request from the National Congress of American Indians (Executive Office of the President, 2021). The same day, Joint Secretarial Order No: 3403 was issued on 'Fulfilling the Trust Responsibility to Indian Tribes in the Stewardship of Federal Lands and Waters,' which officially included the incorporation of Indigenous knowledge to Federal land and resource management as part of the Federal Trust Responsibility (US Department of the Interior, 2021).

In 2022, further efforts toward integration of TEK into policy include verbiage presented in: Executive Order #14072 'Strengthening the Nation's Forests, Communities, and Local Economies,' Executive Order #14049 'White House Initiative on Advancing Educational Equity, Excellence, and Economic Opportunity for Native Americans and Strengthening Tribal Colleges and Universities,' and Executive Order #13990 'Protecting Public Health and the Environment and Restoring Science To Tackle the Climate Crisis.' As a response to the formal recognition of TEK as a valued knowledge system in November 2021, the Biden Administration finally released a formalized plan on 'Indigenous Knowledge Guidance for Federal Agencies' in December 2022 (The White House, 2022). The plan, which is the first of its kind, is intended to support agencies in understanding TEK, further develop relationships with Indigenous peoples, and incorporate TEK into Federal research, policies, management, and decision-making (Executive Office of the President, 2022). A framework such as this cannot be developed in a vacuum and requires ample input and perspective. The guide was developed through the White House Office of Science and Technology Policy and the White House Council on

Environmental Quality, with input from 25 Federal agencies, 100 Native Nations, Indigenous youth, and various public and organizational sources. The Biden Administration has made historic and laudable advancements to prioritize protections for Indigenous groups in land management. This important progress can be built upon by increasing representation of and centering Indigenous peoples in planning, land management, and goverment, and more formally protecting important natural resources and cultural and landscapes.

9. Discussion

In the 20 years since TEK entered the lexicon of western SEK, numerous studies have examined TEK application to land management from both a social and ecological lens. Taken together, studies have advanced our understanding of the nature of TEK, its transmission among knowledge holders, cultural importance, utility in land management and conservation, and benefits as context for understanding ecological change. One critical development has been the identification of a signature of past Indigenous groups within modern ecosystems (Bliege Bird et al., 2008; Bird R. B. et al., 2013; Bird M. I. et al., 2013; Sullivan et al., 2017; Power et al., 2018; Adlam et al., 2021). This finding expanded the ecological role of non-agricultural societies, which was often ignored or minimized, resulting in the fetishization of 'pristine' ecosystems, absent of humans (Vining et al., 2008). Adopting a community-integrated approach to land management, rather than deprioritizing human roles within landscapes, will likely increase the efficacy of management, conservation, and restoration strategies.

Simultaneously, the realization that ignoring the concerns of human populations impedes successful land management is driving numerous agencies and groups to prioritize collaborative planning at initial stages of project development. Conservation movements and land management policies that disregard community input may inadvertently harm local and Indigenous communities and livelihoods, and thus lack long-term stability (Vining et al., 2008; Johansson et al., 2019; Campbell, 2020). A prime example, conservation easements or carbon conservation areas in tropical regions were often established without consulting with local groups, or equitably sharing benefits or payments for ecosystem services. Such mismanagement and exclusion of traditional harvest practices within conservation areas resulted in illegal behavior like poaching, increased conflict and resentment, and further marginalized impoverished communities (Johansson et al., 2019; Campbell, 2020). Similarly, agencies in the US that established barriers to prevent traditional harvest on public lands depressed the ability of Indigenous communities to practice cultural activities, increasing resentment towards the government, despite the fact that little, if any, evidence suggests that traditional harvest negatively impacts target populations (Souther et al., 2021b). Co-developed land management and conservation policies bolster the long-term success of ecological protections (NEPSTAD et al., 2006; Reniko et al., 2018; Schuster et al., 2019; Schang et al., 2020). Prioritizing local and Indigenous perspectives in land management decisions is an important goal simply to support cultural practices and social justice, and likely improves understanding of ecological systems and management outcomes; suggesting that TEK integration into land management should be a primary objective of US land management agencies.

We identified several fundamental gaps in the TEK-literature. Studies rarely included both social and ecological data and infrequently applied inferential statistics, which precluded generalizing to other systems. Few studies were conducted outside of Australia, the US, and Canada, again limiting our ability to understand how patterns vary across landscapes and cultures. The model of coupled social-ecological systems provides a framework to more completely understand TEK and land management (Liu et al., 2007; Long and Lake, 2018). Long and Lake (2018) adopt a coupled social-ecological systems frame to contextualize management outcomes. Specifically, authors describe the feedback loops that have created 'social traps' for many US Indigenous groups, in which separation of Indigenous communities from ancestral lands contributed to mis-management of natural resources, which in turn, degraded ecological systems. Ecological decline then contributed to ecocultural erosion, as loss of access to first foods and sacred spaces further impoverished and degraded the health of communities. Using this frame work, decisions can be made to avoid, prevent or stop social-ecological feedbacks that that result in persistent, undesirable states (Long and Lake, 2018). This is particularly important as climate change creates social-ecological perturbations that could further degrade the function of coupled systems (Long and Lake, 2018). Future research should focus on developing analytical methodology to study and model complex systems, in order to provide generalizable insights and generate projections of coupled-human and natural systems.

Traditional ecological knowledge systems are currently imperiled by a variety of factors, including modernization, globalization (Mistry, 2009; Camacho et al., 2012; Juanwen et al., 2012; Mackey and Claudie, 2015; Amelia et al., 2018), resource exploitation (Rai, 2011; Mackey and Claudie, 2015; Kuklina et al., 2022), development including agriculture, climate change, loss of knowledge holders (i.e., elders), and shifts in land tenure to private land ownership (Pangging et al., 2011; Rai, 2011; Juanwen et al., 2012; Rodenburg et al., 2012; Scales, 2012; Mackey and Claudie, 2015; Schmidt and Pearson, 2016; Selemani, 2020). Within this manuscript, we detailed numerous benefits of TEK to land management, which included providing insights into sustainable management of natural resources, improving ecological assessments, and addressing novel threats driven by global change. Urgent action is needed to enshrine the protection and incorporation of TEK into land management strategies at national levels (Armatas et al., 2016; Kanwar et al., 2016; Keats and Evans, 2020; Das et al., 2021). Creating national-level policies ensures consistency across agencies and may increase the adoption rate of TEK-integrated management approaches. Scaffolding to create comprehensive TEK-policy exists in the US, and is broadly supported by the Biden administration. Concerted efforts to integrate TEK into to land management, particularly in the US, could support ecological and cultural health and reduce the likelihood of global change further harming marginalized groups.

Author contributions

SS conducted the literature review and co-authored the manuscript. SC conducted the policy review and co-authored the manuscript. NL provided content guidance and editing. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.988126/full#supplementary-material

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Silicon pools, fluxes and the potential benefits of a silicon soil amendment in a nitrogen-enriched tidal marsh restoration

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Tidal marshes are important sites of silicon (Si) transformation, where dissolved Si (DSi) taken up by macrophytic vegetation and algal species is converted to biogenic silica (BSi), which can accumulate in the soil, be recycled within the marsh, or be exported to adjacent coastal waters. The role of restored and created tidal marshes in these processes is not well understood, nor is the impact of nutrient enrichment at either the plant or ecosystem level. Here, Si fluxes were examined to develop a Si mass balance in a nitrogen (N)-enriched marsh created with fine-grained dredged material from the Chesapeake Bay, United States. In addition, the effectiveness of Si soil amendments to ameliorate the negative effects of excess nitrogen on *Spartina alterniflora* was examined through laboratory and field experiments. Silicon was exported to the estuary as DSi ($49 gm^{-2} y^{-1}$) and BSi ($35 gm^{-2}y^{-1}$) in stoichiometric excess of nitrogen and phosphorus. Rapid recycling of Si within both marsh and the tidal creeks appeared to be important in the transformation of Si and export from the marsh. Enhanced macrophyte SiO_2 tissue concentrations were observed in the field experiment, with end-of-season mean values of 2.20–2.69% SiO_2 in controls and 2.49–3.24% SiO_2 in amended plots, among the highest reported for *S. alterniflora*; however, improved plant fitness was not detected in either experiment. Thus, tidal marshes created with a fine-grained, N-rich dredged material appear to function as a rich source of Si to the restored marsh and local estuarine environment, an overlooked ecosystem service. Soil Si amendments, however, did not appear likely to alleviate N-induced stress in *S. alterniflora*.

KEYWORDS

dredged material, beneficial use, nutrients, Poplar Island, ecosystem services, *Spartina alterniflora*

1. Introduction

Silicon (Si) is important for vascular plant metabolism and growth (Datnoff et al., 2001) and is essential for marine diatoms (protists), which often form the basis of marine food webs (Ragueneau et al., 2006). It is transported to coastal waters from terrestrial systems *via* riverine and groundwater inputs (Tréguer et al., 1995; Conley, 1997), as particulate and dissolved Si (DSi) derived from the weathering of terrigenous rock, and as biogenic Si (BSi) from terrestrial vegetation. As a link between terrestrial and coastal ecosystems, tidal marshes are positioned to play a key role in regulating Si fluxes.

In terrestrial ecosystems, amorphous Si (ASi) largely consists of BSi derived primarily from Si deposited in plant tissue in the form of phytoliths and other biological sources, combined with mineral (non-biological) non-crystalline forms, and can persist in the soil indefinitely (Conley, 1998). Occluded carbon (C) within phytoliths can contribute to C sequestration through organic matter burial (Parr and Sullivan, 2005; Li et al., 2013). In coastal areas, tidal flooding and groundwater flow promote soil ASi dissolution (Hackney et al., 2000). ASi has a solubility several orders of magnitude greater than crystalline mineral silicates (Van Cappellen, 2003), and regular flooding in salt marshes further promotes ASi dissolution due to higher pH and the catalytic effect of cations in seawater (Loucaides et al., 2008). Higher fluxes of DSi from tidal salt marshes compared with tidal freshwater marshes (Struyf and Conley, 2009) can result in Si leached soils in some mature salt marshes (Müller et al., 2013). This leads to export of ecologically significant amounts of DSi to adjacent subtidal ecosystems (Vieillard et al., 2011; Schoelynck et al., 2014; Carey and Fulweiler, 2014a).

Coastal eutrophication has disrupted the historically diatom-based food web in many coastal ecosystems, including Chesapeake Bay, stimulating diatom growth and resulting in DSi depletion early in the growing season (Officer and Ryther, 1980; Conley and Malone, 1992). Despite its relatively high abundance in terrestrial and many aquatic ecosystems, seasonal Si depletion in eutrophic estuaries has led to shifts in the dominance of algal species in summer and is hypothesized to promote the proliferation of harmful algal blooms in some coastal areas (Cooper and Brush, 1991; Humborg et al., 2000).

The extent to which tidal marshes may buffer the impact of eutrophication on Si depletion in estuarine and coastal areas remains unclear, with a wide range of reported estimates of Si exchange rates (Norris and Hackney, 1999; Struyf et al., 2006; Vieillard et al., 2011; Carey and Fulweiler, 2013; Müller et al., 2013). Despite increased tidal marsh restoration and creation, there are few estimates of Si fluxes from new or restored marshes (Jacobs et al., 2008) and their importance in local Si cycling is not well understood. Fluxes may differ from natural marshes due to substrate differences, e.g., lower organic matter content, and different rates of macrophytic productivity and biogeochemical cycling. Studies of Si fluxes from restored and created marshes are needed to enhance our understanding of how these practices may affect estuarine and coastal Si dynamics (Giblin et al., 2021).

Eutrophication can also have profound impacts on plant growth and morphology, leading to physical changes in tidal marsh soils and geomorphology. The response of *Spartina alterniflora*, the dominant species growing in many coastal marshes, to eutrophication includes enhanced annual biomass production (Mendelssohn and Morr, 2002; Darby and Turner, 2008), a shift in biomass allocation (root:shoot ratio, RSR) in favor of shoot growth (Darby and Turner, 2008) and lodging (collapse of excessively tall culms; Deegan et al., 2012). Nitrogen enrichment of plant tissue can also lead to increased predation by grazers and susceptibility to pathogens, likely due to changes in lignin content, tissue SiO_2 concentrations, and other anatomical and biochemical changes (Marschner, 2012). Long-term exposure to high levels of N and phosphorus (P) may ultimately undermine the structural integrity of salt marshes, leading to peat collapse and increasing vulnerability to sea level rise (Turner, 2011; Deegan et al., 2012).

Although Si has not historically been considered essential for growth of most plants, Epstein (1999) considered it "quasi-essential" due to its important role in mitigating biotic and abiotic stress. Silicon is taken up by plants primarily as silicic acid (H_4SiO_4), the hydrated form of SiO_2. It promotes survival of many taxa, including the Bryophyta (bryophytes), the Lycopsida (club mosses), Equisetopsida (horsetails), Pteridophyta (ferns), and, among the angiosperms, the Cyperaceae (sedges) and the Poaceae (grasses; Hodson et al., 2005). Species within the Poaceae are particularly susceptible to Si deficiency under conditions of high fertility, and often benefit from a Si soil amendment to reduce the effects of N enrichment (Epstein, 2001; Ma et al., 2001). For example, in the cultivation of rice (*Oryza sativa*), a wetland graminoid, Si leaching from paddy soils due to continuous flooding depletes Si availability. The application of soil Si amendments increases Si availability, raises plant tissue SiO_2 concentrations and improves resistance to both biotic and abiotic stresses, resulting in increased yields (Ma and Takahashi, 2002). Several other crop species, including sugarcane (*Sacharinum sacharinum*), turfgrass (*Poa* spp., *Agrostis* spp., *Zoysia* spp.), and banana (*Musa* spp.) are treated with Si soil amendments to increase yield by counteracting the negative effects of N fertilization while minimizing the use of harmful chemicals (Datnoff et al., 2001; Korndorfer and Lepsch, 2001; Ma et al., 2001; Nanayakkara et al., 2009).

In earlier work on native North American marsh grasses, parallels were drawn with cultivated rice by Lanning and Eleuterius (1981, 1983), who speculated that coastal eutrophication could impose N stress on marsh grasses such as *S. alterniflora*. In a survey to provide a baseline of Si plant tissue concentrations in coastal areas that were still considered pristine, *S. alterniflora* was one of the higher Si accumulating species (Lanning and Eleuterius, 1981). *Spartina alterniflora* tissue concentrations are considered intermediate for grasses (Ma et al., 2001), ranging from 0.26–2.28% SiO_2 (Giblin et al., 2021). However, the relationships between tissue concentrations and levels of abiotic stress (Querne et al., 2012) and soil Si availability (de Bakker et al., 1999) remain unclear.

While early Si studies in tidal marshes focused on tissue SiO_2 concentrations, more recent studies have emphasized the Si pools and exchanges of DSi and BSi with adjacent waters (Struyf et al., 2006; Struyf and Conley, 2009; Vieillard et al., 2011; Querne et al., 2012; Carey and Fulweiler, 2013). The created marshes at the Paul S. Sarbanes Ecosystem Restoration Project at Poplar Island (hereafter Poplar Island), in Chesapeake Bay (Figure 1), provide an opportunity to examine Si cycling and fluxes in a mesohaline, N-rich created marsh, and to determine the potential benefit of soil Si amendments to improve *S. alterniflora* fitness under N-enriched conditions. These tidal marshes are being constructed with material dredged from navigation channels in upper-Chesapeake Bay, which has experienced significant ecosystem changes resulting from anthropogenic nutrient

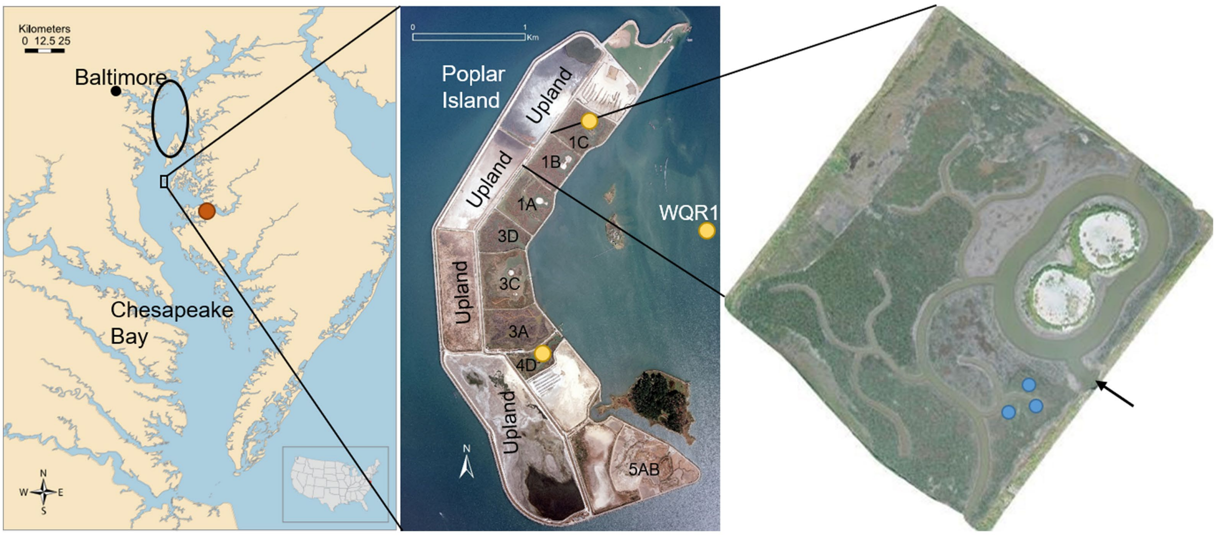

FIGURE 1
Location of study site in Chesapeake Bay, United States (left), showing the source of dredged material (black oval), the natural reference marsh at Horn Point Laboratory (HPL, orange dot), and Poplar Island (black rectangle). Middle inset shows island configuration, with yellow dots indicating dissolved Si monitoring sites (Cells 4D, 1C and Poplar Harbor, WQR1). Right inset is Cell 1B, the site of tidal flux and soil amendment studies, showing the tidal inlet (black arrow) and soil amendment plots (blue dots). Map credit (left),Tracey Saxby, Kate Boicourt, Integration and Application Network (ian.umces.edu/media-library); photo credit (middle and right), U.S. Army Corps of Engineers.

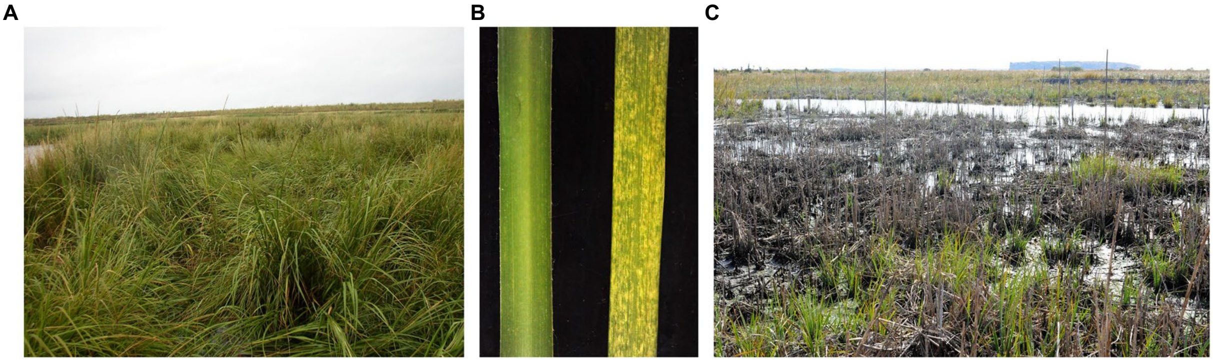

FIGURE 2
Spartina alterniflora characteristics observed at Poplar Island that may be related to nitrogen enrichment include **(A)** lodging; **(B)** increased insect pressure (right blade) compared with natural marsh (left blade); and **(C)** sudden vegetation dieback.

enrichment (Kemp et al., 2005), including seasonal changes in Si availability and trophic shifts (Conley and Malone, 1992). The fine-grained substrate is largely of terrigenous origin (Cornwell and Owens, 2011), and is therefore a potentially rich source of Si. Yet it is also highly enriched in N (Cornwell et al., 2020), resulting in very high porewater ammonium (NH_4^+) concentrations in the created tidal marshes, the N form preferred by *S. alterniflora* (Mendelssohn, 1979). It has resulted in *S. alterniflora* that shows distinctive N induced stress responses (Figure 2), including low root:shoot ratios (Staver et al., 2020), high rates of fungal infection and intense grazing pressure (unpublished data), and lodging. These symptoms may contribute to sudden *S. alterniflora* dieback (Elmer et al., 2012), which has also been observed in these marshes. The site differs from many historical marsh restoration projects in the use of fine-grained, nutrient rich dredged material, in contrast to the sandy substrates with low to moderate nutrient availability typically used in marsh restoration projects (Craft et al., 1999). Similar substrates are increasingly being used, however, in other eutrophic estuaries, e.g., the Gulf Coast of Louisiana (Costa-Pierce and Weinstein, 2002), and are likely to increase with the beneficial use of dredged material for coastal restoration.

Marsh export of Si to local waters to sustain diatom growth and contribute to secondary production, including commercially important fisheries, may be more important in a eutrophic system like Chesapeake Bay than in a more pristine coastal system. In addition, the potential for soil Si amendments to improve *S. alterniflora* plant fitness in this N-enriched environment by reducing the incidence of N-induced symptoms and dieback, and contributing to greater resilience of the marshes to sea-level rise (SLR), has not been examined. We addressed some of these concerns in the present study using (1) data collected as part of the Poplar Island monitoring program to develop a Si mass balance for one newly constructed marsh to examine Si pools and exchanges with the adjacent estuary;

and (2) targeted experiments to test the potential for a Si soil amendment to increase tissue Si concentrations and alleviate the observed symptoms of N stress in *S. alterniflora* at Poplar Island.

