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Non-indigenous and Invasive Freshwater Species on the Atlantic Islands of the Azores Archipelago

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Freshwater systems on remote oceanic islands are particularly vulnerable to biological invasions. The case of freshwater ecosystems in the Azores Archipelago is especially relevant considering the islands' youth and remoteness, and low natural connectivity. This study presents a review of the introduction and presence of non-indigenous freshwater species in the Azores, retrieved from various historical records, paleoenvironmental reconstructions, published records, and field data from two decades of the Water Framework Directive (WFD) monitoring programs. At least 132 non-indigenous freshwater species have successfully established in the Azores, belonging to several taxonomic groups: cyanobacteria (10), synurophytes (1), desmids (1), diatoms (20), plants (41), invertebrates (45), amphibia (2), and fishes (12). Intentional and accidental introductions have been occurring since the establishment of the first human settlers on the archipelago, impacting freshwater ecosystems. The first reported introductions in the Azores were intentional fish stocking in some lakes. Non-deliberate introductions have recently increased through transport-contaminants (51%) associated with the aquarium trade or agricultural products. In the Azores, the highest number of non-indigenous species occur on the largest and most populated island, São Miguel Island (116), followed by Flores (68). Plants constitute the most representative group of introduced species on all islands, but invertebrates, diatoms, and fishes are also well established on most islands. Among invertebrates, non-indigenous arthropods are the most well-established group on all islands except on the smallest Corvo Island. Many non-indigenous species will likely benefit from climate change and magnified by globalization that increases the probability of the movement of tropical and subtropical species to the Azores. Present trends in international trade, importations, and enhanced connectivity of the archipelago by increasing flights and shipping will probably promote the arrival of new species. Augmented connectivity among islands is likely to improve non-indigenous species dispersal within the archipelago as accidental transportation seems to be an essential pathway for non-indigenous freshwater species already present in the Azores.

Keywords: non-indigenous species, invasive species, oceanic islands, freshwater ecosystems, Azores archipelago

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INTRODUCTION

Human activities have for centuries promoted the transport of multiple species across huge biogeographical barriers (Gippoliti and Amori, 2006; Clavero and Villero, 2014), and this has accelerated exponentially since the beginning of the twentieth century (Vander Zanden and Olden, 2008; Clavero and Villero, 2014). The increasing introduction rate and spread of non-indigenous species are among the most critical threats to biodiversity and ecosystem services (Vitousek et al., 1996; Sala et al., 2000). Even though biological introductions may cause no detectable or long-term impact (Williamson and Fitter, 1996), some non-indigenous species, especially the invasive ones, usually display high spreading rates in the introduced environment causing significant impacts, from the alteration of habitats, replacement of native species through predation and competition, the transmission of diseases, and effects on human health and economy (Pimentel et al., 2000; Cowie, 2001; Blackburn et al., 2014; Gallardo et al., 2016). Identifying these invasive species is crucial for prioritizing management efforts (Ricciardi and Atkinson, 2004). Their control is often more practical, cheaper, and more effective soon after detection, and for some, eradication might be possible (Simberloff, 2009; Simberloff et al., 2011).

Freshwater ecosystems provide many benefits to humankind, and the induced changes (e.g., by invasive species) in the goods and services they provide can have a substantial impact on the human well-fare (Gherardi, 2007). Nevertheless, freshwater ecosystems are among the systems most heavily affected by non-indigenous species introduction (Amat-Trigo et al., 2019). The degradation of these ecosystems has caused non-indigenous species to establish and become invasive more easily than in other environments (Sala et al., 2000). Many of these species are effective colonizers that exhibit rapid adaptation in degraded aquatic or riparian habitats characterized by communities with a reduced competition that facilitate such adaptation (Conlan, 1994; MacNeil et al., 2004). The disturbance is commonly assumed to release resources and provide opportunities for invaders (Lozon and MacIsaac, 1997; Davis et al., 2000). Moreover, some invaders that inhabit human-disturbed environments in their native range might have a greater ability to adapt to human-disturbed environments than resident species (Niemelä and Mattson, 1996), giving them the advantages for successful invasion (Shea and Chesson, 2002). Also, systems already impaired by non-indigenous species are susceptible to additional disturbance, as non-indigenous species often facilitate each other's establishment and/or their continued existence, increasing the likelihood and the magnitude of the global environmental impact inflicted by biological invasions (Gherardi, 2007).

Freshwater ecosystems are highly vulnerable to anthropogenic and natural introductions of species and their subsequent spread (Gherardi et al., 2008b; Strayer, 2010; Havel et al., 2015; Tricarico et al., 2016). The effects of intensive human usage and hydromorphological changes to aquatic systems, such as the impoundment of rivers (e.g., dams and weirs, water removal), water quality deterioration (e.g., pollution, eutrophication, acidification), habitat degradation and fragmentation (e.g., channelization and land-use change), resources overexploitation (Ricciardi, 2001), as well as climate change (Rahel and Olden, 2008) have been enhancing the dispersal of aquatic organisms (Gherardi et al., 2008a; Oscoz et al., 2010). Both anthropogenic habitat disturbance and the introduction of non-indigenous species are today the main drivers of biodiversity change in these ecosystems (Didham et al., 2005).