2. Methods

2.1. Site description

Poplar Island is located in mid-Chesapeake Bay, 3.2 km northwest of Tilghman in Talbot County, Maryland, United States (Figure 1). The site experiences a mean diurnal tide range of 0.47 m (NOAA Tides and Currents, station ID 8572271), and a mean surface salinity range (1985–2018) of 10.1–12.5 (US EPA CBP 2019). The study was conducted primarily in one marsh subunit (cell) on the site, Cell 1B, a 12.41 ha tidal marsh completed in 2012. The marsh platform was designed as 80% low marsh (LM, 6.92 ha) and 20% high marsh (HM, 2.51 ha), planted with *S. alterniflora* and *S. patens*, respectively, and 1.79 ha of tidal creeks. The cell also includes a 1.19 ha upland habitat island, which was excluded from the marsh mass balance estimates. The marsh substrate (to a depth of approximately 2 m) is fine-grained dredged material resulting from maintenance dredging of the navigation channels in upper Chesapeake Bay (Cornwell and Owens, 2011), providing a high fertility substrate for the restored tidal marshes (Cornwell et al., 2020). Each marsh is surrounded by sand dikes extending approximately 3 m above mean sea level, and tidal exchange occurs through side-by-side 1.83 m^2 concrete box culverts, simplifying flow estimates and making the site well suited to a tidal flux study. The marsh is connected to adjacent marshes (Cells 1A and 1C; Figure 1) *via* shallow lateral channels designed to facilitate fish passage, but exchange through these channels is less than 5% of tidal exchange at the inlet (Fleri et al., 2019). Upland drainage into the marsh is limited to the area of the surrounding dikes, and the consolidated dredged material substrate limits transport within the sediment profile primarily to diffusion.

2.2. Silicon mass balance

A Si mass balance developed for the Cell 1B marsh (11.22 ha, excluding the upland habitat island) identified potential inputs as atmospheric deposition, tidal exchange with the estuary, and upward diffusion from the sediment below the root zone. Potential outputs were tidal exchange and burial. Measurements of site-specific atmospheric deposition were beyond the scope of our study, so an estimate based on literature values was used. Upward diffusion of DSi from the sediment below the root zone was not estimated and internal cycling, while important, was not quantified in this study with the exception of remineralization from macrophytic vegetation. All other pools and fluxes were based on Si analysis of samples collected as part of the long-term monitoring program at Poplar Island, or as part of targeted experiments from 2012 to 2014.

The pool of Si in marsh vegetation was estimated from 2014 end-of-season biomass measurements (Staver et al., 2020), combined with mean end-of-season tissue SiO_2 concentrations from live *S. alterniflora* shoots (2.37%) and roots/rhizomes (1.06%) from the control subplots in the Si amendment experiment (described below), and standing dead material collected for a decomposition experiment (2.00%) in 2012–2013 (Supplementary Table S1). Tissue SiO_2 concentrations were not determined for *S. patens*, but Giblin et al. (2021) reported a range of 0.29–2.19% SiO_2, similar to that for *S. alterniflora*, so the same tissue concentrations were used to estimate the high marsh vegetation pool. Annual shoot and root production in Cell 1B were estimated from clipped plots (0.25 m^2) and sediment cores (42 cm^2 × 20 cm) harvested in October 2014 (Staver et al., 2020, 2021).

Porewater and solid phase soil concentrations were combined to estimate the total sediment Si pool within the root zone (15 cm depth). Porewater samples were obtained using porewater equilibrators (Hesslein, 1976), deployed and retrieved following Cornwell et al. (2020). Dissolved Si concentrations were determined as SiO_2 using the molybdate blue methodology (Strickland and Parsons, 1968), modified for a Technicon AutoAnalyzer II (Technicon Industrial Method 186-72 W-Modified), with ascorbic acid as the reductant. The sediment porewater DSi pool was estimated from concentrations measured in the control subplots of the Si amendment experiment described below, and assumed a pore space volume of 50%. A representative value from these profiles of 200 $\mu mol\,L^{-1}$ was used to calculate the root zone DSi pool. Sediment solid phase concentrations were determined as BSi for 18 solid phase samples collected in 2011, prior to planting the marsh, using the base digestion technique (Demaster, 1981) modified by Saccone et al. (2006) followed by silica (SiO_2) analysis. The BSi range among those samples was 2.34–3.45% dry weight. The mean value, 2.96% (±0.07 se, $n = 18$), and a bulk density of 1.1 $g\,cm^{-3}$ (Staver et al., 2021) was used to calculate the root zone BSi pool.

An average value for the Si pool in tidal creeks (68.28 $\mu mol\,L^{-1}$) was estimated by using the mean annual ebb concentrations of DSi and BSi (41.96 and 26.46 $\mu mol\,L^{-1}$, respectively) in the tidal exchange study, combined with the tidal creek area (1.79 ha) and an average depth of 1 m.

The Si pool in edaphic algae was not quantified here, although it is recognized that benthic diatoms are often present on the marsh surface and are likely important in Si cycling within the marsh seasonally (Ragueneau et al., 2006). Staver et al. (2020) reported seasonally high rates of carbon fixation in unvegetated sediment cores, but respiration always exceeded carbon (C) fixation. Thus, while the benthic algal community is active, fixed carbon is rapidly recycled and stocks are low. In our study, although it is recognized that diatoms are a part of the benthic algal community and may be important in Si processing, it is assumed that, like C, the Si pool is comparatively small and recycles rapidly.

Annual tidal fluxes of DSi and BSi were estimated from seasonal measurements made during 2014. In addition, dissolved inorganic N (DIN), soluble reactive phosphorus (SRP), total suspended solids (TSS) and chlorophyll *a* (Chl *a*) concentrations were measured to allow examination of correlations with particulates and the stoichiometry of Si and essential plant nutrients N and P. A full description of tidal water velocity measurements and constituent flux calculations can be found in Staver et al. (2020). In brief, seasonal (February, May, July, and November) tidal water velocity measurements were made with a Nortek Aquadopp acoustic Doppler profiler (ADP), mounted on a weighted PVC plate and placed in the center of one culvert, equidistant from the open ends and sidewalls.

Concurrent with the water velocity measurements, an ISCO automatic water sampler was deployed for a 24-h period (two full tidal cycles) in the same culvert at the mouth of Cell 1B. Discreet water samples were collected at hourly intervals from 30 to 40 cm off the bottom of the culvert. The samples were chilled with ice in the ISCO sampler, returned to the lab at the conclusion of the sample period and kept refrigerated during processing. Samples were subsampled for DSi within 24 h, usually immediately upon return from the field (within 2 h). For BSi analysis, 30 ml subsamples were filtered through 0.45 μm polycarbonate filters, which were analyzed according to Saccone et al. (2006). For validation, the DSi concentrations from the tidal flux study were compared with ambient concentrations measured monthly in 2014 at three long term water quality monitoring stations at Poplar Island. Two stations were located in tidal creeks within the interior of Poplar Island marshes Cell 4D (sand substrate, completed 2003) and Cell 1C (fine-grained dredged material, completed 2005), and a third was located just offshore in Poplar Harbor (WQR1; Figure 1).

Burial rates were determined in a litter bag study described in detail in Staver et al. (2020). In brief, litter bags of *S. alterniflora* aboveground (AG) biomass were deployed in the low marsh in three fine-grained dredged material marshes spanning a range of age, Cells 3D, 1A and 1C (constructed in 2005, 2009 and 2011, respectively), and Cell 4D, the low nutrient sand substrate marsh (constructed in 2003) from February 2012 to December 2013. Decomposition rates were not determined separately for *S. patens* or for the high marsh; so for the annual burial estimate the low marsh, the *S. alterniflora* rate was also applied to the high marsh. For this study, litter bag contents were analyzed for BSi as described above (Saccone et al., 2006). Based on the results of this study, which showed minimal dry mass loss during the second year, it was assumed that a steady state in decomposition is reached after 2 years (Staver et al., 2020). This is likely not the case in the high marsh, which constitutes just 20% of the marsh platform, potentially introducing a small error in the marsh estimate. The burial rate was estimated as $B = \mathrm{AP} * \%\mathrm{DM} * \%\mathrm{SiO}_2$ where AP is the area-weighted mean annual biomass production of the high and low marsh (2,131 g dry weight; Supplementary Table S1); % DM is the mean percent of original dry mass of *S. alterniflora* litter remaining in litter bags; and % SiO_2 is the SiO_2 concentration in litter at the conclusion of the decomposition study in the fine-grained dredged material cells (Cells 1A, 1C, 3D).

In a review of global atmospheric Si transport, Tegen and Kohfeld (2006 in The Silicon Cycle) estimate that the mid-Atlantic coast receives between 0.1–1.0 g Si m^{-2} y^{-1}. For atmospheric deposition, we used the estimate of Anderson and Downing (2006) for Iowa, where agriculture is a dominant land use, similar to much of the region surrounding our study site. Atmospheric deposition averaged 0.61 g Si m^{-2} y^{-1} (equivalent to 1.30 g SiO_2 m^{-2} y^{-1}), with highest deposition rates occurring in spring when agricultural activity causes dust to become airborne. While agricultural activity is absent on Poplar Island, it was assumed that dust produced by the use of heavy equipment as part of on-going dredged material management activities is analogous to that produced by agricultural activity, meriting a mid to upper level estimate within the range of Tegen and Kohfeld (2006).

2.3. Silicon amendments

2.3.1. Phytotron experiment

To test Si soil amendment effects on *S. alterniflora* tissue SiO_2 concentrations, a small-scale experiment was conducted in a climate controlled environmental chamber ("phytotron," Environmental Growth Chambers, Chagrin Falls, OH) at Horn Point Laboratory (HPL), Cambridge, MD. Dredged material was collected from Cell 1B in September 2010 prior to planting or tidal exchange. The material was dry sieved (1 cm mesh) to remove large plant debris and soil aggregates. For comparison of the fine-grained dredged material with sand, which is commonly used in marsh restoration, we included an unamended sand treatment using commercially available construction grade (course) sand from a local source.

Containers made of 30 cm sections of 10 cm ID PVC pipe, covered at one end with 1 mm mesh screen, were filled to a depth of 20 cm with either fine-grained dredged material (2,100 g) or sand (2,865 g). The substrate filled containers were conditioned in filtered (2 μm) ambient Choptank River water at HPL (salinity 6.8, 12 μM SiO_2) for approximately 24 h, draining them, and repeating twice. Ten replicate containers per treatment received either no soil amendment (dredged material control and sand control), or a calcium meta-silicate soil amendment (Cal-Sil Corporation, Columbia, TN) which was mixed into the top 10 cm of the substrate in each container by hand, at rates to simulate 1, 2, 4, and 8 Mg ha^{-1}. Porewater samplers (Rhizon MOM 10 cm model 19.21.21, Rhizosphere Research Products) were inserted into the top of the soil in 5 of the 10 replicates of each treatment. One 2.5 cm nursery grown *S. alterniflora* stock plant grown from wild collected seed (Environmental Concern, St. Michaels, MD) was placed in each container after rinsing the nursery substrate from the root mass. Each container was placed in a 19 l bucket, filled to 15 cm depth with filtered ambient Choptank River water. The experiment was conducted under a 15-h light, 26°C, 60% humidity/9-h dark, 22°C, 80% humidity cycle for 93 days. Soil pH (measured at 5 cm depth) was monitored approximately every 2–3 weeks with a Corning model 315 pH meter equipped with a Sensoret model S175CD spear tip electrode.

At the conclusion of the experiment (93 days), stem height was measured, flowering was noted, and AG and belowground (BG) biomass were harvested. AG biomass was rinsed in deionized water and dried to constant weight in a forced draft oven (Grieve model 343). BG biomass was rinsed free of sediment over a 1 mm mesh sieve and similarly dried and weighed. Dried plant samples were ground in a Wiley Mill (1 mm mesh screen) prior to analysis for BSi using the modified wet alkaline digestion technique (Saccone et al., 2006).

2.3.2. Field experiment

In 2012, triplicate experimental plots were established parallel to a tidal creek in the low marsh zone in Cell 1B (Figure 1). Each plot was divided into three 5 × 5 meter subplots (split-plot experimental design), which were assigned to receive either a soil Si amendment, broadcast on the sediment surface at a rate of 6 Mg ha^{-1} and roto-tilled into the top 5 cm using a small rototiller attachment on a Stihl Model 115R string trimmer; tillage without the soil amendment (procedural control); or neither amendment nor tillage (control). The soil amendment was a granular form of calcium meta-silicate (Cal-Sil Corporation, Columbia, TN).

Porewater DSi concentration profiles were measured using 45 cm PVC sediment porewater equilibrators (Hesslein, 1976) on July 24, 2012. Due to limited availability, equilibrators were deployed only in control and amended subplots, but not in the tillage control plots. Porewater DSi measurements were not made in the experimental plots after 2012, but measurements elsewhere in Cell 1B in 2013 ($n = 3$) and 2014 ($n = 5$) were made to assess spatial variation and change over time. DSi concentrations were determined as silicate using the molybdate blue methodology as described above. Although solid phase soil analysis was not conducted on samples from the experimental plots, BSi concentrations from 18 sites in Cell 1B collected in fall 2011 were assumed representative of the substrate in the experimental plots.

Vegetation in the experimental plots was sampled monthly for *S. alterniflora* tissue SiO_2 concentrations. Three representative whole stems were collected from each subplot and analyzed for SiO_2 as described above. For comparison purposes, samples were also collected from the Poplar Island marsh Cell 4D (sandy substrate) and a natural reference marsh (HPL) near Horn Point Laboratory (38°35′32.25″N, 76°7′49.90″W), approximately 29 km from Poplar Island. The subplots were inspected monthly during the growing season (April–September) through 2012–2013 for lodging and muskrat (*Ondatra zibethicus*) grazing, and sampled once toward the end of the 2012 and 2013 growing seasons for fungal infection. Fungal infection rates were determined for fresh *S. alterniflora* stems in the amended and control (not the tillage control) plots in 2012 ($n = 20$ stem sections per treatment plot) and 2013 ($n = 50$ sections per plot). Stem sections were incubated on Peptone-PCNB agar (selective for *Fusarium* species; Elmer and Marra, 2011). Five to 7 days later stem pieces with fungal colonies were counted. Single spores from colonies were sub-cultured on Carnation Leaf agar and held for 10 days at 22°C on laboratory benches. Cultures were examined under 100 × and 400 × magnification for identification based on fungal morphology (Elmer and Marra, 2011).

2.4. Statistical analyses

Pearson Product Moment Correlations were performed to determine relationships between tidal flux components. For the phytotron experiment, statistical analyses included Kruskal–Wallis one-way analysis of variance on ranks (ANOVA) to test for significant effects of a soil amendment on shoot growth and root growth. One-way ANOVA was performed on tissue SiO_2 concentrations, followed by pairwise comparisons based on rank sums (Tukey test). For the field experiment, significant differences in soil porewater DSi profiles between Control and Si amended plots were tested with a split-plot ANOVA, with plot, treatment, and depth as variables. Differences between amended and control treatments in tissue SiO_2 concentrations throughout the growing season in each year (2012 and 2013) were tested with a split-plot ANOVA, with plot, treatment and date as variables. Statistical analyses for the phytotron, tidal flux and fungal (field experiment) data were performed in SigmaPlot 13.0 at $p = 0.05$; analyses for the soil porewater and *S. alterniflora* tissue SiO_2 concentrations (field experiment) were performed in R using the Agricolae package for split-plot experimental designs.

3. Results

3.1. Silicon mass balance

3.1.1. Pools

Sediment BSi is overwhelmingly the largest Si pool in the marsh, followed by the vegetation pool (Table 1). The sediment DSi pool is comparatively small, on the same scale as the water column (tidal creek) pool, which represents a combination of DSi and BSi in the tidal creeks.

TABLE 1 Estimated Si pools for the Cell 1B tidal marsh (11.22ha) at Poplar Island, Chesapeake Bay, including macrophyte vegetation, sediment root zone (top 15cm), and tidal creek water volume in 2014.

Pool	SiO_2 (kg/marsh)
Vegetation	4,035
Sediment—DSi	85
Sediment—BSi	460,561
Water column	73

The sediment pools include dissolved Si (DSi) and biogenic Si (BSi).

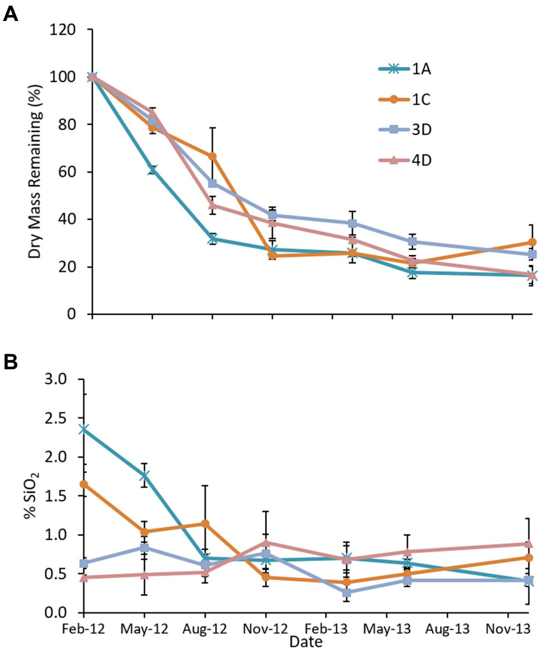

FIGURE 3

Results of the 2012–2013 *Spartina alterniflora* litter decomposition study showing **(A)** mean ($n=3$ litter bags) percent remaining dry weight, and **(B)** litter SiO_2 concentration in four marshes at Poplar Island. Cells 3D, 1A and 1C are dredged material marshes; in Cell 4D the substrate is sand. Error bars represent standard error.

3.1.2. Burial

There was a net decrease in dry mass (Figure 3A) in the three marshes with fine-grained substrate, with the most rapid losses occurring in the first 6 months followed by little change in the subsequent 16 months. Initial BSi litter concentrations varied widely (Figure 3B), with the older Poplar Island marshes, Cells 4D (sand substrate, constructed 2003) and 3D (constructed 2005), having much lower concentrations than the two younger marshes, Cells 1A and 1C during the growing season. Tissue BSi concentrations decreased rapidly in litter with higher initial BSi concentrations (Cells 1A and 1C), but there was little change in litter with lower initial concentrations (Cells 3D and 4D). Using the area-weighted mean biomass (2,131 g m^{-2}), mean remaining dry

TABLE 2 Mean (n=2 tidal cycles) tidal prism and flood and ebb tide concentrations of water column dissolved Si (DSi), biogenic Si (BSi), dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP), total suspended solids (TSS) and chlorophyll *a* (Chl *a*) at the Cell 1B inlet, Poplar Island, Chesapeake Bay in 2014.

Date	Mean tidal prism	Tide	BSi	DSi	DIN	SRP	TSS	Chl *a*
	(m^3)	Stage	(μmol SiO_2 L^{-1})		(μmolNL^{-1})	(μmol P L^{-1})	(mgL^{-1})	(ug L^{-1})
Feb-14	6,028	Flood	7.26	18.57	18.57	0.08	5.09	6.80
		Ebb	17.09	22.64	21.83	0.11	18.15	7.39
May-14	8,820	Flood	19.40	16.96	39.29	0.10	11.50	13.23
		Ebb	26.01	20.44	36.48	0.09	20.37	12.82
Jul-14	9,886	Flood	28.79	48.87	3.30	0.09	30.48	10.36
		Ebb	52.76	92.82	2.34	0.15	30.80	15.12
Nov-14	10,873	Flood	8.11	29.78	3.06	0.11	7.77	3.11
		Ebb	9.99	31.94	4.83	0.17	9.36	3.81

Means are for two full flood tides, except the November ebb, which is the mean of one full and two partial ebb periods. See also Supplementary Table S2.

TABLE 3 Estimated mean (n=2 tidal cycles) tidal fluxes of dissolved Si (DSi) and biogenic Si (BSi; kg SiO_2), dissolved inorganic nitrogen (DIN, kg N) and soluble reactive phosphorus (SRP, kg P) during flood and ebb tides in 2014 at the Cell 1B tidal inlet.

Deployment	Tide	BSi	DSi	DIN	SRP
Feb-14	Flood	2.63	6.71	1.57	0.01
	Ebb	−6.18	−8.19	−1.84	−0.02
	Δ	−3.56	−1.47	−0.27	0.01
May-14	Flood	10.27	8.97	4.85	0.03
	Ebb	−13.77	−10.82	−4.51	−0.03
	Δ	−3.5	−1.84	0.35	0
Jul-14	Flood	17.08	28.99	0.46	0.03
	Ebb	−31.29	−55.06	−0.32	−0.05
	Δ	−14.21	−26.07	0.13	−0.02
Nov-14	Flood	5.29	19.43	0.47	0.04
	Ebb	−6.52	−20.84	−0.73	−0.06
	Δ	−1.23	−1.41	−0.27	−0.02

Delta (Δ) denotes net flux for one tidal cycle. Negative values represent net export; positive values represent net import. See also Supplementary Table S3.

mass (24%) and SiO_2 concentration (0.51%) for the dredged material marshes, annual burial was estimated at 246 kg SiO_2 for the marsh platform (9.43 ha).

3.1.3. Tidal exchange

Ebb concentrations of DSi, BSi and TSS exceeded flood concentrations during all sampling periods (Table 2; Supplementary Table S2). Concentrations of DIN, SRP, and Chl *a* were more variable throughout the year, with DIN ebb exceeding flood in the colder months, but the reverse in the warmer months; SRP ebb exceeding flood except in May; and Chl *a* ebb exceeding flood except in May. The highest concentrations of BSi, DSi, TSS and Chl *a* occurred in July, when nutrient concentrations were lowest.

Estimated net fluxes of both DSi and BSi were negative (export) during all monitoring periods, with the largest net export of both constituents in July (Table 3; Supplementary Table S3). Extrapolating these values to estimate exchange on an annual basis resulted in net export of 3,980 and 5,468 kg y^{-1} of BSi and DSi, respectively, as SiO_2 (Table 4). Biogenic Si dominated exports during the first two quarters of the year, while DSi dominated exports during the latter half of the year.

There were strong correlations between mean BSi and TSS (correlation coefficient = 0.88, p = 0.0036; Figure 4A), and between mean BSi and Chl a (correlation coefficient = 0.82, p = 0.012; Figure 4B). The relationship between mean DSi and Chl *a* was much weaker (correlation coefficient = 0.43, p = 0.285; Figure 4B).

Dissolved SiO_2 concentrations in samples collected in the tidal creeks in Cells 4D and 1C, and in Poplar Harbor varied by a factor of four throughout 2014 (Figure 5). Minimum concentrations were observed in April at all stations, increased during the warmer months and declined after September. Concentrations were consistently highest in Cell 1C, the dredged material marsh, where they were at least double the other stations on all but one sampling date and similar to concentrations measured during the tidal flux study in Cell 1B. Concentrations at the inlet to Cell 4D, the sand marsh, were close to ambient Poplar Harbor concentrations and showed a similar pattern.