Aquatic non-indigenous organisms encompass a great variety of taxonomic groups, including microorganisms, plants, sponges, cnidaria, flatworms, molluscs, crustaceans, fishes, birds, amphibians, reptiles, and mammals (see García-Berthou et al., 2007; Nunes et al., 2015). However, most of the freshwater non-indigenous species that have been deliberately introduced are fishes and plants (Pimentel et al., 2005). Most freshwater species introduced in Europe are native to northern America and arrived in France, United Kingdom, or Germany, and spread from there to southern Europe, e.g., Portugal and Spain (García-Berthou et al., 2005; Boix et al., 2007). For example, the pumpkinseed [*Lepomis gibbosus* (Linnaeus, 1758)] and mosquito fishes (*Gambusia* spp.), which are American fish species (García-Berthou et al., 2005), are very well-established in Europe. One of the major pathways of freshwater species introduction is aquarium species trade, which accounts for 21% of world freshwater fish introductions (Andrews, 1990; Gozlan, 2008; Maceda-Veiga, 2013; Ishikawa and Tachihara, 2014; Nunes et al., 2015) and secondarily, aquaculture (Gherardi et al., 2008b; Nunes et al., 2015). In Europe, introductions related to ornamental trade were mostly freshwater plants (Keller et al., 2011). More than 400 non-indigenous aquatic and semi-aquatic species of plants are currently traded in Europe, and many are considered potentially invasive in European freshwater habitats (Hussner, 2012). Most of those introductions arrived in Portugal via Spain (García-Berthou et al., 2005). Nonetheless, some accidental freshwater introductions in Portugal seem to be related to escapes from cultivation sites and disseminated along watercourses. For example, red swamp crayfish [*Procambarus clarkii* (Girard, 1852)] might have arrived in Portugal from escapes in aquaculture facilities in Spain to the Guadiana river (Gherardi et al., 2002). Most imports to the Azores came from mainland Portugal, through commercial shipping and flights to the archipelago, mainly arriving on São Miguel island (Calado et al., 2014).

Oceanic islands are highly vulnerable to invasive species due to the low levels of diversity, lack of competitors and predators, and the resulting availability of ecological niches (Simberloff, 1995; Sax, 2001; Covich, 2010), offered by the existence of non-saturated assemblages (see Cornell and Lawton, 1992). Moreover, species on islands have small populations with restricted genetic diversity, and this, coupled with limited habitat availability, increases their vulnerability to environmental stresses, including the introduction of non-indigenous species (Russell et al., 2017). Therefore, insular freshwaters are among the most vulnerable ecosystems to invasive species (Raposeiro et al., 2009; Costa et al., 2013; Raposeiro et al., 2017).

The geographic setting of oceanic islands and the Azores archipelago presents a considerable distance across open ocean from a continental source which hampers natural dispersal and species colonization (Bilton et al., 2001; MacArthur and Wilson, 2001). In the Azores, isolation, small island area, young geology, and numerous volcanic eruptions have acted as strong biogeographical filters, resulting in low diversity of native biotic assemblages and a high percentage of freshwater faunal endemism (11% – Raposeiro et al., 2012), when compared to continental systems (Hughes, 2006). Since the establishment of the first human settlements in the islands (official Portuguese colonization in 1432 CE), pressure on the ecosystems has increased exponentially, mainly associated with landscape disturbance due to changes in land use which have resulted in habitat degradation and fragmentation and the introduction of non-indigenous species (Triantis et al., 2010; Connor et al., 2012; Ferreira et al., 2017; Raposeiro et al., 2017; Rull et al., 2017; Vázquez-Loureiro et al., 2019).

The consequences of introduced species have been an object of discussion in several studies (Mooney and Hobbs, 2000; Ricciardi, 2003; Bohlen et al., 2004), including in island ecosystems (Reaser et al., 2007), but the introduction of non-indigenous species and the impact of these in the highly vulnerable insular freshwater systems of the Azores has not yet been thoroughly addressed (Raposeiro et al., 2011a). The inventory of non-indigenous species in the archipelago and knowledge of their introduction pathways, establishment, and spread potential is vital to predicting threats to freshwater native biodiversity and to developing management strategies for local freshwater environments (Raposeiro et al., 2009; Lamelas-López et al., 2017).

This paper updates the knowledge on all non-indigenous freshwater species in the Azores through a broad taxonomic approach from unicellular phytoplankton to vertebrates, presenting what is known of their introduction history, pathways, origins, and ecological and socioeconomic impacts in the archipelago. Furthermore, species' invasion risk and management actions are discussed.

Study Area

The Azores archipelago comprises nine islands of volcanic origin located in the middle of the northern Atlantic Ocean (**Figure 1**), between the latitudes, 36° 45′ N and 39° 43′ N and the longitudes 24° 45′ W and 31° 17′ W, about 1500 km off mainland Portugal (Santos et al., 2004). This archipelago is particularly rich in freshwater ecosystems due to volcanic geomorphology and climatic conditions that prevail in altitude with a total land surface area of 2,325 km^2 drainage corresponding to 763 hydrographic basins (Cruz and Soares, 2018) and many small (maximum length of 29 km) streams (Raposeiro et al., 2013). Following its discovery in 1439, extensive deforestation began in coastal areas of hydrographic basins to establish human settlements that extended in the early 20th century. The intensification of agricultural activity, the excessive application of agrochemicals, building roads, effluent discharge of livestock farms, and the release or non-deliberate introduction of non-indigenous species are some of the main factors currently affecting the water quality and ecosystems services provided by these islands' freshwater habitats (Pereira et al., 2014; Raposeiro et al., 2014).