The mass balance for the Cell 1B marsh indicates that this young marsh is a net exporter of Si as both DSi and BSi on an annual basis

TABLE 4 Estimates of net quarterly and annual fluxes of dissolved Si (DSi) and biogenic Si (BSi) in kg SiO_2, total dissolved nitrogen (TDN, kg N) and soluble reactive phosphorus (SRP, kg P) at the Cell 1B inlet, Poplar Island, Chesapeake Bay, in 2014.

Quarter	BSi	DSi	DIN	SRP
	(kg SiO_2)	(kg SiO_2)	(kgN)	(kg P)
1	−619	−256	−48	−0.83
2	−616	−325	61	0.23
3	−2,528	−4,636	24	−3.62
4	−218	−250	−51	−3.57
Annual (kg y^{-1})	−3,980	−5,468	−14	−7.79
(kg ha^{-1} y^{-1})	−355	−487	−1.25	−0.69

Negative values represent export. Marsh area = 11.22 ha.

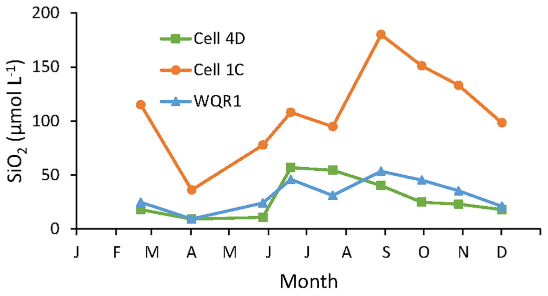

FIGURE 5
Ambient 2014 water column concentrations of DSi in Cell 4D (sand substrate), Cell 1C (dredged material substrate) tidal creeks and a subtidal site in Poplar Harbor (WQR1; Figure 1).

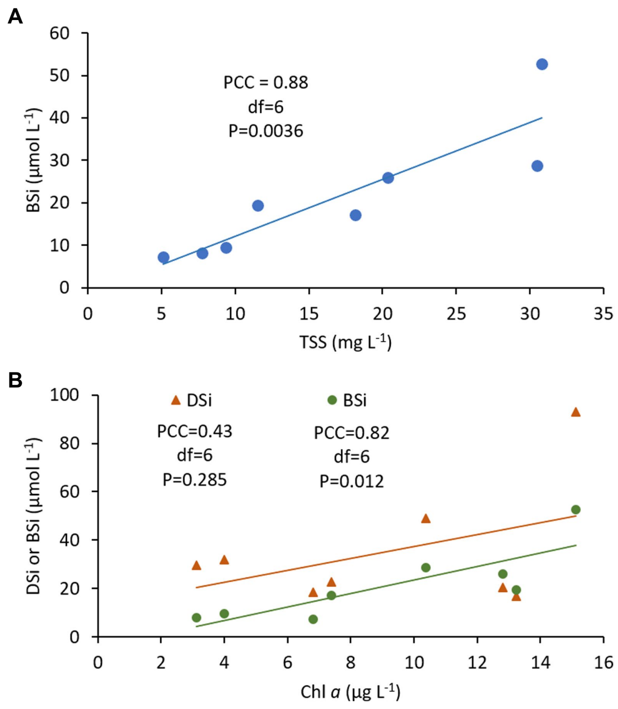

FIGURE 4
Pearson's correlation analysis of volume-weighted mean concentrations of **(A)** biogenic Si (BSi) with total suspended solids (TSS) and, **(B)** dissolved Si (DSi) and biogenic Si (BSi) with chlorophyll *a* (Chl *a*), showing Pearson's correlation coefficient (PCC), degrees of freedom (*df*), *p* value and trend line. Data are from the 2014 tidal flux study at the Cell 1B inlet, Poplar Island, Chesapeake Bay (Table 2).

(Figure 6). The fine-grained dredged material substrate is the primary source of Si, with vegetation mining about half of the exported Si from the root zone.

3.2. Silicon amendment experiments

3.2.1. Phytotron experiment

In the 2012 laboratory experiment, porewater DSi concentrations were similar at all levels of Si amendment (Figure 7A), but somewhat lower on the beginning and ending sampling dates in the sand treatment (no amendment) due to the low solubility of mineral Si in sand. Soil pH increased with application rate, due to the alkalinity introduced by the calcium meta-silicate amendment (Lacroix et al., 2014), and the differences persisted throughout the duration of the experiment (Figure 7B). Shoot biomass at the termination of the experiment was similar across all dredged material treatments, while biomass in the sand treatment was only 5.5% of the mean of dredged material treatments (Table 5). Root biomass was variable across the dredged material treatments, but, again, the sand treatment had only 5.6% of the root biomass of dredged material treatments (Table 5). Analysis (Supplementary Table S4) showed significant differences between treatments in both AG and BG biomass (AG biomass, $p < 0.001$; BG biomass $p < 0.001$). There were no significant differences in tissue SiO_2 concentrations at the termination of the experiment across all treatments ($p = 0.084$).

3.2.2. Field experiment

Background soil BSi concentrations in Cell 1B at the start of the Si amendment field trial ranged from 2.34–3.45% SiO_2, somewhat lower than observations in mesohaline *in situ* Chesapeake Bay channel sediments (3.0–7.0%; Cornwell et al., 1996). In November 2012, at the end of the first growing season, mean soil pore water DSi concentrations ranged from 169 to 788 μmol L^{-1} and 302–1,035 μmol L^{-1} in the control and Si amended plots, respectively (Figure 8A). There were significant differences with Plot*Depth ($p < 0.001$) and Treatment ($p = 0.003$), but not by Treatment*Depth ($p = 0.962$; Supplementary Table S5). Concentrations in the same range were observed in Cell 1B monitoring locations outside the experimental plots in 2013 and 2014 (Figure 8B).

Plant tissue SiO_2 concentrations in the experimental Si amendment field plots at Poplar Island were similar at the beginning of the growing season in both 2012 and 2013, but diverged as the season progressed each year, with an overall increase through the growing season (Figure 9). Differences between treatments were modest. In 2012, there were significant differences within plots over time (Plot*Date, $p < 0.001$) and due to Treatment ($p = 0.002$), but not Treatment*Date ($p = 0.671$). Similar results were obtained in 2013, with significant differences

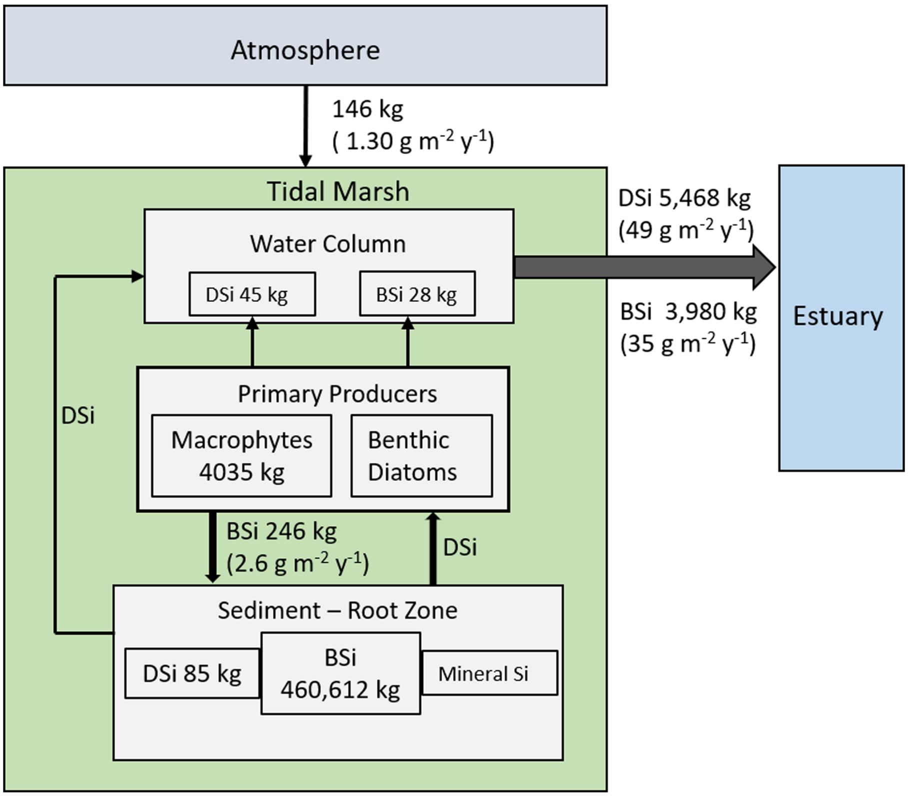

FIGURE 6
Conceptual model of annual SiO_2 mass balance for the Cell 1B tidal marsh at Poplar Island. All fluxes for the marsh are expressed as SiO_2 (annual, kg SiO_2 y^{-1}; area-based fluxes in parentheses, g SiO_2 m^{-2} y^{-1}).

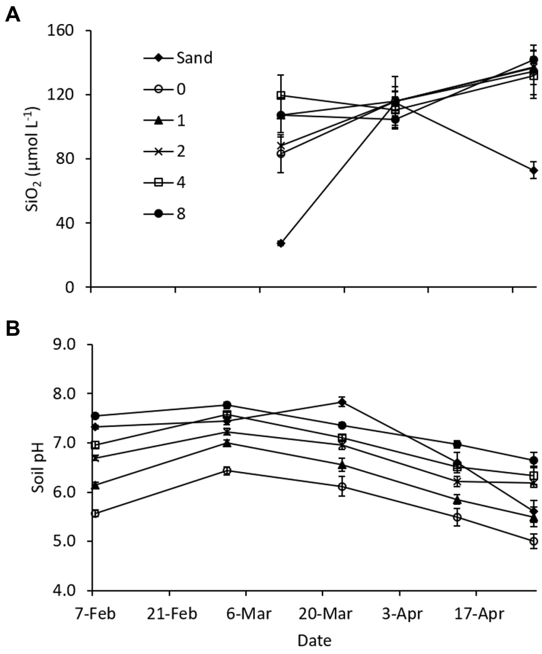

FIGURE 7
Mean **(A)** soil porewater dissolved Si (DSi) concentrations (n=5), and **(B)** soil pH (n=10) in the 2012 Si amendment laboratory (phytotron) experiment. Sand and 0 treatments received no soil amendment; other treatments received a calcium meta-silicate amendment at the rates indicated (Mg ha^{-1}). Error bars represent standard error.

with Time (Plot*Date, $p < 0.001$), Treatment ($p < 0.001$), and Treatment*Date ($p = 0.00147$; Supplementary Table S6).

In both years, mean percent fungal incidence was higher in the control plots than in the Si amended plots (Supplementary Table S7), but the differences were not significant in either year (Supplementary Table S8; 2012, $p = 0.264$; 2013, $p = 0.335$). In 2012, however, there were five different *Fusarium* species found in the samples from control plots (*F. palustre*, *F. proliferatum*, *F. solani*, *F. incarnatum*, and *F. oxysporum*), while only two were found in samples from the Si amended plots (*F. oxysporum* and *F. incarnatum*; Supplementary Table S7). Notably, different *Fusarium* species were dominant in the treated and control plots in both years. *Fusarium palustre*, a species unique to *S. alterniflora* (Elmer and Marra, 2009) that has been associated with *S. alterniflora* sudden vegetation dieback (Elmer and Marra, 2011), was found only in control plots in both years and was dominant in 2 of the 3 control plots in 2013, while *F. proliferatum* dominated amended plots. Both species have been reported from natural *S. alterniflora* stands on the east coast of the United States and are considered pathogenic only when plants are stressed by other factors, e.g., drought (Elmer and Marra, 2011).

No signs of muskrat grazing or lodging were observed in any of the experimental plots in either year. An infestation of stem boring insect larvae in 2013, which appeared to kill the meristem in a high percentage of stems, may have reduced the propensity for lodging by limiting stem height. These stem borers persisted through 2014, based on an informal summer survey.

TABLE 5 Results at the conclusion of the 2012 laboratory (phytotron) experiment showing mean (±standard deviation, *n*=10 containers) aboveground (AG) and belowground (BG) *Spartina alterniflora* biomass (g per 2.4l container), *S. alterniflora* tissue SiO_2 concentration (%) and SiO_2 standing stock (g).

Treatment	AG (g)	BG (g)	Tissue SiO_2 (%)	Standing Stock SiO_2 (g)
0 (Sand)	2.66 (0.91)^{a}	3.02 (1.29)^{a}	1.75 (0.37)	0.10 (0.03)
0	46.51 (0.23)^{b}	47.16 (13.13)^{b}	1.58 (0.23)	1.49 (0.44)
1	50.10 (8.19)^{b}	66.48 (49.60)^{b}	1.68 (0.15)	1.93 (0.76)
2	43.86 (6.83)^{ab}	35.34 (12.21)^{ab}	1.44 (0.27)	1.17 (0.42)
4	49.76 (6.41)^{b}	47.48 (22.47)^{b}	1.53 (0.24)	1.50 (0.52)
8	50.62 (8.55)^{b}	72.13 (31.68)^{b}	1.48 (0.25)	1.85 (0.69)

Treatment indicates soil SiO_2 amendment level in Mg ha^{-1}. Letter exponents for a given variable indicate significant differences in pairwise comparisons ($p \leq 0.05$). See also Supplementary Table S4 for more details on the analysis.

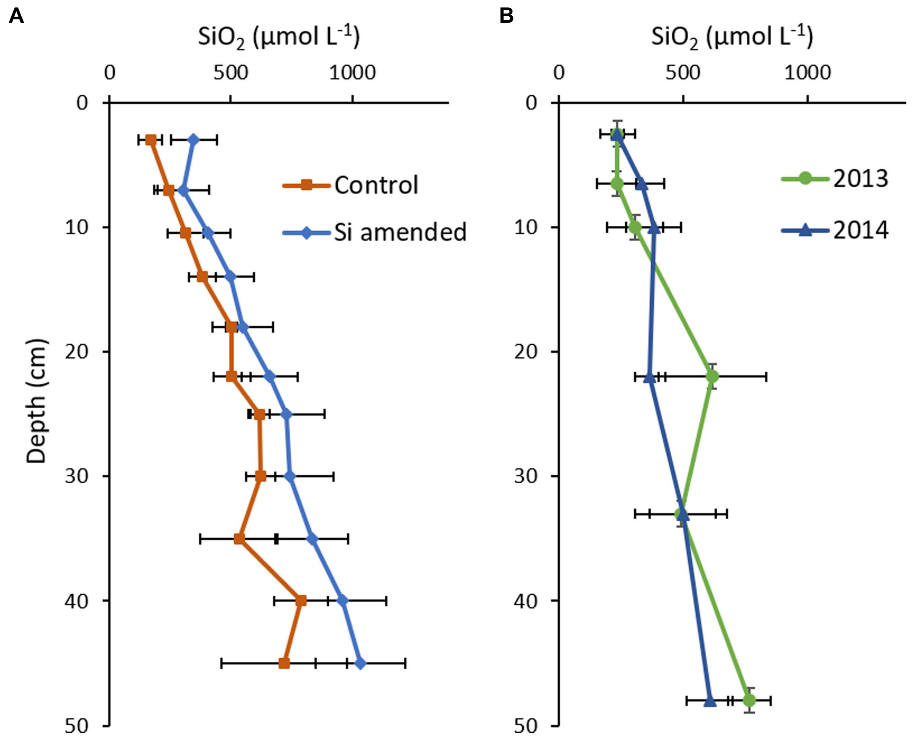

FIGURE 8
Mean porewater dissolved Si (DSi) concentration depth profiles measured in **(A)** 2012 in the Cell 1B experimental Si amendment (orange, *n*=3) and unamended (blue, *n*=3) plots; and **(B)** elsewhere in Cell 1B in 2013 (green, *n*=3) and 2014 (blue, *n*=5). Error bars represent standard deviation.

4. Discussion

4.1. Silicon mass balance

Silicon cycling in the created tidal marsh (Cell 1B, Poplar Island) in Chesapeake Bay is notable for the large net annual tidal export of combined dissolved and biogenic SiO_2. The export of DSi is consistent with Si fluxes reported for other marshes (Struyf et al., 2006; Jacobs et al., 2008; Vieillard et al., 2011). Unlike other marshes, which import BSi with TSS, especially in summer (Struyf et al., 2007), there was a constant export of BSi from Cell 1B. The estimated annual uptake of DSi by macrophytes (4,034 kg) is of similar magnitude as the estimated net annual export of DSi from the marsh (5,468 kg), and is about half the total tidal export (DSi + BSi, 9,448 kg). Combined with the estimate that approximately 6% of the SiO_2 mobilized from the sediment through macrophyte uptake is re-buried with organic matter, the mass balance suggests there is a significant flux of DSi out of the sediment in addition to macrophyte uptake.

The dredged material substrate is the primary source of N for macrophytic growth and the driver of net N export in the Cell 1B marsh (Staver et al., 2021). Similarly, it appears to be the primary source of SiO_2 for uptake by macrophytic vegetation and both benthic and pelagic diatoms, as well as direct fluxes to the water column during flood tides. While direct measurements of sediment DSi fluxes were not made as part of this study, sediment porewater profiles show depletion in the root zone (≤ 15 cm depth) resulting from plant uptake and, likely, direct fluxes when the marsh is flooded, since porewater DSi concentrations greatly exceed those in overlying water.

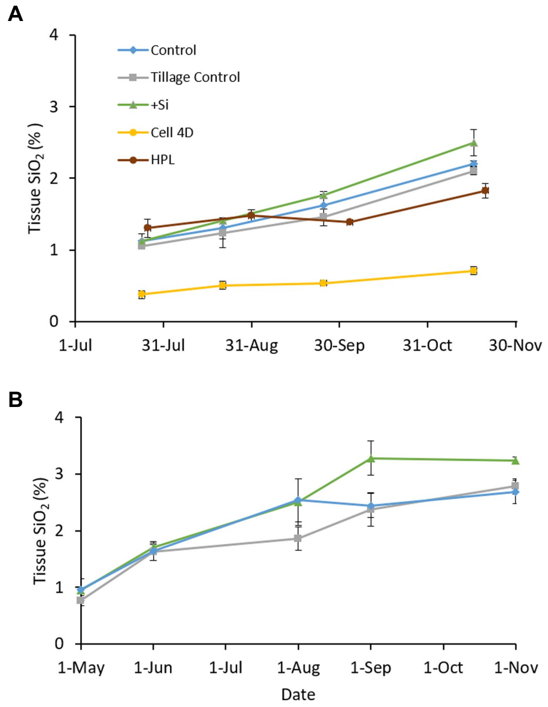

FIGURE 9
Mean (±standard error) *Spartina alterniflora* tissue SiO_2 concentrations in the Si amended and control plots through **(A)** 2012 and **(B)** 2013. Data from the reference marshes, Horn Point Laboratory (HPL) and Cell 4D, were excluded from statistical analyses.

Concentrations below the root zone remain among the highest reported (Müller et al., 2013), 200–1,000 μmol L^{-1} in 2012, exceeding concentrations reported for a natural marsh on Plum Island, MA, 0–300 μmol L^{-1} (Vieillard et al., 2011; Carey and Fulweiler, 2013, 2014a), and a Delaware marsh, 100–900 μmol L^{-1} (Scudlark and Church, 1989). The high concentrations of both BSi and DSi in the dredged sediment likely result from the accumulation of fine-grained particles of terrestrial origin combined with diatomaceous BSi in the deep navigation channels. As the dredged material ages, concentrations will likely decline due to export. There was little change over the course of this study (Figure 9), however, suggesting the large volume of dredged material beneath the root zone will provide a long-term source.

Potential areas of uncertainty in the Si mass balance include heterogeneity in macrophyte biomass production (Wehrhan et al., 2021), and the estimate of tidal fluxes. Biomass is monitored annually in the Poplar Island marshes, and the 2014 data used here is consistent with average production in these marshes. In some years, however, sudden vegetation dieback (Elmer et al., 2012) dramatically reduces *S. alterniflora* production and likely affects Si uptake, recycling and exchange with the estuary. In addition to the influence of macrophyte production, estimates of tidal exchange are constrained by limited sampling. Hourly water sample collection over two tidal cycles was used to estimate seasonal fluxes, and storm events were not represented in our study. The ADPs were deployed for a minimum of 1 week in each season, to ensure the tidal prisms during water collection were representative of that period, but extrapolating to a full three-month season undoubtedly introduces some error. This could be constrained in future efforts through more frequent sampling, e.g., monthly, combined with storm sampling to characterize fluxes associated with extraordinary tides. A smaller error is likely due to an overestimate of burial, for which low marsh decomposition rates were applied to the high marsh where decomposition can be slower due to differences in vegetation and less frequent tidal inundation (Frasco and Good, 1982). Since only 20% of the marsh platform is high marsh, a more accurate burial estimate would have a minimal impact on the mass balance.

In our study, the peak export of DSi and BSi occurred in July when soil temperatures and sediment flux rates are reported to be highest (Scudlark and Church, 1989). However, SiO_2 loss from *S. alterniflora* detritus was most rapid during the spring (Figure 3) prior to peak DSi and BSi export from the marsh (Table 3). The delay may be due to assimilation by benthic diatoms in spring, followed by release as diatoms are shaded by macrophytes or replaced by other algal species during the warmer months.

In Danish marshes, the summer export of DSi is considered a valuable DSi source to coastal waters when ambient DSi concentrations are at a minimum (Struyf et al., 2006; Jacobs et al., 2008). In mid-Chesapeake Bay, the annual minimum occurs in early summer (Conley and Malone, 1992), prior to the peak export by the Poplar Island marshes (Table 3 and Figure 5). Rather, it coincides with a summer peak in ambient DSi resulting from remineralization of diatom BSi following the spring diatom bloom (Conley and Malone, 1992). In the tidal flux study presented here, the positive relationships between BSi and TSS, and BSi and Chl *a* (Figure 4) suggest that much of the BSi export from the marsh is in the form of pelagic diatoms. If this is the case, it suggests that diatoms remain abundant in the marsh creeks despite the high inorganic N concentrations due to the availability of DSi. The Si:N ratio in diatoms is ~1 (Sterner and Elser, 2002), while the molar Si:N ratio of exports from Cell 1B is approximately 6.6 for dissolved forms of Si and N, suggesting that overall the marsh is exporting a surplus of Si relative to N and diatom production in marsh channels is not Si limited. Together, these observations support the hypothesis that DSi depletion in eutrophic estuaries is responsible for the shift in species composition toward non-diatomaceous species, including those which produce harmful algal blooms (Giblin et al., 2021), and may have implications for higher trophic levels. A characterization of temporal changes in algal species composition in the Poplar Island marsh creeks could resolve this question.