MATERIALS AND METHODS

The GBIF Backbone Taxonomy was used to harmonize the taxonomy of the studied groups (GBIF Secretariat, 2019). For the present paper, freshwater species were considered those organisms that complete their entire life cycle in the water [e.g., diatoms (Bacillariophyceae), molluscs (Mollusca), crustacea (Crustacea), fishes (Actinopterygii), cyanobacteria (Cyanobacteria), synurophytes (Synurophyceae) and desmids (Desmidiaceae)], animals that live in aquatic habitats at some point in their life cycle [e.g., some arthropods (Arthropoda), amphibia (Amphibia) and floating, submerged and helophyte plants (Tracheophyta) (Thorp et al., 2014; Bellinger and Sigee, 2015; Dodds and Whiles, 2019)].

Indigenous and non-indigenous species were categorized following criteria in Essl et al. (2018); indigenous species from the Azores were considered those not related to human-modified habitats or activities, occurring in native habitats, and also present in other Macaronesian archipelagos. Species that have human-mediated movement across biogeographic barriers from their presumed native/indigenous origin are considered non-indigenous. In the Azores, this biogeographic filter is evident due to its distance to the mainland (around 1,500 km) and the Atlantic Ocean's physical barrier. Possible pathway analysis and their absence from pristine habitats had to be put into the equation to establish the species as non-indigenous. The review of the introduction and presence of non-indigenous freshwater species in the Azores considered all available records to date (see **Supplementary Material 1**), retrieved from various sources as historical and contemporary records, paleoenvironmental reconstructions, and field data from WFD monitoring programs in place for the last two decades.

According to the Convention on Biological Diversity (Convention on Biological Diversity, 2014), each species' introduction pathway was determined, distinguishing intentional and/or non-deliberate introductions. The species introduction mechanism as importation, transport vector or dispersal corridor association and natural spread from a previously invaded region were considered and addressed to one of five groups (as the CBD 6th pathway is not locally applicable): Release – an intentional introduction for human use in the natural environment (e.g., biological control, fishery, hunting); Escape – the movement of non-indigenous species from confinement (e.g., aquaria, botanic gardens, zoos) to the wild; Transport-contaminants – the non-deliberate movement of organisms transferred through intentional trade (e.g., pets, food diseases, seeds); Transport-stowaway – the movement of organisms attached to transporting vessels and associated equipment and media (e.g., ballast water, boats, fishing equipment's); and Unaided – secondary natural dispersal of organisms that have been introduced elsewhere through pathways 1–5.

Some of the non-indigenous species established in Azorean freshwater habitats were categorized as invasive species following

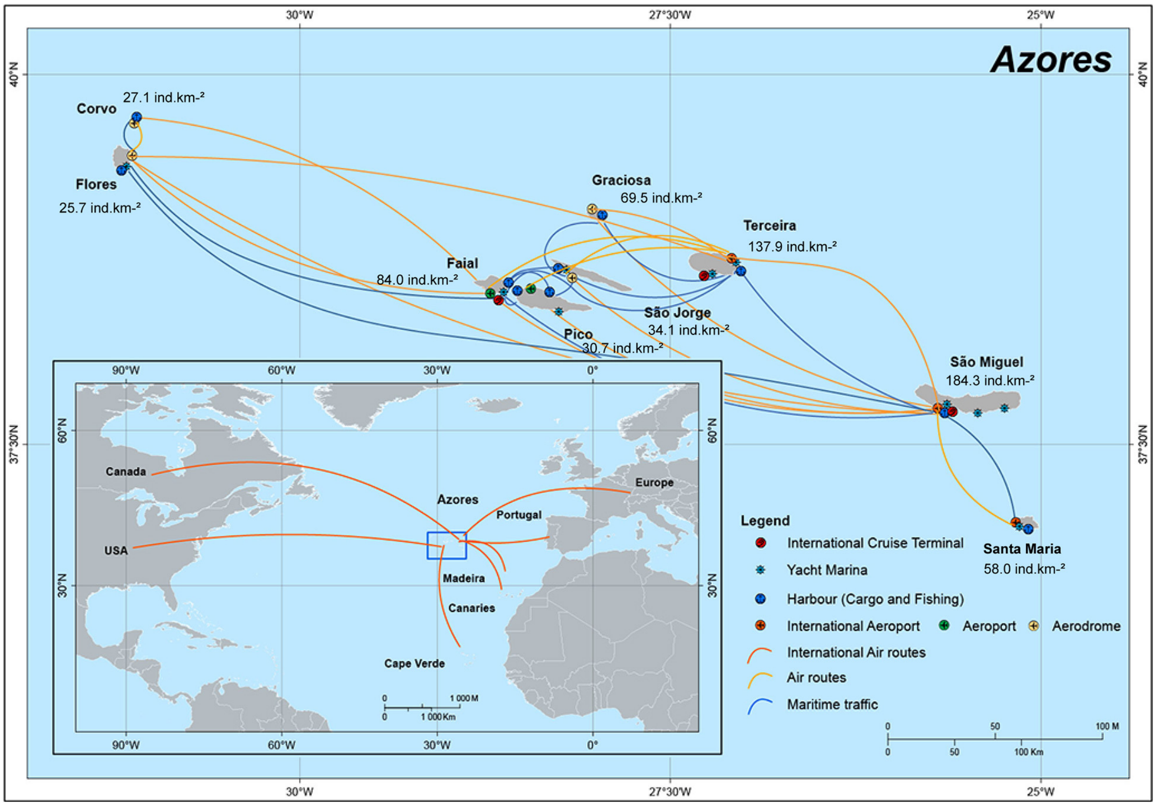

FIGURE 1 | Location of Azores Archipelago on North Atlantic Ocean. Principal routes of entry for non-indigenous species onto the islands are presented.

the definitions of the International Union for Conservation of Nature (IUCN), US National Aquatic Invasive Species Act (NAISA), and the Convention on Biological Diversity (CBD). Thus, invasive species are herein considered as non-indigenous species whose introduction and/or spread outside their natural past or present distribution has led to their establishment and spread in an ecosystem or a natural or semi-natural habitat, being an agent of a change and threat to native biodiversity, economy, environment, human health, recreation, or public welfare.

We used information on the invasive potential of non-indigenous species from Delivering Alien Invasive Species Inventories for Europe (DAISIE), European Alien Species Information Network (EASIN), Global Invasive Species Database (GISD) databases to established them as invasive or non-invasive species. Moreover, field and published data about their spread capacity and proliferation, feeding habits, predation and competition behavior, and preferred habitat were also used as complementary information to define the invasive status of those species and determine their possible negative impact on archipelago's ecosystems.

Literature Review and Historical Records

Historical data can provide important insight to understand biological invasions (Willis and Birks, 2006). The assignment of introduced status to the Azores islands species has also been inferred using historical records, including those from the first 17th century chronicles and reports from naturalist and scientific expeditions of the 19th century. Data on species were extracted from these sources and completed with information retrieved from different peer-reviewed published papers, gray literature, reports, and studies carried out in Azorean freshwater systems. Species introductions associated with developing human economic activities in the archipelago and clear evidence for direct human mediation were considered deliberate introductions, releases, or escapes. The more obvious cases are related to agricultural and ornamental plants introductions (Williamson, 1996; Heywood, 2012). Ornamental plants and fishes deliberately introduced in Azorean lakes for leisure, stocking, and fishing purposes, were the most prevalent, especially during the late 18th century (see Raposeiro et al., 2017 and references associated). Species that might have arrived in the archipelago due to indirect consequences of human actions, such as accidental transport related to habitat modification, eliminating indigenous competitors or predators, were also considered. The date of introduction was considered the date of the first record reported in the literature or the publication date when the introduction date was not mentioned.

Paleolimnology Records

Long-term data are essential to assign indigenous and non-indigenous species status and detect the exact date of a species introduction (Moser, 2004; Willis and Birks, 2006; Smol, 2014).

To overcome the scarcity and incomplete historical records in the Azorean islands, environmental reconstructions based on long continuous sequences of natural archives (sediments older than 1450 AD) were used to establish species presence in pristine conditions before human settlement. Data from recent paleolimnological studies in the Azores (São Miguel, Pico, and Flores islands) that have been focused on climatic and environmental reconstruction using biological proxies, e.g., pollen, plant remains, frustules of diatoms, water fleas, and chironomids (van Leeuwen et al., 2005; Connor et al., 2012; Raposeiro et al., 2017; Rull et al., 2017; Vázquez-Loureiro et al., 2019) were considered for this new approach. For example, van Leeuwen et al. (2005) unequivocally confirm the status of *Selaginella kraussiana* (Kunze) A. Braun as native on the Azores islands. As a consequence, species only collected in sediments post-1450 AD were considered non-indigenous. Despite the usefulness of paleolimnological records as an essential tool to understand native biota, the preservation of organisms in the sediments depends on the type of organism and the environmental conditions at the time of sedimentation (Heiri et al., 2009; Smol, 2014). So, the absence of species in the paleolimnological registry does not, *per se*, qualifies them as non-native. To overcome this, paleolimnological data was only used to access the status of diatoms, which are well preserved in lake sediments. Only the species that were consistently present in the sediment after human arrival was considered non-native, while all species that occurred sporadically were excluded.

Field Records

Field data from WFD monitoring programs carried out between 2000 and 2020 covering several water masses on all islands were also used to compile plants, macroinvertebrates, microalgae, and cyanobacteria data. Due to the different distribution of water masses among islands, the number of sampling events is not the same for every island: 4 on Faial, 12 on Terceira, 55 on Corvo, 60 on Santa Maria, 212 on Pico, 421 on Flores, and 1101 on São Miguel. Records of recent fish releases on different islands were obtained by net-fishing field data for various projects (authors' unpublished data).