The retention of macrophyte detritus within Cell 1B due to the limited tidal exchange appears to contribute to robust rates of vertical accretion (Staver et al., 2020), although it is not clear what effect it may have on Si burial rates. Struyf et al. (2007) report that young Dutch marshes have higher deposition and burial rates than mature marshes, with rates of both declining after the marshes reach an elevation in equilibrium with sea level. The resulting recycling efficiency ranges from 15% in young marshes (85% buried) to 60% in mature marshes (40% buried). The young marshes at Poplar Island also have higher rates of vertical accretion and may follow a similar trajectory. However, upward diffusion of sediment N and DSi from below the root zone likely persists for years to decades and may result in persistently higher recycling rates and lower burial rates for a longer period than in the Dutch marshes.

Although the marshes studied by Struyf et al. (2007) were formed on former agricultural land, they did not consider the effects of soil N on Si recycling or burial. This was examined in a study of two Rhode Island marshes exposed to different levels of N (Carey and Fulweiler, 2013). Nitrogen enrichment was associated with higher sediment BSi and DSi concentrations, as well as higher plant tissue concentrations. Increased Si availability due to high TSS deposition and high rates of recycling induced by N enrichment were thought responsible for the elevated sediment and plant concentrations, although there was likely also a difference in Si inputs. The results presented here suggest that at the ecosystem scale, increased primary production resulting from N enrichment enhances sediment SiO_2 mobilization, remineralization and export. Thus, through continuous export of DSi these marshes may help mitigate the negative effects of eutrophication on spring and summer diatom populations in the surrounding estuary, potentially enhancing their role in support of fisheries (Baker et al., 2020).

4.2. Silicon amendments

At the plant scale, there has long been speculation that *S. alterniflora* could develop a growth induced Si deficiency in response to N enrichment (Lanning and Eleuterius, 1981, 1983), and several studies have examined the interactions of marsh macrophytes, stress (biotic and abiotic) and Si availability. Results of amendment studies have been mixed, with some species showing enhanced tissue concentrations in response to Si enrichment (Schaller et al., 2012; Mateos-Naranjo et al., 2013), while others did not (de Bakker et al., 1999). The role of tissue Si concentrations in regulating *S. alterniflora* growth and resistance to pathogens, grazing and abiotic stressors also remains unclear (Querne et al., 2012; Bazzano and Elmer, 2017).

In our study, it was hypothesized that N availability in the Poplar Island marshes, combined with the numerous indications of N stress in *S. alterniflora*, made this an ideal site to examine whether growth induced Si deficiency can be mitigated by soil Si amendments, as in some crop species. The results of our small-scale phytotron experiments growing *S. alterniflora* in dredged material enriched with calcium meta-silicate were, however, inconclusive. While Si amendments had a pronounced effect on soil pH, there was not a large difference in plant growth or tissue Si concentrations with increasing Si amendment. Plants grown in sand were stunted compared with those grown in fine-grained dredged material, likely due to N deficiency, but they contained similar tissue Si concentrations (Figure 9). The experiment was only 12 weeks long, and since DSi is taken up passively by *S. alterniflora*, this experiment may not have reflected the results that would be obtained in a longer growing season. However, these data highlight the effect of N enrichment on soil Si mobilization by macrophytic vegetation through increased biomass production. This likely contributes to an increase in DSi availability within the marsh and to the large net total SiO_2 export from the Cell 1B marsh.

In the two-year field experiment, tissue concentrations were similar in Si-amended and control plots early in each growing season, but differences developed and increased as the season progressed. In contrast to the phytotron experiment, it appeared that soil SiO_2 amendment can help mitigate root zone depletion and produce a modest effect on tissue concentrations. This effect persisted through year two following soil amendment. Thus, it appears that in an N-rich environment, SiO_2 uptake potential can exceed supply even where availability is high.

Also noteworthy in the field experiment was that tissue Si concentrations of *S. alterniflora* plants from Cell 4D, which has a sand (low nutrient) substrate, were substantially lower than plants from the dredged material plots, while plants from the HPL reference marsh, with higher soil porewater NH_4^+ concentrations (unpublished) were closer to the dredged material marsh controls. These results align with the results of Carey and Fulweiler (2013) that plants exposed to higher N availability contain higher tissue Si concentrations. What is not clear is whether this is due to differences in N availability and plant growth, or differences in Si availability or uptake. Nitrogen enrichment delays senescence, and passive Si uptake persists as long as the plants are transpiring. A prolonged growing period for N enriched plants could result in higher tissue Si concentrations at the end of the growing season through passive uptake in the absence of increasing biomass. Active uptake has also been reported for *S. alterniflora* (Carey and Fulweiler, 2014b), but the steady increase in tissue SiO_2 throughout the growing season in the field experiment suggest that passive uptake is the primary mode of Si acquisition in the Poplar Island marsh.

The question of whether increased tissue concentrations confer resistance to stress in *S. alterniflora* was not resolved by these studies. Neither lodging nor grazing by *O. zibethicus* were observed in or near the experimental plots during the course of the field experiment. Fungal analysis suggested that there could be a protective mechanism conveyed by Si enrichment, at least with respect to the more pathogenic strains found in *S. alterniflora*. Bazzano and Elmer (2017) found Si amended *S. alterniflora* in greenhouse trials did not, however, differ in susceptibility to *F. palustre* or in herbivory by marsh crabs when compared to untreated plots.

Although some increases in *S. alterniflora* tissue Si concentrations were observed in response to amendments in this study, associated improvements in fitness and production were not observed even under extreme N enrichment, as has been reported for *O. sativa* and some other crop species. Both species are members of the same family, *Poacea*, known to have higher tissue concentrations than most other vascular plants. *S. alterniflora*, however, has been designated an intermediate Si user accumulating Si primarily through passive uptake, with tissue concentrations of 0.5–1.0% dry weight (Querne et al., 2012), whereas *O. sativa* is considered an accumulator, showing both passive and active uptake and tissue concentrations > 1.0% (Ma and Takahashi, 2002). Notably, tissue concentrations in our study were within the range considered to be characteristic of accumulators, but we hypothesize that this results from N-enrichment, which can delay senescence, allowing Si uptake to continue later in the growing season (Marschner, 2012). The reasons for generally lower tissue Si concentrations in *S. alterniflora* compared with *O. sativa* are unclear, but may be related to Si availability in brackish to saltwater versus freshwater environments, or to physiological requirements related to perennial (*S. alterniflora*) versus annual (*O. sativa*) life cycles.

4.3. Conclusion

The present study has demonstrated that newly constructed fine-grained dredged material marshes can provide a source of both dissolved and biogenic Si to local waters in stoichiometric excess (relative to algal requirements) of exported N and P, an overlooked ecosystem service. High nutrient availability drives high rates of macrophyte production, which appear to enhance mobilization of sediment DSi and remineralization. The tidal creeks also appear to be important in the transformation and export of Si. Effects on the composition and shifts of the local benthic and pelagic algal community are unknown, but may be important locally for higher trophic levels, a potential area for future study.

Soil amendment with calcium meta-silicate resulted in slightly enhanced tissue concentrations in *S. alterniflora*, but improved plant fitness was not detected in this study, even in this N rich environment where symptoms of N stress were abundant. The accumulation of evidence from this and other studies appears to cast doubt on the concerns of Lanning and Eleuterius (1981, 1983) that N stress in *S. alterniflora* results from a Si deficiency.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

LS, JS, and NN conceived and designed the tidal flux study. LS, JS, JC and WE designed the experiments. LS and NN performed the tidal flux study and LS performed the experiments. LS, MO, and WE performed sample analysis. LS, NN and KS performed data analysis. LS wrote the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1097380/full#supplementary-material

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Invertebrate communities of Bay of Fundy salt marsh pools: comparison of a natural and recovering marsh

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Disturbed salt marshes may recover with little additional management once tidal inundation is restored. We assessed the success of such recovery by comparing the invertebrate biota of Bay of Fundy salt marsh pools in a reference site at Dipper Harbour to that of Saints Rest marsh that had been drained for over a century and to which tidal flooding had been returned ~50 years prior to our study. The sediments and vegetation of salt marsh pools were sampled seasonally throughout one year. Average biomass of pool invertebrates ranged from 1.8 to 4.0 g dry wt m^{-2}, depending on the amount of vegetation cover in the pools. The most abundant organisms of the pools were the gastropod *Ecrobia truncata (=Hydrobia tottentei)*, Tubificidae (=Naididae) oligochaetes, and Chironomidae (=Chironomini). We compared overall abundance and biomass of the invertebrates in the pool communities, assessing the month of sampling, pool elevation, and source marsh as explanatory variables. Our analyses revealed that marsh origin of pools seldom explained a significant amount of variance, and when it did, the proportion of variance explained was usually lower than elevation of pools and month of sampling. Diversity of invertebrates found in all pools was higher at the recovering site with species richness >40% higher than in the reference site. We conclude that after an estimated 50 years since dyke failure and return of tidal flooding to Saints Rest marsh, that the ecosystem function represented by pools and their fauna has recovered.

KEYWORDS

invertebrate diversity, invertebrate biomass, salt marsh restoration, salt marsh pools, elevation gradient

1 Introduction

Tidal salt marshes are generally flat wetlands considered to be highly productive and dominated by a small number of extremely salt tolerant plant species (Mitsch and Gosselink, 2015). Many tidal salt marshes contain permanently flooded pools that add diversity and value to the habitat provided by the marsh. Pools provide habitat for fish (Smith and Able, 1994; Adamowicz, 2002) and invertebrates (Nicols, 1935, Bromley and Bleakney, 1979, Clarke et al., 1984), and, in turn, valuable feeding sites for birds (Burger et al., 1982; Clarke et al., 1984; Erwin, 1996). Clarke et al. (1984) found that bird use was strongly correlated with pool density in Massachusetts salt marshes, particularly for shorebirds, herons, and terns. These pools may be particularly important on macrotidal coasts such as the Bay of Fundy, where some surfaces of the salt marshes are flooded only intermittently, at extreme (spring) tides (Byers and Chmura, 2007). Standing pools of water on the surface of the marsh provide a refuge for organisms, such as fish and aquatic invertebrates, which would not be able to survive on the marsh surface between flood tide events.

Despite their apparent ecological importance in salt marshes, relatively few studies have focused specifically on the invertebrate biota of pools in natural or restored salt marshes. Early studies found few species in pools (Nixon and Oviatt, 1973; Campbell and Denno, 1978). The challenge of isolation and identification of invertebrate fauna also may discourage investigators from using them as an indicator of restoration success (Laymen and Rypel, 2020). Most salt marshes in the Bay of Fundy (85%) have been altered or lost, with dyking and drainage of marshes beginning in the 17th century by early French Acadian settlers (Butzer, 2002). Beginning in 2010 managed realignment, the construction of a new dyke inland followed by strategic breaching of the original dyke, has been employed to restore some of these drained marshes. Over the first 8 years of monitoring at the first managed realignment site, vegetation at the restored and reference sites showed increasing similarity but recovery of invertebrate populations lagged (Virgin et al., 2020). Indeed, studies of other restored marshes indicate that some components of the ecosystem recover more quickly than others. For instance, creek use by nekton can return to the condition of an undisturbed marsh in as little as one year (Roman et al., 2002), but Allen et al. (1994) found that the forage value for *Fundulus heteroclitus* of a restored marsh had not recovered after 15 years. In Connecticut, Warren et al. (2002) reported that invertebrate populations may take over 20 years to recover.

On the Bay of Fundy some historic dykes have been breached by storms and tidal marshes subsequently left to recover without human intervention or management. These sites have served as natural laboratories to examine the long-term outcome of salt marsh restoration with respect to surface hydrology (MacDonald et al., 2010) and vegetation (Byers and Chmura, 2007). In this study we compare a previously dyked and drained marsh at Saint John, New Brunswick (Saints Rest marsh, now a protected site) to that of an undisturbed marsh in Dipper Harbour, New Brunswick to determine the extent of recovery of the pool invertebrate fauna. Saints Rest marsh had been subject to an unmanaged recovery following the breaching of the dyke that occurred 50 years prior to this study. As environmental conditions vary with pool elevation (Noël and Chmura 2011), we hypothesized that invertebrate communities would vary with pool elevation, thus include this as a variable in our analyses.

2 Methods

2.1 Study sites

The Bay of Fundy has a steep gradient in tidal range, varying from 4 m near the mouth of the Bay to >16 m at its upper reaches (Canadian Hydrographic Survey, 2005). On the New Brunswick coast of the Bay of Fundy as the tidal range increases, so to do the sediment supply and rates of sediment deposition in the salt marshes (Chmura et al., 2001). The greater the distance between marshes, the greater is the difference in these conditions, and the shift in tidal range also causes a shift in the elevation of mean high water (Gordon et al., 1985). Thus, proximity along the coastline is an essential consideration in selecting reference sites to compare to restored marshes. The Dipper Harbour marsh was the only undisturbed marsh with an appropriate geomorphic context (a single main channel) and accessibility for our year-round study. (See Figure 1 in Noël and Chmura (2011) for the location of each marsh on the Bay of Fundy coast.)

Saints Rest marsh, located on the lower Bay of Fundy in Saint John, New Brunswick, has a long history of human use and alteration including dyking and ditching dating back at least 140 years, construction of roads, use as a rifle range, and currently a sewage treatment plant discharges into the head of the creek. (See Figure 2 in Noël and Chmura (2011) for a map of Saints Rest marsh and location of pools.) The relatively undisturbed reference site, Dipper Harbour marsh, is 28 km southwest of Saints Rest marsh. (See Figure 3 in Noël and Chmura (2011) for a map of Dipper Harbour marsh and location of pools.) Additional descriptions of the marshes have been provided by Thomas (1983); Chmura et al. (1997); MacDonald et al. (2010), and Byers and Chmura (2007).

Based on surrounding vegetation we selected pools to sample that represented three marsh elevations: “high”, “mid” and “low”. At each marsh one pool from each elevation was selected for environmental analyses as described by Noël and Chmura (2011) – these were the first to be sampled and referred to as our “main” pools.

2.2 Invertebrate sampling

A Wildco™ hand corer with a diameter of 5 cm was used to collect sediment samples to a depth of 15 cm. The sample size was determined to be adequate after constructing a species area curve from repeated sediment samples (5) collected in one pool at Dipper Harbour, although large differences in abundance from sample to sample were noted.

Sediment samples were collected from a pool at each of the three elevations in each marsh during July 28–30, 2004. Between August 25 and September 2 these pools were sampled again, along with 5 additional pools on each marsh, for a total of 8 pools per marsh. The 3 pools first sampled on each marsh were sampled again in May 2005. In each pool, sediment samples were taken ~0.5 m and ~2.5 m in from the edge of the pool and combined for further analyses. The sediment samples were sieved through a 0.5 mm screen and the portion retained was placed in a 5% buffered formalin solution for a few days, then transferred to a 50% isopropyl alcohol solution for preservation until sorting and identification. The samples were transferred to a rose bengal staining solution for 1.5 h to stain the invertebrates so they could be more easily sorted from roots and other debris in the sample using a dissecting microscope. Meiofauna (defined as those passing through a 0.5 mm screen), such as ostracods, foraminifera and copepods, were quantified when encountered in the

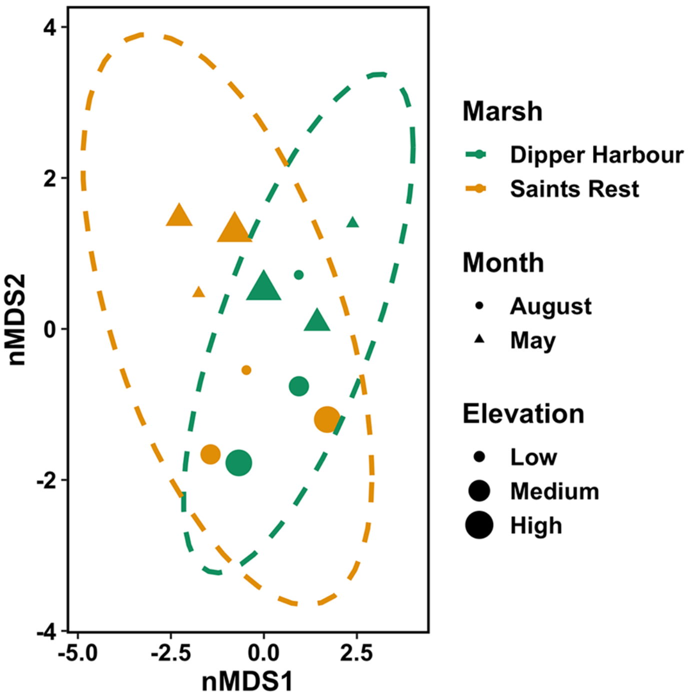

FIGURE 1
nMDS ordination plot for invertebrate fourth-root of invertebrate dry mass in vegetation of pools from July 2004 to July 2005 at Dipper Harbour and Saints Rest salt marshes using Euclidean distance. Each symbol represents the assemblage of invertebrates in a sample. Plot ellipses represent the 95% confidence regions for group clusters. Stress=0.12.

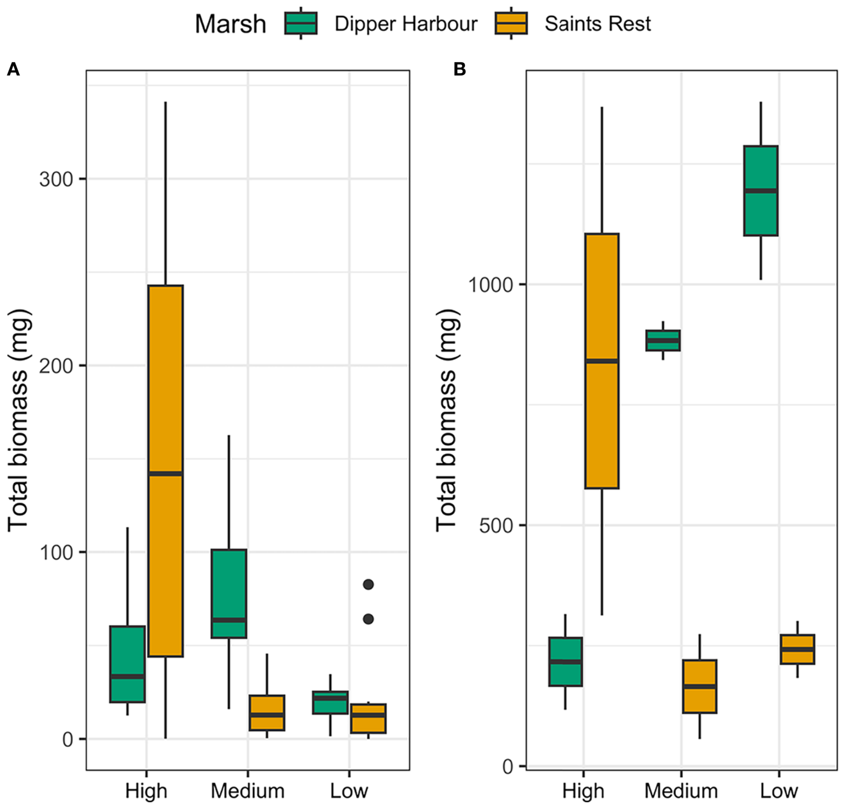

FIGURE 2
Box plots showing total biomass (mg) of **(A)** all macrofauna found in 300 cm^{-3} sediment samples and **(B)** all invertebrates (mg) in 0.25 m^2 samples of vegetation in pools from July 2004 to July 2005 at Dipper Harbour and Saints Rest salt marshes. The horizontal bar represents the median; lower and upper box edges are 25th and 75th percentiles, respectively; whiskers are 1.5 × 25th and 75th percentiles, and dots are outliers.

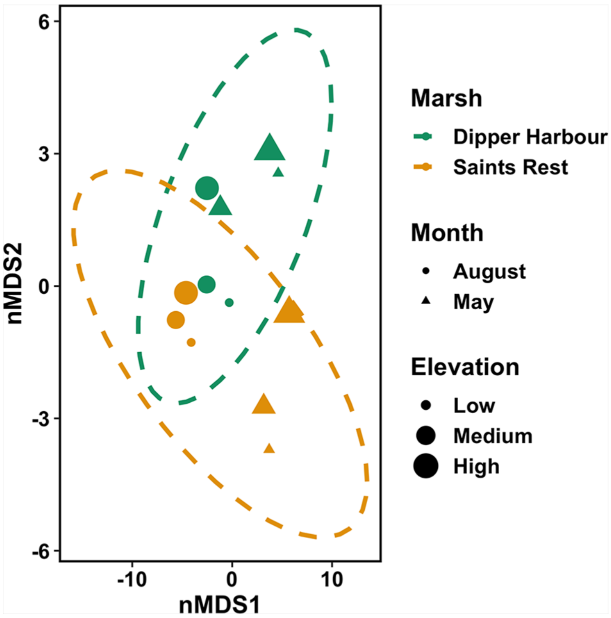

FIGURE 3
nMDS ordination plot for invertebrate fourth-root abundance of invertebrates in vegetation of salt marsh pools from July 2004 to July 2005 at Dipper Harbour and Saints Rest salt marshes using Euclidean distance. Each symbol represents the assemblage of invertebrates in a sample. Plot ellipses represent the 95% confidence regions for group clusters. Stress=0.04.

samples. However, due to the mesh size used these counts cannot be considered complete and so only macroinvertebrates were included in the final analyses of invertebrate communities in the sediments.

On 5 dates from July 2004 to July 2005 the percent cover of aquatic vegetation was visually estimated in the main pools at Dipper Harbour and in the main pools on 4 dates over the same period at Saints Rest (Table 1). In mid-August 2004 and again in May 2005, a single 0.25 m^2 sample of aquatic vegetation (widgeon grass, *Ruppia maritima*, and filamentous algae) was cut from each of the 6 main study pools at a randomly selected location within the pool, and removed carefully so as to not dislodge any invertebrates. Samples taken in August were rinsed multiple times over a 0.5 mm mesh screen. The May samples were not rinsed, which allowed for accurate meiofauna counts as well as macrofauna. The algae and *R. maritima* were separated and the wet weight of each was determined for all samples.