RESULTS AND DISCUSSION

Taxonomic Groups and Area of Origin of Non-indigenous Species

At least 132 non-indigenous species are established in Azorean freshwater ecosystems (see **Supplementary Material 1**), belonging to different taxonomic groups (**Table 1**). Plants (41), invertebrates (45), diatoms (20), and fishes (12) presented the highest number of records, followed by cyanobacteria (10), amphibia (2), synurophytes (1), and desmids (1). Plants and arthropods are the most representative contributing with 31.1 and 19.7%, respectively, of the total number of non-indigenous species, followed by diatoms (15.2%) and fishes (9.1%) (**Table 1**). Freshwater non-indigenous fauna represents a total of 59 species, of which 23.7% are vertebrates. Invasive species account for 51.5% (68 species) of Azorean non-indigenous freshwater species (**Table 1**). All amphibians and fishes, except for the native eel *Anguilla anguilla* (Linnaeus, 1758) are considered invasive species in the archipelago. Plants and mollusks also presented a higher percentage of invasive species (82.9 and 66.7%, respectively) than the other groups (**Table 1**). More than 60% of vascular plant flora in the terrestrial realm, all the mammals (except the Azorean bat) and reptiles are reported to be non-indigenous (Silva et al., 2008). As for marine species, the number of non-indigenous species reported for the Azores by Tsiamis et al. (2019) is 53 species, most of them macroalgae and invertebrates.

TABLE 1 | Number and percentage (in brackets) of freshwater non-indigenous (NIS) and invasive species in different taxonomic groups.

Group	Non-indigenous species (% of total NIS)	Invasive species (% for the group)
Cyanobacteria	10 (7.6%)	5 (50.0%)
Synurophyceae	1 (0.8%)	0 (0.0%
Desmidiaceae	1 (0.8%)	0 (0.0%)
Bacillariophyceae	20 (15.2%)	1 (5.0%)
Tracheophyta	41 (31.1%)	34 (82.9%)
Platyhelminthes	4 (3.0%)	2 (50.0%)
Nematomorpha	1 (0.8%)	0 (0.0%)
Cnidaria	2 (1.5%)	1 (50.0%)
Annelida	6 (4.5%)	2 (33.3%)
Mollusca	6 (4.5%)	4 (66.7%)
Arthropoda	26 (19.7%)	5 (19.2%)
Amphibia	2 (1.5%)	2 (100%)
Actinopterygii	12 (9.1%)	12 (100%)
Total	132	68 (51.5%)

The Azorean non-indigenous species are predominantly Palearctic (mostly invertebrates, amphibians, and fishes) and unknown (mostly cyanobacteria, diatoms, and desmids) in origin. Neotropic and Nearctic regions are also represented in non-indigenous species in the Azores in plants, Platyhelminthes, Mollusca, and fishes (**Figure 2**). According to historical records, some non-indigenous species might have been transported inadvertently by the Portuguese during the initial human colonization of the islands (archeophytes, i.e., introduced before 1500; Mandak and Pysek, 1998). However, the latest introductions in the late 19th century were deliberate releases with economic purposes for fish stocking or as ornamental plants for gardens. The first record of a species introduction is the goldfish [*Carassius auratus* (Linnaeus, 1758)] in 1792 (Ribeiro et al., 2009) (**Figure 3**), which is also the first record for freshwater species' introduction in Portugal (Kottelat and Freyhof, 2007). It is often difficult to be sure whether humans have introduced insular species or whether they are, in fact, native. Paleolimnology records helped solve this question, especially in well-preserved groups as diatoms, plants, and some invertebrates. In the Azores, the significant impacts revealed by the sedimentary record are concurrent with the Portuguese colonization, providing evidence for strong anthropogenic landscape transformations leading to eutrophication (Connor et al., 2012; Raposeiro et al., 2017; Rull et al., 2017). Eighteen diatom taxa only appear in the