The filamentous algae from the August samples were identified to genera. Invertebrates in sediment and vegetation samples were hand sorted under a dissecting microscope. Small species and diagnostic features (such as chironomid heads) were mounted on slides and examined under a compound microscope. Invertebrates were identified to the lowest practical taxonomic level using the resources listed in Supplementary Table 1. Voucher specimens were placed in the permanent collection of the Atlantic Reference Centre in St. Andrews, New Brunswick.

Dry weight was determined for species of macrofauna that comprised more than 10% of the total invertebrate abundance of 3 or more samples. To determine dry weight, specimens were randomly selected from samples which contained a large number of individuals of the species to be weighed. With the exception of *Ecrobia truncata* and *Gammarus mucronatus* there was little variation in the size and wet weight of most species among samples. For this reason, a subset from the summer and spring sampling periods were weighed separately for only these two species. One to 100 individuals of each species representing more than 5% of total species abundance of samples from the 6 main study pools were dried and weighed. The number of individuals weighed was higher for smaller species. Specimens were soaked in distilled water overnight to remove alcohol, then oven-dried at 120°C for 24 h. To calculate g m^{-2} we normalized the area of sampled and assumed a 15-cm sediment depth, as this was the depth cored.

2.3 Analyses

Our analyses were designed to compare pool vegetation and invertebrates of the reference marsh, Dipper Harbour to that of the

TABLE 1 Percent cover of aquatic vegetation in high (H), mid (M), and low (L) marsh pools from July 2004 to July 2005.

		July 30	Aug 20	Sept 16	May 23	July 5
Dipper Harbour						
H	*Ruppia*	90	90	90	5	45
	Algae	5	5	<10	5	25*
	Bare	5	5	0	90	35
M	*Ruppia*	80	90	55	<1	80
	Algae	20*	30*	<10	10	30*
	Bare	15	10	45	90	<5
L	*Ruppia*	35	40	40	<1	15
	Algae	15	15	15	15	40
	Bare	50	45	45	85	45

(Continued)

TABLE 1 Continued

		July 30	Aug 20	Sept 16	May 23	July 5
Saints Rest						
H	*Ruppia*	–	25	**	**	**
	Algae	–	10	**	**	**
	Bare	–	65	**	**	**
M	*Ruppia*	–	<5	<5	0	0
	Algae	–	35	<10	25	45
	Bare	–	60	85	75	55
L	*Ruppia*	–	5	<1	0	0
	Algae	–	20	25	40	30
	Bare	–	75	75	60	70

– No observation made; *total >100% due to cover of algae growing epiphytically on Ruppia; ** no bottom visibility.

recovering marsh, Saints Rest. Pool elevation (high, mid, and low) and sample month were tested as explanatory variables. All statistical analyses were performed using R.

Species Richness, the Shannon-Wiener index of diversity ($H=-\sum p_i \ln p_i$, where p=the proportion of taxa i to total taxa count of sample) and equitability ($J=H/\ln S$, where S=species richness) were calculated for all samples and for combined data for each pool (Begon et al., 1990). Species Richness was based on, for example, the total number of species found in sediments of all low pools, and the total found in sediments of all pools in the marsh. The Shannon Wiener index calculation was based on average abundance of species in each pool elevation across all sample events.

To examine the variation in species composition and invertebrate biomass, we used non-metric multidimensional scaling (nMDS) of the two marshes using the fourth-root taxa abundance and biomass data. We used Permutational multivariate analysis of variance (PERMANOVA), with Euclidean distances, to test significance of independent variables on the abundance and biomass of invertebrate taxa (Anderson, 2001) using the Vegan package in R (Oksanen et al., 2008). Note that we only evaluated main effects and not any possible interactions. All the PERMANOVA analysis were done in fourth-root transformed data. Bar plots of taxa abundance data are made with fourth-root transformed data. Bar and boxplots for taxa and total dry biomass are shown in absolute values without transformations. To determine the importance of species in their contribution to dissimilarities between grouping variables we performed SIMPER analysis (Clarke, 1993). As the difference between the marshes was the primary question of this study, our analyses and visualizations primarily focus on contrasting the two marshes. Within-group dispersion was assessed with the vegan package *betadisper* (Oksanen et al., 2008). If dispersion between groups is unequal, the statistical significance identified using PERMANOVA may result from dispersion patterns rather than the species composition differences. We used ANOVA to test if the dispersions of one or more groups were different. To compare the total biomass in vegetation and sediment samples in the marshes we used a t-test. As the variance in total biomass differed, we used unequal variance t-test. Similarly, to test the differences in total biomass along elevation gradient and across sampling months we used Kruskal Wallis test because of differing variance in the groups.

3 Results

3.1 Pool vegetation

The only vascular plant that grew in most pools was *R. maritima* (widgeon grass), though isolated stems of *Sporobolus alterniflorus* (=*Spartina alterniflora)* frequently encroached into the pools with sloping sides and pools with sloping sides near the upland sometimes graded into stands of *Bolboschoenus maritimus* (=*Schoenoplectus robustus)*. *Zostera marina* occurred in a few of the lowest elevation pools. Thick mats of filamentous algae grew in virtually all pools from May to late fall (Table 1). No attempt was made to quantify the abundance of each species of filamentous algae, though it was noted that *Cladophora* sp. was the dominant species of the algal mats and *Ulva* (=*Enteromorpha)* sp. tended to occur in some areas of the pools. Less common algae identified from the pools included *Rhizoclonium* sp., *Cylindrocapsa* sp. and *Ectocarpus* sp. Cyanobacteria (Cyanophyceae) were epiphytic on species of algae, on *R. maritima*, and also on bits of wood and rhizomes mixed in with the samples.

3.2 Invertebrates

3.2.1 Invertebrates in pool vegetation

Fauna in pool vegetation averaged 0.86 g dry weight per 100 g of wet vegetation. The average weight of vegetation in a 0.25 m^{-2} sample was 65 g, giving an average macroinvertebrate biomass of 2.24 g m^{-2}. We considered counts of 21 invertebrate taxa found in our samples from pool vegetation for our statistical analyses (Supplementary Table 2). Eight taxa were retained for analysis by biomass (Supplementary Table 3). There was no significant difference in biomass within vegetation samples across sampling months or as a function of elevation. Marsh explains 20% of the variability (Table 2), but there is no clear separation of marshes visible in the corresponding nMDS ordination plot (Figure 1). Although total invertebrate biomass within pool vegetation showed some difference between the marshes (including a differing elevational pattern; Figure 2B), the effect of marsh site was not significant (t=1.29, df=10, p=0.22).

The nMDS ordination plot (Figure 3) of invertebrate community composition based upon abundance in the 6 main pools showed that communities of the two marshes are generally distinct in May, but not in August. There was no significant difference in species composition recovered from vegetation samples based on elevation or marsh, while there was a significant difference by sampling month (Table 2). Sampling month explained 44% of the variability. Comparing dispersion between marshes using ANOVA revealed no significant difference between the two marshes (F=4.56, df=1 & 10, p=0.06). SIMPER analysis identified the cumulative combinations of the most influential taxa as, in descending order, copepods, ostracods, Tubificidae (=Naididae) and *Ecrobia truncata* in distinguishing the difference in communities in August 2004 and May 2005. Whereas ostracods, copepods, Tubificidae, Ceratopogonidae and Chrinomidae (=Chironomini), in descending order, explained 54% of the differences observed between marshes in vegetation samples (Figure 4).

The overall species richness (the total in all pools) of invertebrates in vegetation of Dipper Harbour pools was 16 while that at Saints Rest was slightly higher, 19, and this pattern was consistent when considering pools at individual elevations (Table 3). Diversity, as expressed by the Shannon Weiner Index (based upon abundances) was also higher at Saints Rest, when considering the total in all pools, yet its value was lower in for the low and high elevation pools at Saints Rest.

3.2.2 Invertebrates in pool sediments

We considered counts of 23 invertebrate taxa found in our samples from pool sediments for our statistical analyses (Supplementary Table 4). Marsh, sampling month and elevation significantly contribute to difference in abundance of the invertebrate communities (Table 3). The largest variation was explained by sampling month (15%), followed by elevation (7%), with marsh contributing the least (5%). A comparison of variance between Saints Rest and Dipper Harbour marshes showed a significant difference in beta dispersion (F=18.79, df=1 & 48, p<0.001), with Saints Rest having higher variance (Figure 4). The SIMPER analysis showed that most influential taxa contributing a cumulative 70% of the dissimilarity between the two marshes are, in descending order, *Ecrobia truncata*, Tubificidae (=Naididae), Chironomidae (=Chironomini), Coroxidae, Ephydridae, *Gammarus mucronatus* and *Manayunkia aestuaria* (Figure 5).

The average total biomass of invertebrates in the pool sediment was 1.79 g dry weight m^{-2}. When combined with the biomass of invertebrates in the vegetation, the potential total pool biomass was 4.03 g m^{-2} if there was 100% vegetation coverage. Seven taxa were retained for analysis by biomass (Supplementary Table 5). Although invertebrate total biomass in sediment samples showed some difference between the marshes (Figure 2A), an unequal variance t-test showed that the pattern was not statistically significant (t=0.56, df=35.03, p=0.57). Similarly, using the Kruskal-Wallis test there was no significant difference in biomass in sediment samples across sampling months (Chi-sq=1.53, df=2, p= 0.46). However, a Kruskal Wallis test on sediment samples revealed a statistical difference in total biomass as a function of elevation and higher elevation tended to have higher biomass values (Chi-sq=7.96, df=2, p=0.02).

TABLE 2 Results of PERMANOVA with Euclidean distance with 10,000 permutations for biomass and abundances of invertebrates in vegetation of pools at Dipper Harbour and Saints Rest salt marshes from July 2004 to July 2005.

	Treatment	Df	R^2	F	p-value
Biomass					
	Elevation	2	0.07	0.47	0.890
	Marsh	1	0.20	3.30	0.030
	Month	2	0.16	2.17	0.070
	Residual	7	0.54		
Abundance					
	Elevation	2	0.09	1.00	0.410
	Marsh	1	0.13	2.76	0.070
	Month	1	0.44	9.57	0.001
	Residual	7	0.32		

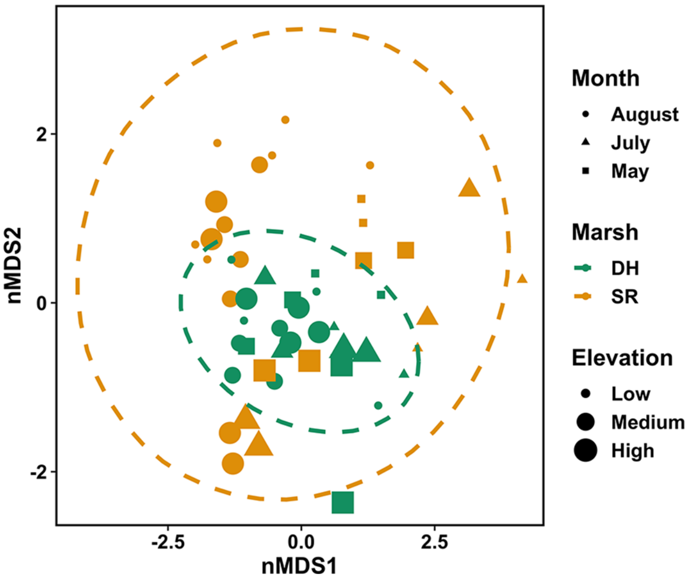

FIGURE 4
nMDS ordination plot for fourth-root abundance of macroinvertebrates in sediments of salt marsh pools from July 2004 to July 2005 at Dipper Harbour and Saints Rest salt marshes using Euclidean distance. Each symbol represents the assemblage of invertebrates in a sample. Plot ellipses represent the 95% confidence regions for group clusters. Stress=0.17.

Using fourth root data of the dry mass for the invertebrate community revealed that both marsh and month show significant influence, albeit marsh explains slightly less of the variability (Table 3). A comparison of variance between Saints Rest and Dipper Harbour marshes showed a significant difference in beta dispersion (F=15.20, df=1 & 48, p<0.001), with Saints Rest having higher variance (Figure 6). SIMPER analysis of dry biomass in fourth root data showed that *E. tuncata*, Chrinomidae (=Chironomini), and *G. mucronatus* explain 70% of the dissimilarity between two marsh types (Figure 7).

The cumulative species richness (the total in all pools) of invertebrates in sediments of Dipper Harbour pools was 17 while that at Saints Rest was 40% higher, i.e., 24 (Table 4). Diversity, as expressed by the Shannon Weiner Index (based upon abundances) was also higher for the total in all pools at Saints Rest, as well as for the mid and low elevation pools there.

4 Discussion

4.1 Vegetation

Vegetation in the pools of both salt marshes was highly dominated by the one vascular plant, *R. maritima*, and *Cladophora* sp., a filamentous green alga. The higher percent cover of this aquatic vegetation in Dipper Harbour than in Saints Rest marsh overall (Table 1) was likely due to much greater bird use (grazing) of the pools in Saints Rest marsh that we observed. Large

TABLE 3 Results of PERMANOVA with Euclidean distance with 10,000 permutations for abundance and biomass of invertebrates in sediments of pools at Dipper Harbour and Saints Rest salt marshes from July 2004 to July 2005.

	Treatment	Df	R^2	F	p-value
Abundance					
	Elevation	2	0.07	2.41	<0.005
	Marsh	1	0.05	3.29	<0.006
	Month	2	0.15	4.87	<0.001
	Residual	44	0.71		
Biomass					
	Elevation	2	0.07	2.11	0.060
	Marsh	1	0.06	3.30	0.020
	Month	2	0.08	2.41	0.040
	Residual	44	0.78		

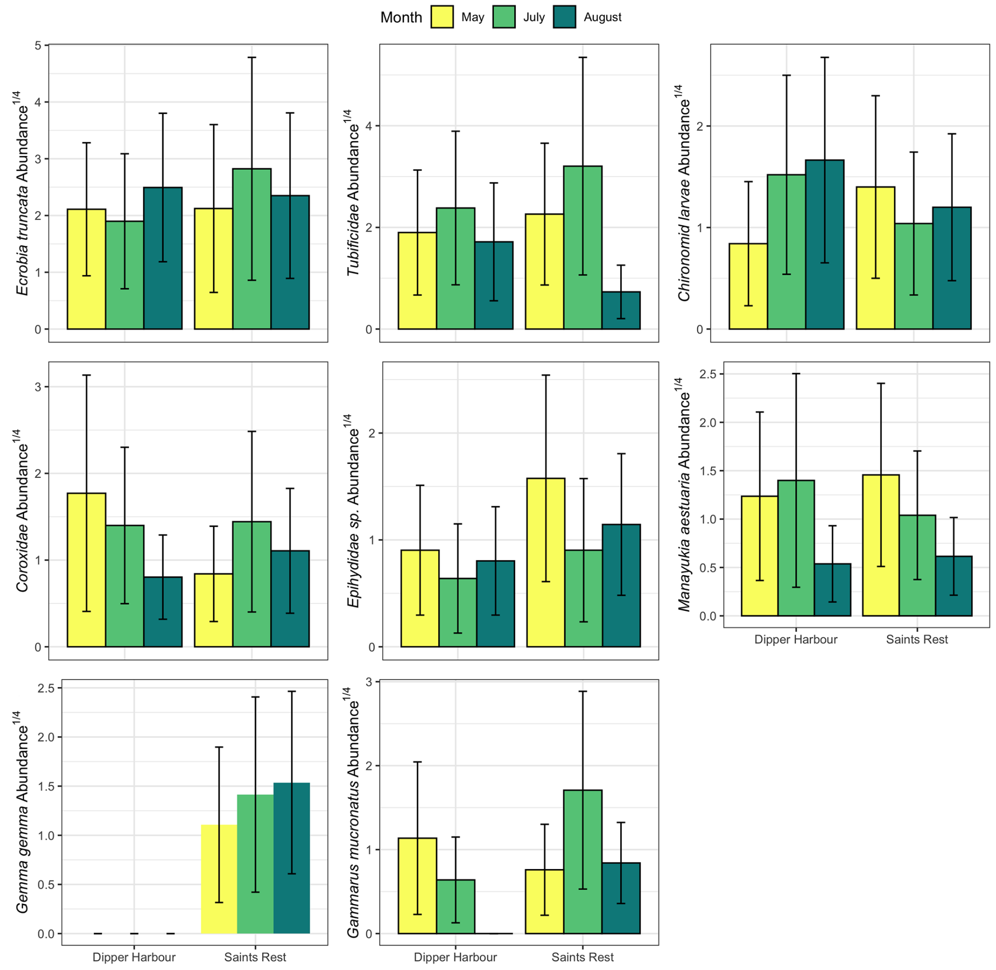

FIGURE 5
Mean (and se) of fourth-root abundance of the most influential macroinvertebrates taxa contributing a cumulative 70% of the dissimilarity between the two marshes in 300 cm^{-3}-samples of sediments from salt marsh pools sampled in May, July and August in 2004 and 2005 and averaged for pool elevation. For each marsh n=6 for May and July and in August, n=12 and 14 for Saints Rest and Dipper Harbour, respectively.

flocks of Canada geese and black ducks were frequently observed in the pools at Saints Rest while birds observed at Dipper Harbour were generally in small groups or solitary. Flooding lifts algal mats and allows them to float out of pools, and we assume that the more frequent flooding of low marsh pools was responsible for the low amount of vegetation observed in them. As compared to 2004, the decreased cover of *R. maritima* in 2005 may be due to the much drier summer weather causing extensive drying of most of the pools.

4.2 Invertebrates

Our analyses showed that pool elevation and month of sampling often explained more of the variability in invertebrate samples than whether they came from the reference marsh at Dipper Harbour or "recovering" Saints Rest marsh. The marsh origin had no significant influence in abundance of invertebrates in communities within pool vegetation. Although it was a significant influence on abundance of invertebrates in pool sediments, marsh origin explained the least amount of the variability (5%). Lower abundances of some species in Saints Rest pool sediments were likely due to more intensive grazing at this site, as noted above.

The observation of more intensive grazing at Saints Rest and our diversity indices suggest that the invertebrate communities in its pools have as much value as those in the reference marsh at Dipper Harbour. Overall diversity, as revealed by the Shannon Weiner Index or Species Richness, is similar or higher in Saints Rest, the recovering marsh. Although it may take greater than 20 years for invertebrate populations to recover (Warren et al., 2002) the status of invertebrate populations in pools at Saints Rest indicated that populations will take less than 50 years for this component of the marsh ecosystem to recover.

4.2.1 Importance of pools to wildlife

Our data and observations indicate that Saints Rest marsh is supporting the critical function played by invertebrate populations, as a food source for higher trophic levels, adding to that provided by mudflats. Over the course of our study, migrating shorebirds were frequently observed feeding in the marsh pools at high tide at Saints Rest marsh. Mudflats in the upper Bay of Fundy are highly valued as

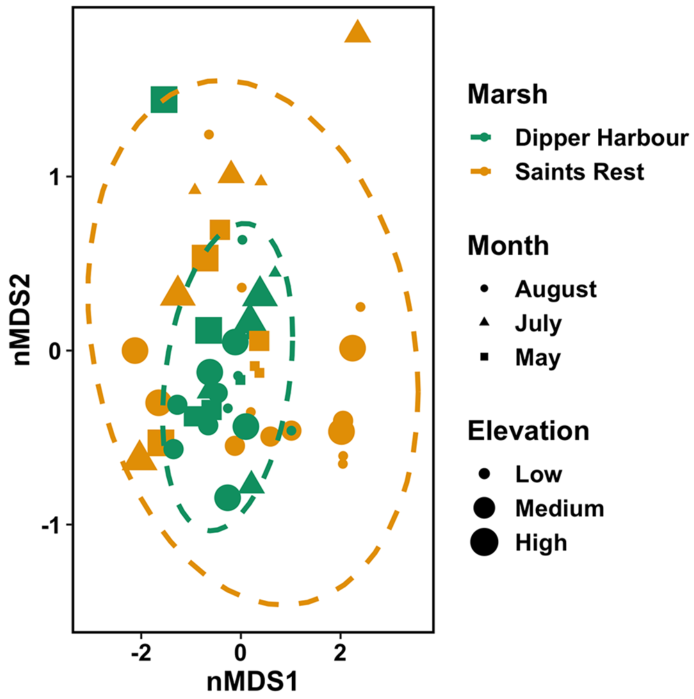

FIGURE 6
nMDS ordination plot for fourth-root of macroinvertebrate dry biomass (mg) in 300 cm^{-3}-samples of sediment collected from pools from July 2004 to July 2005 at Dipper Harbour and Saints Rest salt marshes using Euclidean distance. Each symbol represents the assemblage of invertebrates in a sample. Plot ellipses represent the 95% confidence regions for group clusters. Stress=0.11.

a feeding ground for migrating shorebirds. For instance, they are a critical stopover site for Semipalmated Sandpipers (*Calidris pusilla*) which feed on *C. volutator*, polychaetes and likely ostracods (MacDonald et al., 2012; Quinn and Hamilton, 2012; Gerwing et al., 2016). As compared to mudflats, some species of shorebirds feed primarily in the marsh on the return migration in spring (Hicklin and Smith, 1979) and our marsh pools provided a number of the same prey taxa as mudflats. In the lower Bay of Fundy Gratto and Thomas (1984) reported prey species of sandpipers included species characteristic of marsh pools such as *E. truncata*, Chironomid larvae and pupae, all found at Saints Rest. In addition to direct foraging in pools, insects emerging from pools are a food source for passerines, such as the salt marsh sharp-tailed sparrow, *Ammodramus caudacutus* (Greenlaw and Rising, 1994). Insect remains from at least four different taxa were observed at Saints Rest (Supplementary Table 2).

The importance of marsh pools and other shallow littoral habitats to fish as nursery, foraging and refuge sites is well recognized (e.g., Raposa and Roman, 2001; Adamowicz, 2002; Raposa, 2003; Able et al., 2005). Though not quantified, we observed mummichogs (*Fundulus heteroclitus*) in all sampled pools in all seasons and frequently in high abundance. Important prey items of mummichogs, such as amphipods, tanids, copepods and polychaetes (Kneib and Stiven, 1978), were collected in all of the pools sampled (Supplementary Table 2).