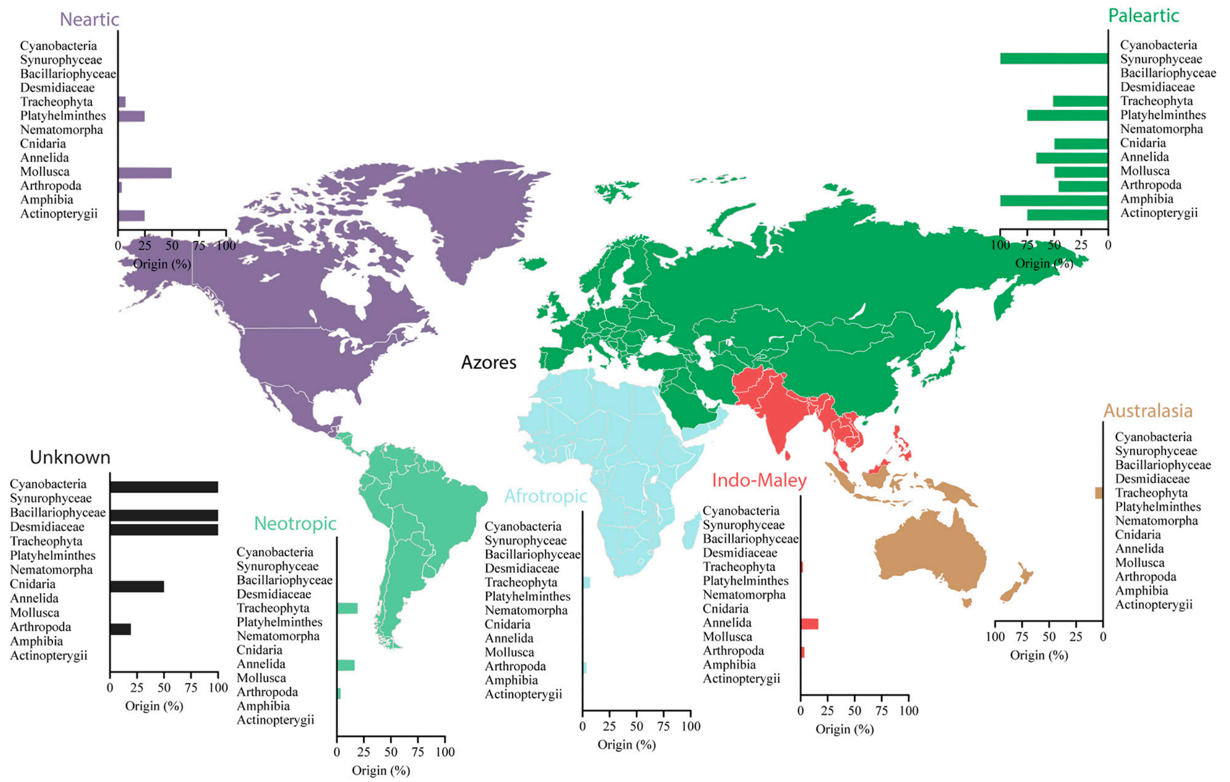

FIGURE 2 | Percentage of freshwater non-indigenous species from different native distribution areas recorded in the Azores.

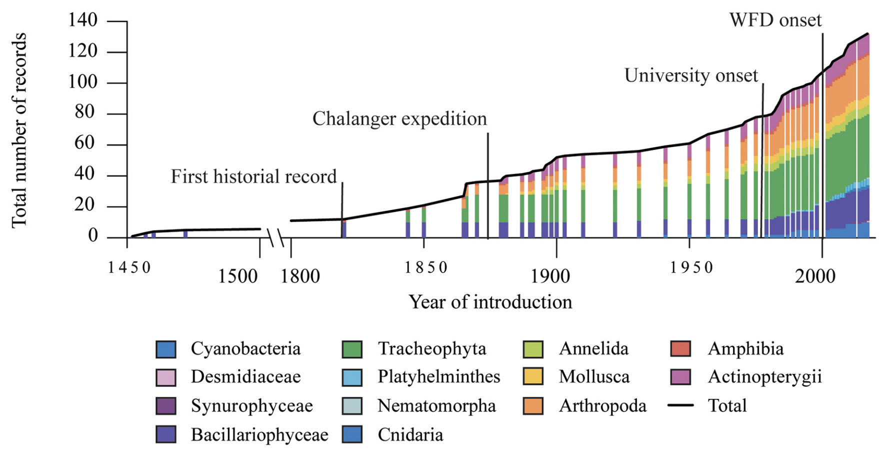

FIGURE 3 | Records of non-indigenous species introduced in Azorean freshwaters from 1450 to 2020 over 50 years intervals.

records after the Portuguese settlement providing evidence that these species are non-indigenous [e.g., *Gomphonema minutum* (C.Agardh) C.Agardh, *Fragilaria crotonensis* Kitton, *Asterionella formosa* Hassall].

Fishes and plants represented the groups for which first introductions have been reported (**Figure 3**) since the 19th century. The onset of the 19th-century naturalist expeditions to the archipelago, e.g., Challenger, encompass a growing number of studies on freshwater biota, increasing the number of non-indigenous species recorded. The number rose again in the second half of the 20th century when more studies on the lakes were carried out (**Figure 3**) due to the local university's establishment and when the international airport in São Miguel started its regular operation. The number of freshwater species reported vastly increased in the last two decades, with new records of non-indigenous species resulting from the extensive sampling efforts in freshwater ecosystems due to WFD monitoring programs' implementation. During this period, the records for cyanobacteria also started to become relevant.

Non-indigenous Species Distribution in the Archipelago

In the Azores archipelago, the highest number of non-indigenous species occurs on São Miguel Island (116), followed by Flores (68), Pico (65), and Terceira (56) (**Figure 4**). Although plants are the most represented group of introduced species on all islands, from 31.0% in São Miguel to 69.0% in São Jorge, invertebrates, diatoms, and fishes are also well established in São Miguel, Santa Maria, Pico, Flores, and Corvo islands. Non-indigenous species do not present a clear distribution pattern linked to human factors such as population density and/or the number of ports. Taxonomic distribution differences among islands are also not apparent (**Figure 4**). These results seem to be related to the sampling efforts associated with WFD monitoring programs during the last two decades in several islands (see field records in the section "Materials and Methods"). However, Terceira, Graciosa, São Jorge, and Faial showed higher percentages of non-indigenous plants (60.7, 63.0, 69.0, and 58.5%, respectively) than the rest of the groups (**Figure 4**). São Miguel and Flores are also the islands with higher habitat availability for freshwater species. Therefore, a higher number of successful introductions can be expectable as mentioned by several authors (Raposeiro et al., 2011a, 2013; Gonçalves et al., 2015). Habitat availability could also explain the distribution of specific groups, such as cyanobacteria and diatoms. Most non-indigenous cyanobacteria and several diatoms are planktonic and therefore restricted to islands with lakes. A similar situation is observed in the fish group, where most of the species were introduced in the lakes of São Miguel island during several decades, from where they were more recently spread to the rest of the archipelago.

Among invertebrates, non-indigenous arthropods are the most well-established group on all islands (from 18.5% in Pico to 26% in Graciosa) except for Corvo where arthropods only represent 4.2% of introductions (**Figure 4**). The poor records on this island may be related to a lower number of studies, limiting the data available for this group.

Most invasive species are restricted to just one archipelago island (**Figure 5**), mainly on São Miguel, Flores, and Pico islands (Raposeiro et al., 2011b; Gonçalves et al., 2015). Half of invasive fish and amphibia and all invasive Annelida and Platyhelminthes are only present on São Miguel island (**Figure 5**). Being the largest and most populated island, São Miguel has greater connectivity with mainland Portugal, Europe, and America (**Figure 1**), becoming the main entrance of invasive species in the archipelago. This island is the main entry point of traded goods in the archipelago, functioning as a distribution hub for other islands. São Miguel is also the island with the most significant contribution to the archipelagos economy reflected in the economic indicators as importation/exportation of agriculture and fisheries' products or tourism (FMS, 2013). The increased human pressure in São Miguel island leads to a higher habitat degradation posing more opportunities for opportunistic non-indigenous species to establish (Silva and Smith, 2004; Cardoso et al., 2013). This island has also hosted a higher number of studies (Johansson, 1976; Borges et al., 2010), and it has thus been more intensively sampled, which might also be reflected in the present results. Invasive plants, fishes, and arthropods present a larger dispersion in Azorean freshwater habitats, with several species established in eight islands (**Figure 5**). Amphibians occur on nine islands; however, this extended distribution is represented only by the green frog, *Pelophylax perezi* (López-Seoane, 1885). Other invasive species, Mollusca, Cnidaria, and Cyanobacteria, are scattered on three or four islands (**Figure 5**).

Principal Introduction Pathways

Most non-indigenous species were probably accidentally introduced to the Azores archipelago, mainly inadvertently

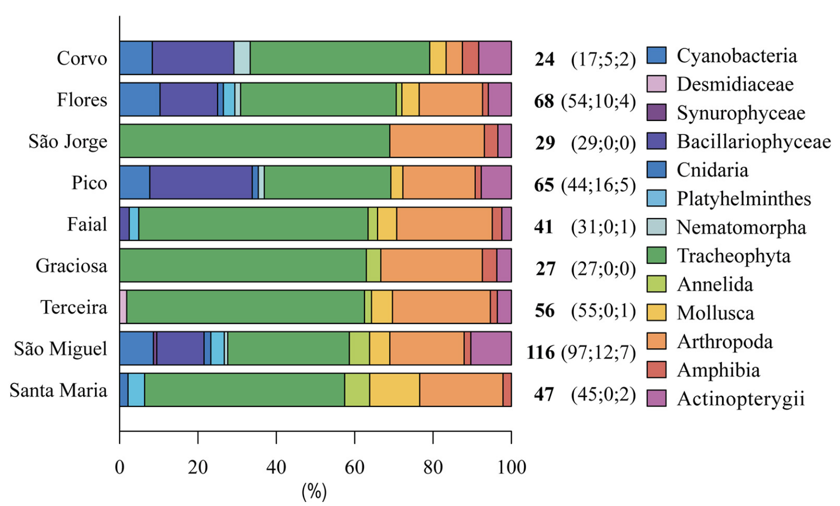

FIGURE 4 | Percentage and **total number** (number of literature records; the number of paleolimnology records; field records) of non-indigenous species included in different taxonomic groups registered in freshwaters habitats for each Azorean island.

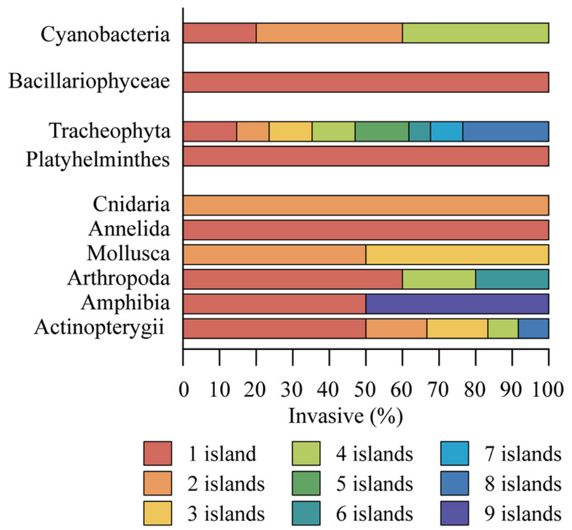

FIGURE 5 | Percentage of invasive species of the different taxonomic groups present in one to nine islands. Synurophytes, Desmids, and Nematomorpha were not included due to the absence of invasive species in these groups.

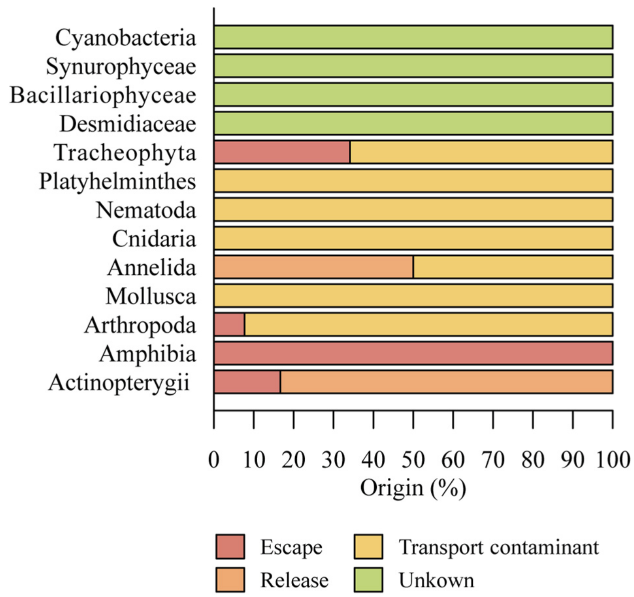

FIGURE 6 | Main introduction pathways of non-indigenous species in the Azores.