The abundance of several species of meiofauna observed, particularly in the un-sieved vegetation samples demonstrated that much of the diversity and production of these pools may be missed when meiofauna are not captured (Supplementary Table 2). For instance, marsh pools have been shown to have very diverse copepod communities, relative to macroinvertebrate diversity (Ruber et al., 1994). Some species of meiofauna are important prey items to fish (Kneib and Stiven, 1978; Ward and Fitzgerald, 1983), some species of birds (Gratto and Thomas, 1984; Gaston, 1992), and are important in transferring energy to higher trophic levels as prey for macroinvertebrates.

5 Conclusions

Approximately 50 years after dyke failure and return of tidal flooding, the invertebrate fauna of pools in the originally drained marsh was nearly indistinguishable from that of the reference marsh. We consider that the marsh has “recovered” with respect to pool fauna. The high invertebrate diversity and presumably secondary production of Bay of Fundy salt marsh pools is thus another ecosystem service to be considered when determining the value of restoration of its salt marshes.

When comparing restoration to reference sites to assess the progress of salt marsh restoration it is important to compare pools

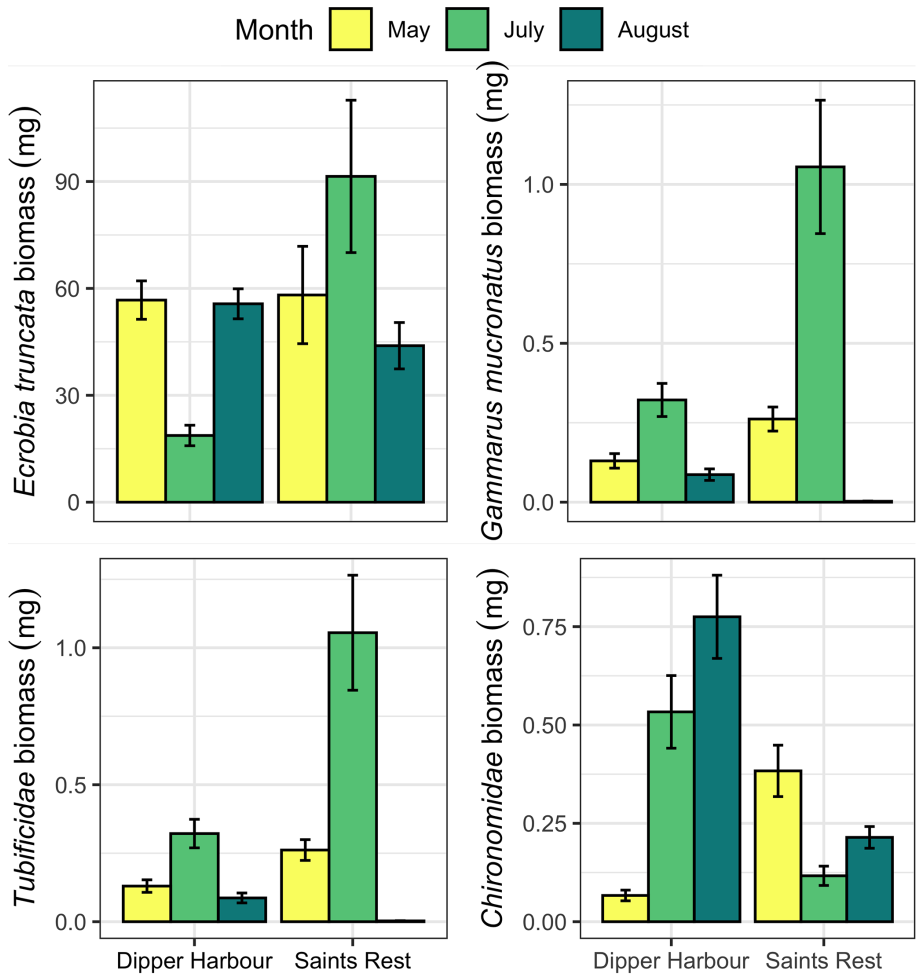

FIGURE 7
Mean (and se) of dry biomass (mg/300 cm^{-3}-sample) of the four most abundant macroinvertebrates in 300 cm^{-3}-samples of sediments from pools at Dipper Harbour and Saints Rests salt marshes, averaged over pool elevation for July 2004 to August 2005. For July and May, n=6 for DH and SR. For August samples n=14 for SR and n=12 for DH.

at similar elevations and time of year as these factors influence the invertebrate fauna found in pools. Including pools over a gradient of elevations will help to reflect the environmental variability that affects invertebrate species composition. In fact, a consideration in planning for salt marsh restoration should be to create pools with varied elevations. Future studies of pool invertebrates also should not be restricted to populations in the vegetation as the sediment samples have greater potential to reveal differences.

TABLE 4 Cumulative measures of diversity (e.g., total number of species found in low pools) calculated as species richness (S), Shannon Weiner Index (H) and eveness (J) of invertebrates in pools at high, mid and low elevations at Saints Rest (SR) and Dipper Harbour (DH) marshes from July 2004 to July 2005. H calculations are based upon average abundances.

Vegetation	S	H	J	Sediment	S	H	J
DH high	11	1.60	0.67	DH high	12	1.64	0.66
DH mid	13	1.17	0.46	DH mid	8	0.72	0.33
DH low	13	1.76	0.69	DH low	17	1.70	0.60
DH all samples	16	1.3	0.46	DH all samples	17	1.53	0.54
SR high	13	1.45	0.57	SR high	13	1.30	0.51
SR mid	14	1.62	0.61	SR mid	12	2.01	0.81
SR low	14	1.62	0.61	SR low	22	2.38	0.77
SR all samples	19	1.6	0.55	SR all samples	24	2.23	0.70

Data availability statement

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

Author contributions

PN and GC conceived the study, PN designed and executed the field and laboratory research. PN and BS conducted the analyses. All authors contributed to the article and approved the submitted version.

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Conflict of interest

Author PN was employed by the company J.D. Irving Limited.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.994533/full#supplementary-material

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Global trends in geospatial conservation planning: a review of priorities and missing dimensions

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Introduction: Biodiversity underpins resilient ecosystems that sustain life. Despite international conservation efforts, biodiversity is still declining due to ongoing anthropogenic threats. Protected areas have been widely adopted as a strategy for conserving biodiversity. The use of spatial conservation planning, which prioritizes areas for protection based on geo-referenced biodiversity and ecological information as well as cost of action and their feasibility, has gained popularity in the conservation discipline in the last few decades. However, there remain gaps between plans and implementation, and negative social impacts on local communities can occur, such as tension and conflict between differing priorities, perspectives, and views.

Methods: To better understand the state of the spatial conservation field and support translating research into practice, a mixed-method approach of bibliometric (n=4133 documents) and content analysis (n=2456 documents) was used to analyze and identify key research priorities, collaborative networks, and geographic and thematic patterns.

Results: We identified that research conducted by westernized nations dominated the field, with the United States, the United Kingdom, and Australia being responsible for almost two-thirds of the research globally, with research interest exponentially growing since 2010. Additionally, while there has been some refinement over time of algorithms and models, Zonation and Marxan methods developed in the 2000s remain the predominant choices of software, with a majority focus on marine ecosystems, birds, and mammals. We found a major gap in the use of social dimensions in spatial conservation case studies (only n=146; 6%).

Discussion: This gap highlights a lack of collaboration in conservation science between researchers and local communities who are affected by management decisions. We recommend including spatially explicit social dimensions from the onset of projects through participatory approaches, along with the acknowledgement by researchers of the importance of including diverse views in conservation planning to enhance implementation and outcomes that are relevant in local contexts. We suggest an increased reflection on types of data used for conservation but also on researchers' personal values, biases, and positionality to encourage more ethical, applicable, and collaborative conservation science.

KEYWORDS

conservation, review - systematic, spatial prioritization, VOSviewer, social dimensions

1 Introduction

Biodiversity is integral to functioning and resilient ecosystems (IPBES, 2019). The persistence of ecosystem services sustained by functioning ecosystems provides the stability needed to support life (Mooney et al., 2009; Sandifer et al., 2015). The importance of conserving biodiversity and ecosystems for societal well-being has become evident with the creation of a multitude of governing bodies, agreements, and goals such as Convention on Biological Diversity (CBD) to the creation of the Sustainable Development Goals (SDGs) (UN, 2015). Beginning in 1992 with the signing from 150 government leaders, the CBD now hosts a range of action agendas, frameworks, conferences, partnerships, protocols, and programs that are updated over time all pertaining to supporting the needs of global biodiversity (CBD, 2022). However, the health of ecosystems is deteriorating and biodiversity is declining (MEA, 2005; IPBES, 2019) despite local, national, and international efforts to meet conservation targets (Butchart et al., 2010; Johnson et al., 2017). As the planet continues to warm and becomes dangerously close to crossing climate-induced tipping points (Brovkin et al., 2021; IPCC, 2022), effective management of landscapes is needed now, more than ever.

Although decisions and actions for managing landscapes have existed for millennia through Indigenous custodianship (Roos et al., 2018; Fletcher et al., 2021a; Roberts et al., 2021), protected areas and other area-based conservation actions, in particular, have recently been adopted widely, at an increasing rate, by industrial society and contemporary scientific disciplines as a strategy for conserving biodiversity (Radeloff et al., 2013; Gillespie, 2020). Protected areas are defined as a clear, defined, recognized, dedicated geographical space that is managed through legal or other effective means for the long-term conservation of nature associated with ecosystem services and cultural values (Day et al., 2019). Protected areas make up 17% of terrestrial and inland water and 10% of marine and coastal areas protected formally (UNEP-WCMC and IUCN, 2021). These numbers are expected to increase in response to global initiatives like “30 by 30” that aims to designate 30% of Earth as formally protected areas by 2030 (CBD, 2022). While strict protection categories for protected areas exist (Dudley et al., 2010), there is debate about whether they are more effective than non-strict areas with multi-use management strategies (Elleason et al., 2021). While some studies have found strict protected areas are more effective (Carranza et al., 2014), others have found that non-strict areas can contribute to climate change mitigation by reducing tropical forest fires (Nelson & Chomitz, 2011) and biodiversity conservation by providing habitat for vulnerable species (Chauvenet, 2023).

To achieve desired conservation targets, spatial conservation planning approaches for identifying where to put new protected areas have gained popularity in the conservation science discipline in the past two decades (Sarkar et al., 2006; Kukkala & Moilanen, 2013; Alvarez-Romero et al., 2018). These approaches identify areas of high ecological importance using spatial information about characteristics of a landscape including, but not limited to, irreplaceability, distribution, and abundance of species, (Margules & Pressey, 2000; Wilson et al., 2009; Wiersma & Sleep, 2016). Spatial conservation approaches have been excellent at integrating ecological data and biophysical processes into spatial prioritization models (Pressey et al., 2003; Harris et al., 2019), and more recently, they have begun to embrace the importance of incorporating climate change data (Jones et al., 2016). Despite seeking to provide answers to questions about how to distribute limited conservation resources and identify priority locations (Wilson et al., 2007), geospatial conservation approaches have yet to fully bridge the gap between planning and implementing conservation activities (Knight et al., 2008; McIntosh et al., 2018).

In systematic conservation planning the impact on stakeholders can be considered through cost variables, such as the cost of acquiring land for a protected area (Kukkala & Moilanen, 2013) or opportunity costs (Adams et al., 2010). However, the unexpected consequences of designing protected areas on stakeholders remain somewhat unaddressed (Shafer, 2015; Larrosa et al., 2016). These include more abstract and difficult to account for situations such as negative social impact and creation of conflict between differing interests for local communities (West & Brockington, 2006; West et al., 2006). Additionally, decision-support tools are reflective of the inputs, settings, and decisions about methodology, and hence, they can favour certain interests and introduce bias into research outputs (Game et al., 2013). Considering social dimensions in conservation planning, like landscape values or cultural and social ecosystem services, has the potential to overcome some of these inadvertent ramifications of technologically heavy approaches. For example, in-person PPGIS workshops with stakeholders were used in the Upper Peace River Watershed to identify overlapping hotspots for non-economic priorities during the decision-making process for a hydroelectric dam (Darvill & Lindo, 2015).

As post-2020 global biodiversity targets are considered (Xu et al., 2021; Leadley et al., 2022), it is crucial to evaluate assumed benefits by assessing the on-ground effectiveness of management decisions. In this paper, we do this by assessing the research trends to understand, quantify, and consolidate the current state of geospatial conservation planning including knowledge gaps. To achieve this aim, we used a mixed method approach including bibliometric and content analysis to assess temporal, thematic and geographic patterns in the literature (Hood & Wilson, 2001; Van Eck & Waltman, 2014). Specifically, we assessed who published the research, where does this research occur, and what methods, themes and topics are prioritized. Finally, we evaluate the main considerations and concerns for future spatial conservation research.

2 Materials and methods

2.1 Bibliometric analysis

To evaluate the growing body of knowledge on geospatial conservation planning, bibliometric data on relevant publications was assessed to provide insights about key research priorities, collaborative networks, and research trends and gaps (Van Eck & Waltman, 2010; Waltman et al., 2010). The bibliometric review method is becoming more popular (Mingers & Leydesdorff, 2015) and has been used more recently to assess global research efforts for environmental topics such as in mountain regions (Verrall &

Pickering, 2020), adaptation to climate change (Nalau & Verrall, 2021), climate change research in the Arab world (Zyoud & Fuchs-Hanusch, 2020), marine spatial planning (Chalastani et al., 2021) among others. To understand the complexities of landscape decision-making processes, it is necessary to first assess how the geospatial conservation planning discipline has evolved, including evaluating priorities focused on when making decisions about the future.

Since it is challenging to identify all research documents on a topic with a single literature search, interactive query formulation was used. This involved collecting and screening preliminary results to ensure that a comprehensive final search term was used to systematically search for relevant literature (Wacholder, 2011; Verrall & Pickering, 2020). We used common geospatial terms paired with specific systematic conservation planning terms to gather a database that was representative of the body of literature in both breadth and depth. The final document search was conducted in the Scopus and Web of Science databases (Falagas et al., 2008) on July 30th, 2021 (Figure 1). This search yielded 4079 and 3407 documents from Scopus and Web of Science respectively and bibliometric data were downloaded for data cleaning in Microsoft Excel (2019). Next, duplicates and some miscellaneous document types were removed (i.e., note, letter, survey, and editorial materials) before topical abstract screening was used to remove any untargeted and unintentional results that were outside of the conservation scope of this review (i.e., applied mechanics and engineering). Even if it is impossible to collect 100% of relevant literature, systematic type reviews provide a framework for identification that is both reproducible and transparent (Moher et al., 2009; Mingers & Leydesdorff, 2015).

A final document count of 4133 peer-reviewed journal articles, books, book chapters and conference papers were included in the

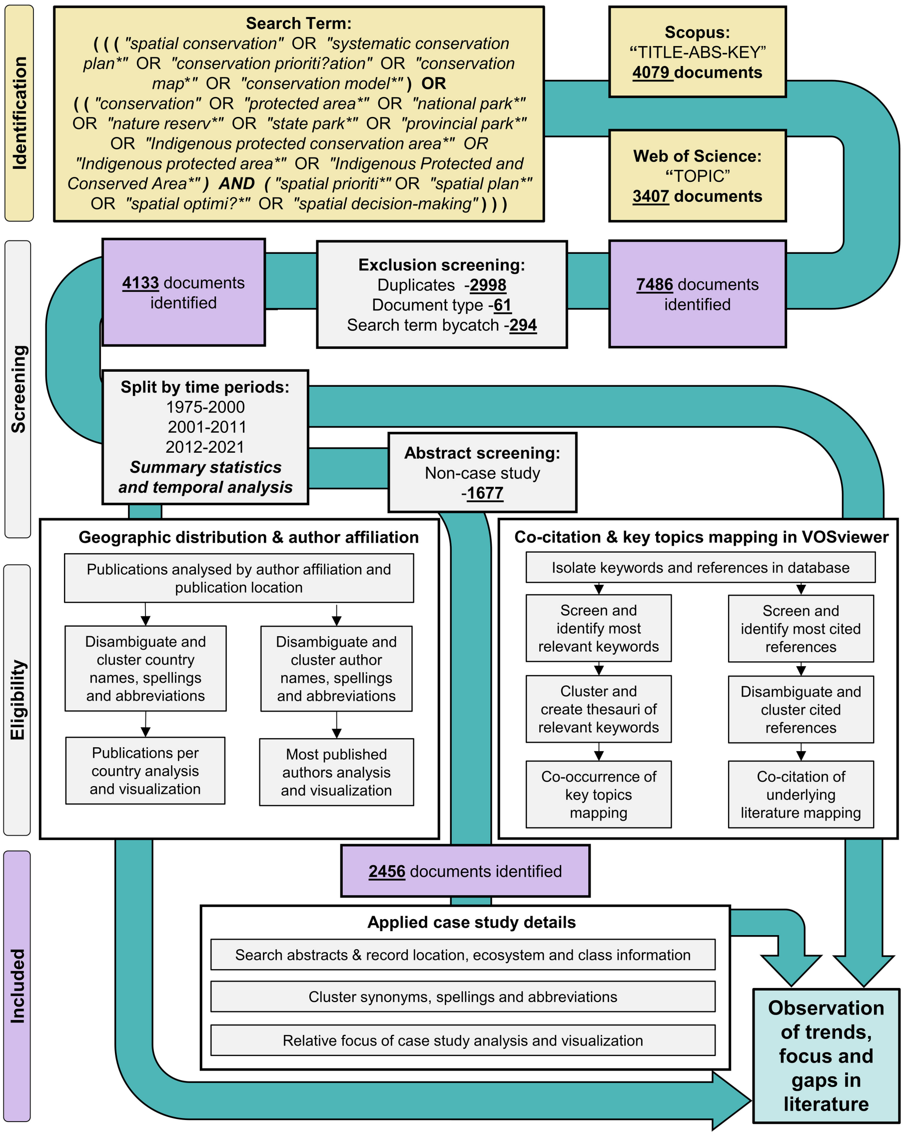

FIGURE 1
Methodological overview of study design including search term, screening process, and analysis summary for all time periods (1975-2000, 2001-2011, 2012-2021).

final bibliometric analysis (Figure 1). Prior to analysis, the final database was split into three time periods that correspond with the introduction of protected area targets from the Convention on Biological Diversity (CBD; 1975-2000, 2001-2011, 2012-2021) to assess the evolution of predominant research trends in the geospatial conservation planning discipline. To assess the literature database author key words, geographic spread of research, underlying co-cited literature, and leading researchers were analyzed in the bibliometric program VOSviewer (Van Eck & Waltman, 2010; Waltman et al., 2010). Some bibliometric data were clustered prior to final analysis by the creation of thesauri to reduce ambiguity (i.e., 'gis' and geographic information systems, 'mammal' and 'mammalian'), where a smart-moving algorithm was used to identify relationships and patterns within the dataset (Van Eck & Waltman, 2017) (Table S1). There is an overlap of terms within these categories due to the targeted nature of the search term, however through the clustering of common words used together, there are certain trends that can be identified. These relationships are visualized through nodes and lines where size and thickness are proportionate to the relative number of occurrences (Waltman et al., 2010).

2.2 Case study and content analysis

To better understand how this discipline is applied on the ground, the literature database was systematically assessed to identify articles that were appropriate for content analysis. The criteria we used to identify these articles was 1) they must be peer-reviewed case studies, 2) they employed geospatial conservation planning methods, and 3) they needed to be tied to a specific time and place, as opposed to theoretical and hypothetical models (Figure 1). Abstracts were screened to assess their relevance to the case study criteria to identify eligible documents for sub-set content analysis (Figure 1; Table S2). There were 32 publications excluded for lack of abstract, 131 because they were books or book chapters and 1515 documents excluded for not meeting the case study criteria of employing geospatial methods to a specific time and place, leaving 2455 documents remaining for content analysis (Table S2). Case study details were recorded in Microsoft Excel (2019); this included coding for region, nation, environment, ecosystem, organism type, organism class, endemicity, invasiveness and incorporation of social dimensions (type and method of collection). We included social dimensions that were spatially explicit, collected in a participatory manner, and integrated into spatial models such as landscape values (e.g., Karimi & Hockings, 2018). We used the author's own classification of ecosystems and location when recording details where possible and recorded where any of the data was not present. Finally, prior to final content analysis, author classifications of ecosystems were clustered into broader ecosystem type categories (e.g., 'bog', 'fen' and 'marsh' grouped to singular 'wetlands' category; 'prairie', 'plain' and meadow' grouped to singular 'grass- and arid-lands'; Table S3) to reduce ambiguity and improve comparative assessments to identify more detailed research trends presented in the following results.

3 Results

3.1 Characteristics of the literature over time

The initial results of the database searches yielded a total of 4133 relevant documents that were divided into three time periods early (1975-2000), recent (2001-2010) and emerging (2011-2021), with 83.7% of the literature falling in the latter, suggesting a recent increase in interest on this topic (Table 1; Figure 2). Most of this literature was published predominantly in English (n=3909; 94.6%) with the remaining published languages covering >2% of the overall documents (Table 1; Table S4). This database consisted mainly of peer-reviewed journal articles (n=3501; 84.7%; Table 1). Collectively, there were 1776 sources that published on geospatial conservation planning with Biological Conservation (n=231; 5.6%), Marine Policy (n-150; 3.6%) and Conservation Biology (n=122; 3%) leading the database for the journals with the greatest number of documents (Table S4). There were a few publications that were heavily cited. For example, 19 of 25 of the most cited authors were co-authors on a single document that has 3650 citations overall (Halpern et al., 2008) compared to the highest cited document in the emerging time period (2011-2021) (Chan et al., 2012) (512). Of the 4133 documents that were examined, 2456 case studies were identified where spatial conservation methods were applied to a specific time and geographic location (Figure 2).

3.2 Geographic trends and priority ecosystems

The database included papers by authors from 154 countries, however, 30 of these countries have only published once (Table S4). From these countries there were 13999 individual authors who have contributed to this body of literature, of which 80.2% have only published once (Table 1). Almost 60% of the literature has been published by authors associated with only three countries (n=2464); United States (26.4%), Australia (16.8%) and United Kingdom (16.4%) (Table 1). Of the top 25 published countries, only six are outside of North America and Europe (Table S4). The number of countries publishing on this topic has increased steadily over the three time periods (20 to 77 to 149). Similar to other global reviews (Verrall & Pickering, 2020; Nalau & Verrall, 2021), on a continental scale, authors from organisations in many countries are represented at some level but large gaps still exist in Central and Northern Africa, Western and Central Asia, Central America and the Caribbean (Figure 3A). While comparing the distribution of published research versus location of the case study areas, there are similar trends in terms of where receives the most attention (Figures 3A, B). Of the 2456 documents with a case study approach, there were 4486 specific geographic locations on which data was recorded, with more countries represented compared to where the studies were published (232 vs 154) (Table 1; Table S7).

Similarly, there are ecosystems that have received more attention than others, most notably marine environments (n= 758; 30%), specifically open water marine ecosystems (n= 489;

TABLE 1 Bibliometric overview of publications split by time periods.

Categories	1975-2000		2001-2010		2011-2021		Total	
	#	%	#	%	#	%	#	%
Publications	105	2.6	568	13.7	3460	83.7	4133	100
Article	90	86.7	447	78.7	2964	85.7	3501	84.7
Proceedings Paper	11	10.5	50	8.8	207	6.0	268	6.5
Review	4	3.8	43	7.6	176	5.1	223	5.4
Book Chapter	0	0.0	24	4.2	97	2.8	121	2.9
Book	0	0.0	4	0.7	16	0.5	20	0.5
Language								
English	88	83.8	535	94.2	3286	95	3909	94.6
Chinese	1	1	4	0.7	71	2.1	76	1.8
German	9	8.6	8	1.4	19	0.5	36	0.9
Spanish	0	0	3	0.5	29	0.8	32	0.8
Polish	5	4.8	4	0.7	7	0.2	16	0.4
Country								
United states	28	26.7	160	28.2	904	26.1	1092	26.4
Australia	5	4.8	77	13.6	611	17.7	693	16.8
United Kingdom	8	7.6	86	15.1	585	16.9	679	16.4
China	1	1.0	14	2.5	302	8.7	317	7.7
Canada	4	3.8	34	6.0	265	7.7	303	7.3
Most Published Authors								
Possingham, HP	0	0.0	21	3.7	98	2.8	119	2.9
Moilanen, A	0	0.0	17	3.0	55	1.6	72	1.7
Pressey, RL	1	1.0	15	2.6	53	1.5	69	1.7
Klein, CJ	0	0.0	9	1.6	26	0.8	35	0.8
Hermoso, V	0	0.0	0	0.0	34	1.0	34	0.8
Most Cited Authors								
Pressey, RL	3368	58.5	1982	6.6	1635	3.1	6985	7.9
Halpern, BS	0	0.0	3560	11.9	1981	3.8	5541	6.3
Possingham, HP	0	0.0	1828	6.1	3532	6.7	5360	6.1
Micheli, F	0	0.0	3560	11.9	534	1.0	4094	4.6
Margules, CR	3368	58.5	592	2.0	0	0.0	3960	4.5
Citations								
Total	5757	6.5	29963	34.0	52535	59.5	88255	100
Most Cited	3368	–	3560	–	512	–	3560	–
Average	55	–	53	–	15	–	21	–
Number of Authors								
Total Authors	208	1.5	1729	12.4	12565	89.8	13999	100
Authors with only one publication	200	96.2	1544	89.3	10100	80.4	11233	80.2
Authors per publications	2.0	–	3.0	–	3.6	–	3.4	–

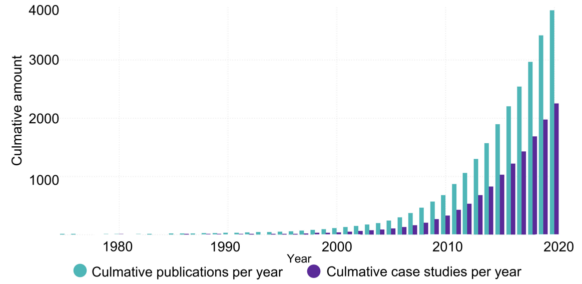

FIGURE 2
Cumulative publications and case studies over time.

19.4%) (Table 2). This may be attributed to a significant focus on the Mediterranean Sea (e.g, Kyprioti et al., 2021). Alternatively, freshwater environments (n= 341; 13.4%), specifically wetland ecosystems (n= 73; 2.9%), have received less attention despite their significant importance worldwide (Moomaw et al., 2018). The most studied ecosystem in terrestrial environments were forests (n=243; 9.6%) and were also the most studied ecosystem in South and Central America (Figure 4A). Anthropogenic landscapes were studied in 13.4% of all case studies (n=339) most often when focused on areas of historic and current human settlement (n= 339; 13.4%) which were the most studied ecosystem in Eastern & Southern Asia region (Figure 4A). There were however many cases of studies focusing on non-specific ecosystem (n= 558; 22.1%; Table 2), instead focusing on areas defined by geo-political boundaries that may make up multi types of ecosystems or range of species across a landscape (e.g., Botello et al., 2015).

3.3 Key topics and themes

Synonymous words were grouped to produce a total of 7593 author keywords used to illustrate key themes within the literature (Figure 5; Table S1). Keywords were grouped by VOSviewer based on their frequency of use, co-occurrence, and connection to each other to illustrate general research themes within the database. We named these sub-categories into five broad research themes: 1) sustainability and land-use planning; 2) spatial conservation planning; 3) habitat suitability and distribution 4) marine spatial planning and management and 5) ecological conservation and prioritization (Figure 5A) based on the relatedness of clustered keywords. While there is an overlap of terms within these categories due to the targeted nature of the search term, there are certain trends that can be identified. Category 1 (Figure 5A), there was a clear clustering of keywords that focused on landscape-level management approaches in socio-environmental systems centered around 'ecosystem services' and 'spatial planning'. The inclusion of 'governance', 'stakeholders' and 'urbanization' showcases a potential human-centric focus for this research (e.g., Kabisch, 2015). Expectedly, the largest cluster (2; Figure 5A) was centered around designing, planning, and analyzing protected areas using complex spatial tools and methods (Figure 5A; Table S#). Variations of 'Marxan' appear to be the predominant software choice for prioritization to support meeting 'conservation targets'

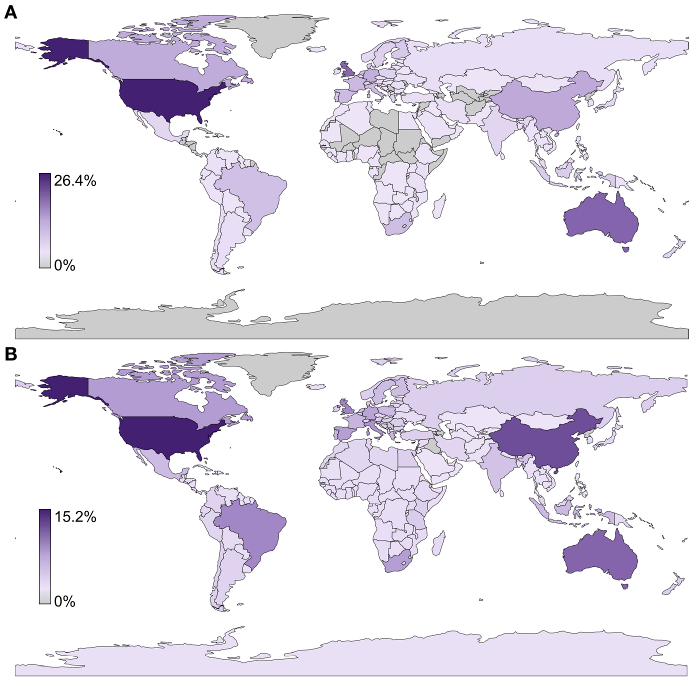

FIGURE 3
(A) Geographic distribution of published literature in the spatial conservation discipline over all time periods (1975-2021) and **(B)** Geographic distribution of case studies in the spatial conservation discipline over all time periods (1975-2021).

TABLE 2 Occurrence of environments of focus and ecosystem types.

Environment type	Ecosystem	#	%
Marine		*758*	30.0
	open water	489	19.4
	coastal	166	6.6
	reef	91	3.6
	mangrove	7	0.3
	non-specific	5	0.2
Terrestrial		*530*	21.0
	forest	243	9.6
	mountain	96	3.8
	grassland	80	3.2
	tropical & rainforest	*45*	1.8
	island	*37*	1.5
	tectonic & exposed rock	*5*	0.2
	non-specific	24	1.0
Freshwater		*341*	13.5
	riverine	149	5.9
	watershed	118	4.7
	wetland	73	2.9
	non-specific	1	0.0
Anthropogenic		*339*	13.4
	historic and current human settlement	158	6.3
	agriculture	116	4.6
	energy	65	2.6
Non-specific		558	22.1

such as ‘natura 2000’ and other ‘protected area’ targets (e.g., Kukkala et al., 2016). The next biggest cluster (4; Figure 5A) was focused on marine spatial planning and environments despite the search term not specifically targeting this literature (Figure 1; Figure 5A). There was a secondary focus on resource management and making decisions about balancing multiple preferences with the inclusion of terms like ‘fisheries’, ‘marine reserves’, and ‘zoning’ that consider ‘local and traditional knowledge’ (e.g., Bennett et al., 2018).

The two smallest clusters; ‘habitat suitability and distribution’ (3) and ‘ecological conservation and prioritization’(5), contained highly specialized terms such as ‘species distribution modelling’ and ‘phylogenetic ecology’ (Figure 5A; e.g., Cadotte & Jonathan Davies, 2010). These keywords may not be necessarily specific to spatial conservation planning in their application like the other clusters, but the context of the research is inherently spatial because it included studies about the way flora and fauna interact with the landscape. The broadness of these disciplines over time and landscapes may explain the inclusion of comprehensive terms like ‘climate change’ and ‘biodiversity’ as top keyword in this is research theme category, which relative research focus has increased over time (Table S8). Figure 5B represents the time period of the largest change in research focus in this body of literature occurred between the years 2014 and 2017 (Figure 5B) where research shifted from optimizing reserve design and selection to focusing on the concepts that motivated conservation initiatives such as ‘ecosystem services’ and ‘biodiversity’. Additionally, this has been a move to including more of a human element with terms like ‘socio-ecological systems’ and ‘human impact’ becoming more popular (e.g., Lazzari et al., 2019).

Examining these ecological attributes of flora, fauna and fungi at the case study level can provide insight into research priorities in terms of the specific organisms. About half of the case studies focused on at least one species of vertebrates (n=924; 34.6%), invertebrates (n=190; 7.1%) or vegetation (n=241; 9%) (Table 3). Most of the research on vertebrates was focused on birds, mammals, and fish (79.4%), while amphibians and reptiles were not as commonly studied (Table 3). When reptiles were studied however, they were more likely than other vertebrates to be studied in the context of being rare, endangered, or threatened (35.8%), particularly when it came to turtles (e.g., Shillinger et al., 2010). Terrestrial plants and invertebrates were more likely to be studied than their aquatic counterparts (Table 3). Terrestrial vegetation was the most studied rare, threatened, or endangered organism (n=67; 23.5%) and the most studied invasive organism (n=12; 50%).

3.4 Influential literature, institutions, and methodological choices

To understand how a body of knowledge influences future research, it is important to first identify the fundamental concepts and ideas that are driving it. Overall, the network of the top 25 most cited and co-cited publications is well-connected; meaning the field is cohesive as there are no major concepts and theories evolving separate from much of the literature. Instead, the documents that are cited most often, are widely and consistently cited throughout this whole body of literature (Figure 6). Of these 25 publications, 84% were published in the 2000s, implying that this is currently the most influential period for the discipline (Figure 6; Table S5). Australian institutions such as the University of Queensland and James Cook University have contributed the most over time to this body of literature with 251 and 114 documents respectively (Table S9). Nelson Mandela Metropolitan University, Conservation International and Duke University were among the earlier key contributors, while Deakin University, Imperial College London and University of Western Australia have been rapidly contributing post-2017 (Figure S1).

There was a clear use of method manuals in research such as Moilanen et al. (2009) and key papers such as Margules & Pressey (2000), demonstrating that these technical works has been pivotal in guiding the research and application of spatial conservation (Figure 6). This popularity could be because these books include

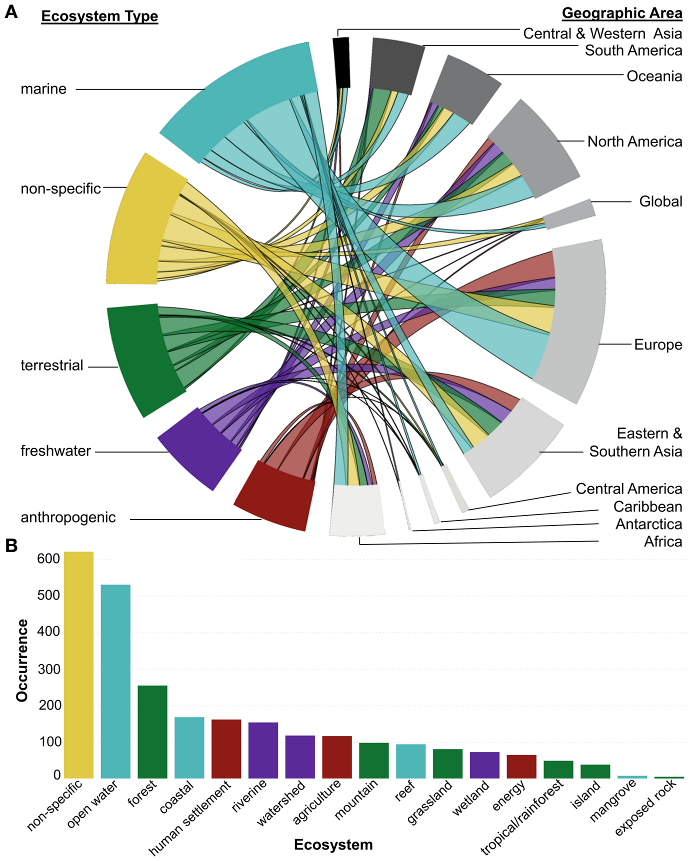

FIGURE 4
(A) Relative focus on environment type by case study region and **(B)** occurrence of ecosystem for case studies over all time periods (1975-2021).

many chapters of different methods that can be cited separately in a range of spatial conservation applications. While 22 of the 25 most co-cited documents were journal articles, they provide the basis of common methods and theories that are used within current geospatial conservation planning discipline (i.e., Watts et al., 2009), and within broader ecological and climate research (i.e., Hijmans et al., 2005).

While the technical aspects of conducting spatial conservation mapping and modelling are well represented, human dimensions and societal implications of the application of these types of approaches are largely missing. When it came to applying these methods on the ground, we found of the 2456 case study applications only 146 (6%) incorporated social dimensions collected through a participatory approach into their models (Table S6). Most often this research has occurred in Oceania (n=32), Africa (n=29), North America (n=26) and Europe (n=26) and has focused on marine ecosystems (n=58; i.e., Buscher et al., 2021). Additionally, there has been an increase in use of this type of method over time, with 54% of instances occurring from 2015 (n=79). Unsurprisingly, the most common type of social dimension that was integrated into research methodologies was preferences and priorities (n=98). Values, which were often conceptualized as ecosystem services to participants, were the next social dimension to be most often integrated (n=35) including situations of multiple or single values at a time (Table 4). Local knowledge was integrated into case studies 25 times, such as local fishers' knowledge on species and habitats (Pittman et al., 2018) and Indigenous Traditional Ecological Knowledge (TEK) (Noble et al., 2020). Finally, human perception was integrated only 8 times into case studies possibly because of the abstract nature and difficulty quantifying qualitative information into models (i.e., landscape changes, threats).

The number of times each data collection method was used was relatively uniform across the options however, interviews were used the most (n=55) followed by participatory mapping (n=54). This included 30 times non-digital (i.e., paper, or laminated maps with stickers, drawing or stackers) and 20 times digitally (both in person via tablets and via online interactive interfaces), and were often used in conjunction (ie., Kockel et al., 2020). Workshops and focus group settings were used 40 times followed using surveys and questionnaires to elicit data to be included in analysis. It is important to note that only one method was used 47 times, while the remaining occurrences used multiple forms of data collection (i.e., an interview that included a one-on-one mapping exercise; Noble et al., 2021). There were some cases where the method of collection was undisclosed (n=28). While authors noted a participatory process and included data collected in their model, the focus of research was on the model and it was not elaborated on how the data was collected (i.e., stakeholders were

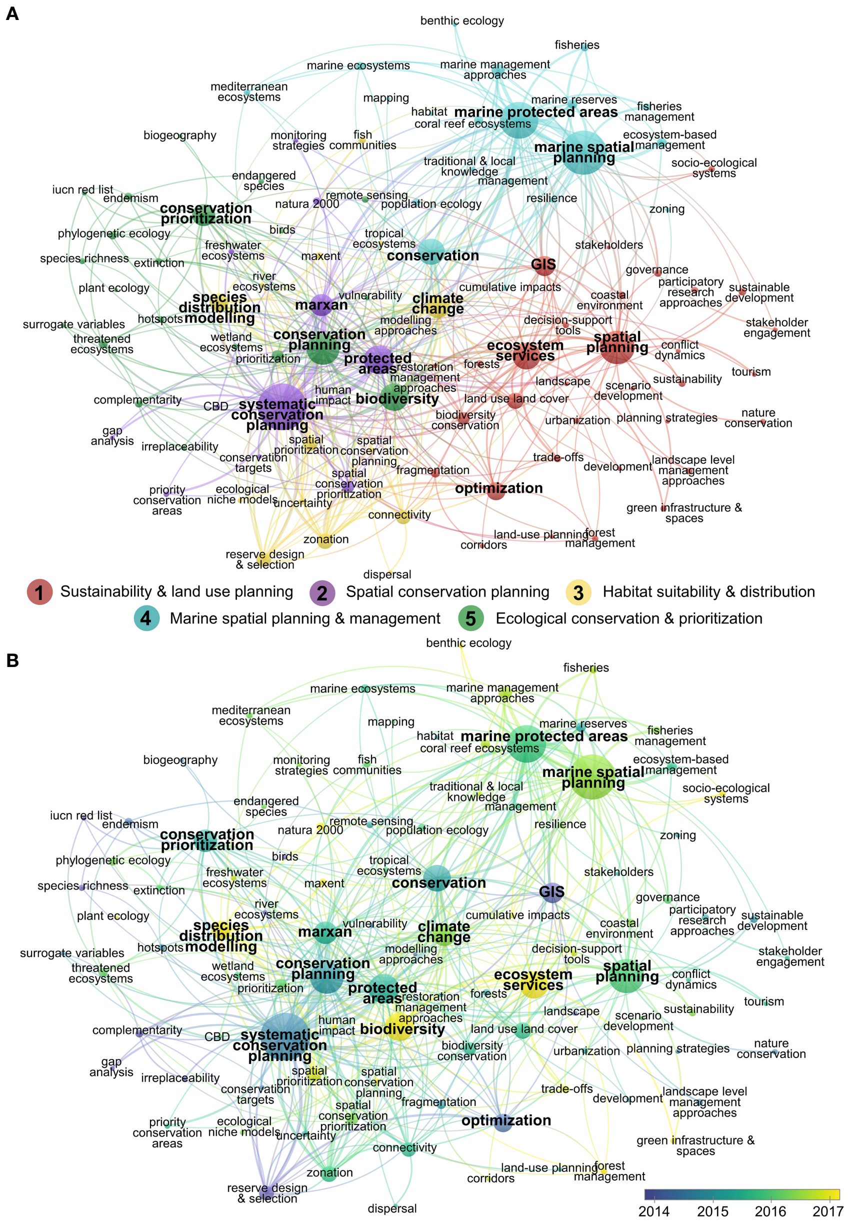

FIGURE 5
VOSviewer map of keywords for top 100 with 25 occurrences and 5 document minimum line strength with **(A)** theme titles and **(B)** the period of most thematic change (2014-2017) over all time periods (1975-2021) where purple represents common keywords pre-2014 and yellow represents common keywords post-2017 as current research focus.

"brought together" or priorities were developed by a stakeholder working group).

4 Discussion

This investigation has provided a comprehensive overview of the general trends in peer-reviewed geospatial conservation planning literature. Our analysis has examined bibliometric characteristics of the literature and foundational theoretical concepts as well as geographic trends in authorship and case study application, research priorities and key themes within the discipline. At this juncture, we focus on understanding how these trends have contributed to the evolution of knowledge within the discipline and how geospatial methods have been applied on the ground against the background of a technological and theoretical discipline.

4.1 Characteristics of research and global priorities

4.1.1 Inception and evolution over time

This review provides insight into the field of spatial conservation planning as a sub-discipline of conservation biology,

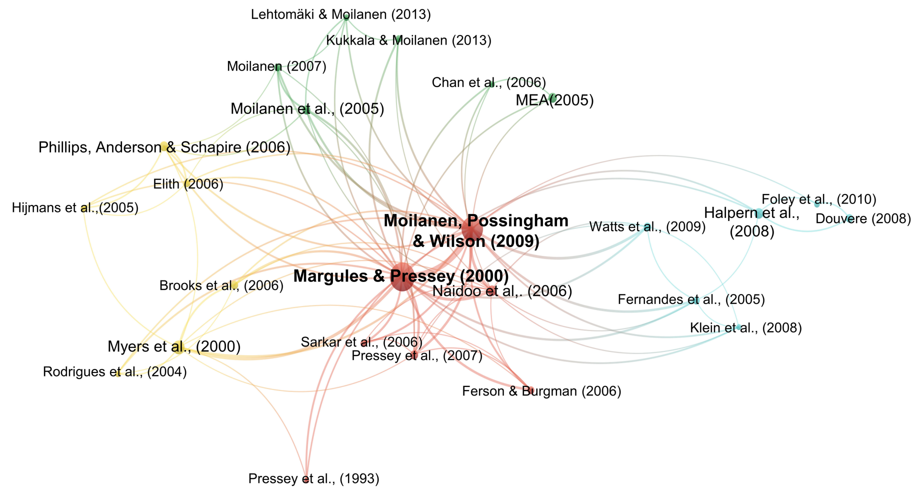

FIGURE 6
VOSviewer map of underlying co-cited literature for top 25 most cited documents with 25 occurrences or more for all time periods (1975-2021).

TABLE 3 Occurrence of taxonomic grouping and class and conservation status for case studies.

Taxonomic grouping	Class	#	%
Vertebrates		924	34.6
	Birds	261	9.8
	Mammals	249	9.3
	Fish	224	8.4
	Reptiles	81	3.0
	Amphibian	70	2.6
	Non-specific	39	1.5
Invertebrates		190	7.1
	Terrestrial	111	4.2
	Aquatic	77	2.9
	Non-specific	2	0.1
Vegetation		241	9.0
	Terrestrial	221	8.3
	Aquatic	16	0.6
	Non-specific	4	0.1
Other			
	Fungi	4	0.1
Non-specific		1315	49.2
Conservation status		#	%
	Endangered, rare, or threatened	328	12.3
	Invasive, noxious, or exotic	27	1.0

and how it has grown over time, especially in the past decade. Following the publication of '*Systematic Conservation Planning*' in 2000 (Margules & Pressey, 2000), and coinciding with systematic conservation planning principles being adopted in the CBD's Strategy for Biodiversity in 2002, there was increasing application of geospatial approaches for nature conservation. The tools that are being used to help conservation practitioners and researchers plan for protected areas are increasingly becoming more sophisticated from a technological standpoint since the centralization of approaches by key methodological publications (Moilanen et al., 2009; Watts et al., 2009). Interestingly, while the amount of research has rapidly increased over the past two decades, the main tools being employed have remained mostly constant. Marxan and Zonation are undoubtedly the primary choices of software for carrying out this type of analysis (e.g., Lehtomäki et al., 2015; Rivers-Moore et al., 2021), with the emergence of web-based tools and program extensions like 'prioriztr' in R (e.g., Southee et al., 2021). Choices in conservation planning support tools can influence the output and should be chosen based on the overall goals of the planning process. These decisions enable researchers and practitioners to make informed decisions about how to achieve their desired goals whether that be, but not limited to, cost-effectiveness, resource allocation, stakeholder engagement, threat mitigation, or corridor design and connectivity. For example, between Marxan and Zonation, both can support different overall goals such as more efficient results for the former and greater connectivity for the latter as demonstrated in a case study from the English Channel (Delavenne et al., 2012). Even though the main choices of methodology have remained dominant for the past two decades, there has been some refinement through changes to existing software as they have been applied more (i.e., from Marxan to Marxan with Zones), pointing to some reflection and advancement within the discipline about methodological choices.

TABLE 4 Examples of the integration of social dimensions from reviewed case studies including the type of dimension, method of participatory collection, software or program used and recommendations for future use and research.

Type	Examples from review	Collection	Software/ program	Recommendations for application
Values	Raymond et al. (2009)	Interviews, participatory mapping (in-person, non-digital)	GIS	-Improve methods in eliciting community input to effectively identify and map atmosphere asset values, associated supporting services, and threats, emphasizing the importance of developing a modified typology for a more comprehensive understanding of supporting services for participants.
	Ruiz-Frau et al. (2011)	Interviews, participatory mapping (in person, non-digital)	ArcGIS	-Adopt a more flexible approach in future Marine Protected Area (MPA) studies, allowing participants to select smaller areas that align with their preferences, as the current methodology of forcing the choice of larger, highly protected MPAs led to concerns about potential impacts on specific societal sectors. -Include a higher number of participants in interviews to capture variation in opinion with and between different stakeholder groups. -Give more attention to the potential disproportional representation of different sectors and possibly apply weightings to final valuation maps.
	Bryan et al. (2011)	Interviews, participatory mapping (in-person, non-digital)	GIS	- For effective co-management decisions, ecologists should engage in a two-way process with local communities, particularly in areas of low ecological value and high social value, by transcending normative aspects and providing evidence-based tools to enhance collaboration.
	(Jarvis et al., 2016)	Crowdsourced Voluntary Geographic Information (VGI)	ArcGIS, RStudio	-Ask participants how they had heard of the opportunity to participate in the study to determine the effectiveness of different recruitment types i.e., print, online, and/or news media. -Encourage participants to initially identify areas of personal importance before identifying values to effectively capture value diversity, including anthropocentric, biocentric, and anthropocentric–biocentric orientations at each point.
Perceptions	(Paloniemi et al., 2018)	Surveying/ questionnaire, interviews, workshops	Zonation	-Engage in iterative communication with planners, landowners, and stakeholders to scale up the prioritization, with emphasis on the importance of collaboration throughout the prioritization process i.e., discussion overall aims, analysis and findings more openly, to improve ownership. -Offer alternative prioritization analyses to present to stakeholders in workshops, aiding in the identification of specific areas for targeted marketing of voluntary conservation through subsequent local meetings and personal communication.
	(Goodman et al., 2006)	Workshops	Remote sensing, ArcGIS, Marxan	- Include, collect, and supplement the system with a wider range of data and biodiversity elements to refine targets for conservation and improve the chance that the plan will be implemented.
Preferences/ priorities	(Brown et al., 2019)	Surveying/ questionnaire, participatory mapping (digital online)	Custom Google maps application, ArcGIS	-Broaden survey recruitment efforts to improve representation, particularly in rural and remote areas, and consider alternative social data collection methods that are potentially more preferred i.e., face-to-face interviews. -Validate ecological data in locations identified as having both high quality habitat and social acceptability. -Include estimated land values for the economic feasibility of prioritization outputs. -Devise a manner to account for “super mappers” who can potentially influence overall results i.e., limiting the number of markers.
	(Teh et al., 2013)	Interviews	Protected Area Suitability Index (PASI)	-Pay attention to power dynamics in the participatory process, particularly where financial, scientific, and technological resources are uneven, to avoid influencing of pre-defined objectives by seemingly more powerful stakeholders. -View index scores as relative to each other and not as absolute values. It is the user’s interpretation of the score in the local context that matters the most.
Local knowledge	(Leroux et al., 2007)	Interviews, participatory mapping (in-person, non-digital)	GIS, Marxan	-Caution given to the scaling of datasets to avoid the overestimation of overlap between heritage sites and protected areas. Make comparisons at a finer scale where possible and appropriate. -Develop co-operative working groups with local organizations to better facilitate exchange of information between researchers and the community and incorporate community interests.
	(Pittman et al., 2018)	Surveying/ questionnaire, participatory mapping (digital online)	Custom Google maps application, ArcGIS, MaxEnt	-Consideration of caveats for future use i.e., that the tool will need to be updated periodically and future users will need to assess the weight of evidence and uncertainty for each scenario.

(Continued)

TABLE 4 Continued

Type	Examples from review	Collection	Software/ program	Recommendations for application
	(Noble et al., 2020)	Interviews, participatory mapping (in person, non-digital)	ArcGIS	-Develop better coordination and mechanisms to prioritize addressing conflicting issues between stakeholders i.e., land council's management of the land-sea connection involved beach sand replenishment whereas other stakeholders felt this was damaging to habitat and could reduce cultural and community well-being. -Address and acknowledge the potential that some stakeholders may not feel comfortable giving responses due to their positions in government that may misrepresent the governments agenda particularly conversations involving contentious issues or topics. -Give value to local and Indigenous knowledge along with scientific information through a communicative process that addresses local concerns. Visual aids like maps could be used as a starting point to facilitate this knowledge exchange.

Assessing the evolution of a research body overtime can provide insights into the potential trajectory of research in the future. Overtime, the areas of focus in this body of research have also diversified including shifts from single species (e.g., Pyke, 2005) through ecosystem level and multi species conservation plans (e.g., Osipova & Sangermano, 2016) to integrating complex issues in socio-ecological systems, like climate change impacts, ecosystem function, and the value of ecosystem services (Anderson et al., 2021). This is aligned with recent calls to integrate climate change into geospatial decision-support tools and has been recognized as an important consideration as the climate continues to warm and species and ecosystems are faced with novel threats (Jones et al., 2016). The context in which these tools are applied, however, is becoming increasingly more diverse with wider application, as the amount of case studies is also rising as the discipline grows. Applying and connecting these approaches on broader geographic scales are important to avoid fragmented and isolated conservation efforts that reduce biodiversity (Haddad et al., 2015), which may hinder the ability to reach conservation targets.

4.1.2 Geographic mismatches

While there are several trends and central themes that have emerged in this review, there were imbalances in who is conducting the research versus where research is being conducted. Similar to many studies that have taken a broad approach to understand how research evolves over time, we found a clear inclination towards publications from westernized nations, with almost two thirds of the research driven by three countries. While the USA and United Kingdom are consistently recorded as leading nations when it comes to peer-reviewed published research (e.g., Hill et al., 2021), Australia surprisingly made up a large portion (16.8%) of the locations where research is conducted (e.g., Hermoso et al., 2012). This may be because some of the most cited and published authors are or have been affiliated with Australian research institutions (e.g., Possingham, H. P.; Pressey, R. L.; Klein, C. J.).

When it came to where research was conducted or applied in case studies, trends were still skewed towards North America and Europe but there was a greater diversity of nations represented. Central African and Western and Central Asian nations were not represented in terms of authorship but species and ecosystems inside their borders were represented at the case study level (e.g., Memariani et al., 2016). This trend was also apparent when examining highly studied regions such as the Mediterranean. While research was conducted at a scale that included the entirety of the Mediterranean Sea, publication credit was dominated by European nations over non-European nations, particularly in Northern Africa and nations of the Arabian Peninsula and Levant. This is not uncommon in peer-reviewed academic literature, specifically in the Arab world (Zyoud & Fuchs-Hanusch, 2020), but creates the potential that western researchers can perpetuate "helicopter" research by conducting research in the Global South without involvement from local collaborators (Haelewaters et al., 2021; Pettorelli et al., 2021). This poses a potential blind spot in managing conservation problems by excluding local and traditional knowledge systems and ideologies that are outside of westernized and colonial worldviews in regions by non-western governance systems. Potential strategies or solutions to overcome this trend could include building higher research capacity in non-western nations through funding of truly collaborative and meaningful research partnerships with western nations who have high conservation research capacity (Zhang et al., 2023).

Whether it was at the bibliometric or case study level, a key biogeographic theme that emerged was that marine environments were the most studied. This preference for marine ecosystems within the geospatial literature is not reflected in the proportion of formally protected areas globally, with more terrestrial and inland water protected (17%) in comparison to marine and coastal areas (10%) (UNEP-WCMC and IUCN, 2021). This imbalance in protected areas may account for this discipline evolving with such a heavy focus on protecting marine ecosystems, as Marine Protected Areas (MPAs) can be difficult to implement and barriers to implementation remain poorly understood (Schultz et al., 2022). Furthermore, some of the lesser studied terrestrial ecosystems such as mountains and wetlands provide important ecosystem services like fresh water and climate regulation that are integral to the survival of society (Moomaw et al., 2018) but remain under-studied in comparison to their importance. As there is increasing pressure with global change, understanding, and conserving these ecosystems and associated services will become increasingly important.

4.1.3 Species vs. ecosystem focus

This review identified two distinct areas of focus when it came to applying geospatial conservation planning. In general, the case studies examined here either focused on the ecosystem for its overall value, or on species and their habitat range. While it is important to consider the protection of individual species in the landscape, it is also important to acknowledge that species do not exist in isolation and certain interactions and assembles affect the stability of complex ecological communities (Qian & Akçay, 2020), mostly comprised of vegetative structures. Furthermore, vegetation forms the primary structural components of most terrestrial ecosystems but was studied far less than the fauna that often depend on vegetation for habitat and resources here. This is a broader problem in ecology and society with the manifestation of the plant awareness disparity, or the inability of people to notice plants in their environment (Parsley, 2020).

Understanding how biodiversity dynamics operate on the landscape is also an integral part of the geospatial conservation planning process. However, there has been a long-recorded mismatch between conservation areas and biodiversity globally (Brum et al., 2017; Willer et al., 2019). This was demonstrated in our analysis, with a dominant focus on specific species of flora and fauna. Prior research has demonstrated that human emotions can influence support to protect mammals and birds, over invertebrates and reptiles (Prokop & Fančovičová, 2013; Castillo-Huitrón et al., 2020), which may explain why birds and mammals were chosen to be studied over reptiles, amphibians and invertebrates overall in this review. However, there is also the potential that the ease of visual access to studying mammals and birds could be a contributing factor as to why researchers choose to focus on them. There was one exception to this trend with the majority of the studies that focused on reptiles, focusing on sea turtles specifically. Though this may be due to their popularity as charismatic mega-fauna and vertebrates often receive more funding for conservation (Mammola et al., 2020). In contrast, aquatic and terrestrial invertebrates are integral to the functioning of healthy ecosystems and provide many ecosystems services that are vital to ecosystem stability (Prather et al., 2013; Chen, 2021) but received relatively little focus here, with some exceptions (e.g., Gormley et al., 2015). Understanding this phenomenon is critical for conservation researchers and practitioners to understand and avoid the creation of "paper parks" that fail to meet conservation needs and targets (Dudley & Stolton, 1999).

4.2 Translating research into practice

Though we can learn from the quantitative insights provided through this investigation, we can also gain insights and learn from the observations made during the literature review process. Such generalized social science insights may equally inform and guide better research and management priorities and actions (Bennett et al., 2017).

4.2.1 Considerations for application

While systematic approaches to geospatial conservation planning provide structure to complicated technological processes, researchers and practitioners still need to take caution when creating these plans. Overall, the conflicting interests of users and the active selection of which data to include demonstrates that plans are not neutral. Since plans and maps can be designed to be reflections of the people involved in making them (Wood, 2010; Sonbli & Black, 2022), it is important to consider the influence and reflect on the wider implications of scientific practice by researchers when developing conservation plans and policies (Pasgaard et al., 2017). Though geospatial conservation planning is focused on nature, decision-support tools that assign dollar value to landscapes can create situations that struggle to balance economic costs with ecological or social benefits. For instance, the focus on cost-effectiveness by spatial conservation prioritization has led to a bias towards placing MPAs in areas that are least threatened (Boon & Beger, 2016).

Moreover, such methodological decisions can enforce or support existing political and societal tensions that have effects for local communities. For example, this review found the coastal areas of the Mediterranean have been a focus, but most studies chose to acknowledge Israel as an independent state while referring to Palestine as a territory, without acknowledgement of its occupation (e.g., Mazor et al., 2013), when it was even acknowledged. Biases, whether conscious or unconscious can have an impact on the chosen research design, data interpretation and decision-making throughout a project, impacting the overall outcomes (Pannucci & Wilkins, 2010). Introspection on one's positionality, whether in a social, cultural, or political context, can help researchers to understand how their own situations may shape research priorities and methodological choices. Reflecting on our own personal values, biases, and positionality may help to encourage more ethical, applicable and collaborative conservation science (Beck et al., 2021).

Severe cases where social aspects of conservation is not considered can manifest in the form "green-grabbing", the dispossession of lands for the sake of conservation (Fairhead et al., 2012). One example is the displacement of the Stoney Nakota Peoples for the creation of Banff National Park (Dang, 2017), one of the oldest, most iconic and the most visited protected areas in Canada (Parks Canada, 2008). Nevertheless, the input of Indigenous Peoples is integral to the conservation of nature worldwide, with 80% of remaining biodiversity protected and managed by just 6% of the world's population who identify as Indigenous (Garnett et al., 2018). While few studies explicitly acknowledged the local history of landscapes that predate colonization (e.g., Leroux et al., 2007; Benner et al., 2019), arrangements that aim to return land back to Indigenous Nations in the form of conservation areas provide a potential solution that can support the righting of previous wrongs (Indigenous Leadership Initiative, 2021). Additionally, land management practices like Indigenous fire stewardship can reduce climate-driven catastrophic bushfires through cultural burning (Fletcher et al., 2021b) and can lead to an increased rate of biodiversity (Hoffman et al., 2021). Considering the importance of Indigenous stewardship worldwide, conservation planning must strive to include diverse perspectives into future conceptualization, designation, and management of protected areas.

4.2.2 Enhancing implementation and outcomes

Our results demonstrated a plethora of geospatial conservation plans across the planet. What is not clear is if these plans came to fruition. Considering geospatial conservation planning is centered around the idea of using resources wisely, it is important to consider the time, knowledge, and funding of the researchers as a resource too. A review by McIntosh et al. (2018) that examined the outcomes of 1200 systematic conservation planning projects discovered that there were only 43 case studies that reported outcomes of implementation. Additionally, there are common mistakes that inhibit sufficient conservation priority setting including not acknowledging conservation plans as prioritizations, poor articulation of problems and ignoring the risk of failure (Game et al., 2013). Understanding why these projects have not made it to the implementation phase and how they can be implemented at an increased rate are important questions to answer if prioritization methods are to be used for effective and tangible conservation.

While this review found there has been some progress in integrating more holistic and interdisciplinary approaches into conservation planning with keywords like ‘stakeholder’ and ‘socio-ecological systems’ as an increasingly popular research topic over time. They were, however, rarely linked to the technical approaches (e.g., Marxan or Zonation) and were instead clustered among the marine environments section. This may be due to the high volume of marine studies examined in this review, though, a recent review of marine spatial planning (MSP) reported that that 50% of plans used qualitative methods to conduct MSP (Chalastani et al., 2021). One way to overcome the subjugation of biophysical interests in geospatial conservation planning might be to include social dimensions from the onset of projects (Strickland-Munro et al., 2016), which were only included in models 6% of the time in this review. Although it can be useful to focus on ecological elements and umbrella or flagship species for a cost-effective way of maximizing biodiversity representation (McGowan et al., 2020; Ward et al., 2020), gathering information and perspectives of local stakeholders and incorporating them into prioritization scenarios could move proposed systematic conservation planning past the theoretical phase into the implementation era (Knight et al., 2010).

4.3 Limitations and recommendations

4.3.1 Scope and nature of reviews

While this review was able to identify trends in geospatial conservation planning, there are certain limitations to the scope of analyzing such a large quantity of literature. To start, there are certain biases in the methodological framework used here including the tendency for databases used to favour certain geographic locations, types of knowledge, and languages (Hamel, 2007; Pickering & Byrne, 2014). This includes not accounting for knowledge and terminology used outside of this specific scientific discipline and only analyzing academic uses of geospatial conservation planning examined here that excludes grey literature and traditional knowledge (Franceschini et al., 2016; Mongeon & Paul-Hus, 2016). While bibliometric reviews are powerful at analyzing thousands of publications and identifying broad themes in a literature (Vinkler, 2010), they are restricted to the level of detail contained within bibliometric data (i.e., title, abstract, keywords etc.). While the deeper look into the subset of case study analysis was conducted partially overcome this challenge, we were still limited by our own ability to only comprehend English language case studies, and how and what authors chose to report in their findings. For example, there is the potential for more details about a project to exist, but not be reported in published literature, and therefore not included in this analysis. Nevertheless, this research was a worthwhile exercise despite the limitations and has made substantial contributions to understanding how geospatial conservation planning has evolved. As environmental impacts intensify with global change, is important that the geospatial conservation planning discipline evaluates its trajectory before research trends stray from tangible on-ground management actions.

4.3.2 Recommendations for future research directions

With access to the right technology, data and knowledge, spatial prioritization approaches have a history of being a viable method to create conservation plans that support effective decision-making for managing landscapes to preserve biodiversity and ecosystem services (Wilson et al., 2007). Future research, however, should focus on integrating more social dimensions and participatory approaches into the planning process. Even though there has been some instances identified in this review it is still not common practice to include social dimensions beyond demographic and economic surrogates, into these models despite the effort made by some researchers to use participatory methods to collect this information (e.g., Karimi & Hockings, 2018; Noble et al., 2020). For this to be a viable option for integrating perceptions into landscape research, the social data such as landscape values or locations of social and cultural ecosystem services, collected needs to be spatially explicit in order to be functional (Dorning et al., 2017). However, such an approach requires pre-planning and intentional data capture on the part of researchers through collaboration with the local communities where the research is taking place. To do this, taking a more stakeholder focused and bottom-up approaches can allow space for alternate forms of governance and models of land management to be considered in and becoming part of planning processes (Ban et al., 2013; Cornu et al., 2014; Whitehead et al., 2014; Noble et al., 2019) and allow time and space for social values to be translated to operational spatial information. Finally, to overcome the research-implementation gap that exists in conservation prioritization (Knight et al., 2008), more detail on design choices, and implementation results and outcomes of projects could be better reported to share insights with others who are considering this type of research.

5 Conclusion

Spatial conservation prioritization approaches are becoming increasingly popular over time. While there remains a clear focus on certain geographic regions, ecosystems and species, approaches are beginning to take into consideration more than just ecological data like climate data and social information and knowledge. To ensure that these spatial prioritization approaches are successful they should be situated in a larger conservation effort that is inclusive of local values, perspectives, and histories. Since social and ecological systems are coupled, focus should be placed on continuing the momentum for more participatory methods that integrate social dimensions with ecological values. Paying special attention to how we address power imbalances, particularly the ways in which we promote inclusive and ethical participation, and what types of knowledge and information we are prioritizing in decision-making tools is vital to the progress of this discipline.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: The datasets analyzed for this study can be found at https://doi.org/10.5281/zenodo.7787297.

Author contributions

Conceptualization, GC and AC. Methodology, GC and AC. Validation, GC and AC. Formal Analysis, GC. Investigation, GC. Data Curation, GC. Writing – Original Draft, GC. Writing – Reviewing & Editing, GC, AC, and JN. Visualization, GC. Supervision, AC and JN. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

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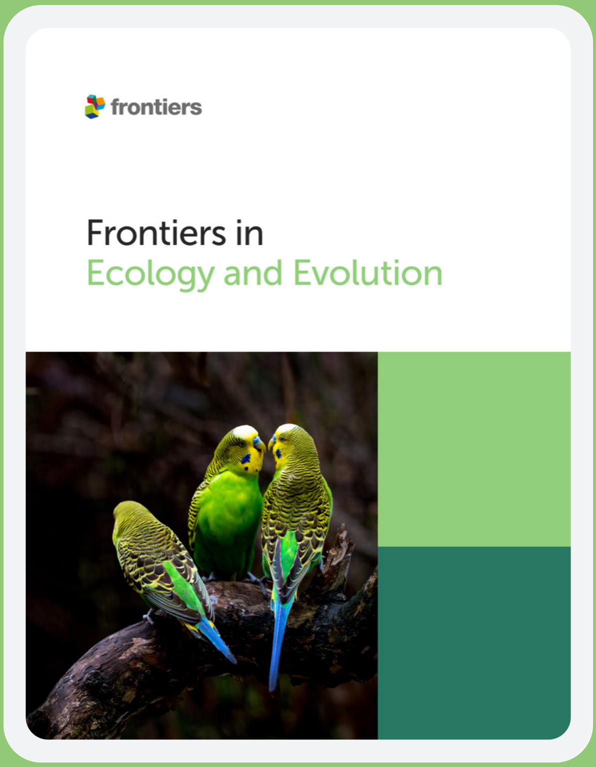

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