by the aquarium trade, attached to plants, as eggs, or in resistant life stages ("Transport-contaminant" pathway), such as Mollusca [e.g., *Ferrissia fragilis* (Tryon, 1863), *Physella acuta* (Draparnaud, 1805) and *Galba truncatula* (O. F. Müller 1774)], Platyhelminthes (e.g., *Dugesia* sp.) and Cnidaria (e.g., *Hydra vulgaris* Pallas, 1766 and *Craspedacusta sowerbii* Lankester, 1880). Arthropods may have been accidentally transported with agricultural products, including food, or packing material, including Coleoptera (mainly species of Hydrophilidae) and Diptera. Agricultural trade is also involved in the introduction of associated pests, such as the turfgrass pest *Tipula oleracea* Linnaeus, 1758 ("Transport-contaminant" pathway) (**Figure 6**).

Ornamental trade was inadvertently involved in the release and spread of many aquatic plant species that might have been imported for use in private or botanical gardens, an important leisure activity of the 19th century in islands as São Miguel, Terceira, and Faial. These aquatic species such as *Zantedeschia aethiopica* (L.) Spreng, *Nymphaea alba* L. or *Eichhornia crassipes* Mart. (Solms) escaped, invading large extensions of freshwater habitats ("Escape" pathway) (**Figure 6**). Another example of species that might have been introduced via domestic aquarium trade, probably by releases in private tanks and later escapes, eventually ending up in native aquatic ecosystems, is the crayfish, *P. clarkii*.

Some species might have been transported accidentally on fishing equipment, airplane wheels, and shoes, among others ("Transport-stowaway" pathway), but this introduction pathway is not easy to determine. The introduction pathway for most non-indigenous species in Azorean freshwaters was categorized as transport-contaminant movement (51.0%) (**Figure 6**). In addition to these accidental introductions, other species have been intentionally introduced. Since the late 18th century, intentional release is the main introduction pathway for fishes such as *Cyprinus carpio* Linnaeus, 1758, *Perca fluviatilis* Linnaeus, 1758, and *Esox lucius* Linnaeus, 1758 among others, attributed to angling activities in Azorean lakes. A well-known example of deliberate introduction is the release of *Gambusia holbroki* Girard, 1859 for biological control of mosquito populations on the mainland and Cabo Verde, another Macaronesian archipelago (Cabral and Marques, 1999; Salgueiro et al., 2019). However, in the Azores, the introduction of *G. holbrooki* was probably related to escapes from private aquaria. After the last known *Rutilus rutilus* (Linnaeus, 1758) introduction in 1983 in Lake Azul (Raposeiro et al., 2017), deliberate releases into the wild stopped. Annelids introduction pathway seems to be escapes related to leeches for medical purposes in the late 19th century (Chaves, 1949). Nevertheless, releases (10.0%) and escapes (15%) are less significant introduction pathways for non-indigenous freshwater species in the Azores (**Figure 6**) when compared with Transport/contamination pathway.

As for Cyanobacteria, Synurophytes, Diatoms, and Desmids, the introduction pathways remain uncertain. Natural dispersion of freshwater microalgae and cyanobacteria is mainly related to transportation by migratory waterbirds (Proctor, 1959) or other organisms (e.g., insects, mammals) (Kristiansen, 1996; Coste and Ector, 2000), water or wind (Sharma et al., 2007). Especially on remote oceanic islands, like the Azores, migratory waterbirds, which can transport microorganisms to very distant places, are probably the most important natural vectors of microalgae and cyanobacteria (Guerne, 1887; Proctor, 1959). Although the presence of non-native microalgae and cyanobacteria could be explained by the interplay of these natural dispersion mechanisms with ecological changes in target areas that enable their establishment (Cellamare et al., 2010), human facilitated transport (e.g., introduction of non-indigenous aquatic plants and fishes) is the most probable pathway of their invasion into new areas across the globe (Cellamare et al., 2010; Kaštovský et al., 2010) and in the Azores.

The international airport in Ponta Delgada (São Miguel) was inaugurated in 1969, and in the following three decades, escapes and transport/contaminant pathways were more critical than introductions. After 2000, escapes became a less clear pathway, which might be related to law enforcement related to living imports. Other pathways such as escapes and transport/contaminant, the first related to ornamental and aquariology trade, and the second with agriculture/livestock importations, are still very relevant and primary pathway in recent years (**Supplementary Material 1**).

Ecological and Economic Impacts

It is widely accepted that invasive species affect biodiversity and ecosystems and have socio-economic impacts (Pimentel et al., 2000). Traditionally, ecologists and invasion biologists have solely focused on the impacts of invasive species on biodiversity and ecosystem functions (Sala et al., 2000; Courchamp et al., 2017). However, the adoption of ecosystem services where biodiversity is considered within the context of human well-being has emphasized the need to consider people's health, wildlife, and domestic animals (Pejchar and Mooney, 2009). Most of the time, it is challenging to quantify long-term ecological impacts because freshwater ecosystems adjust and evolve in response to invasions. However herein we present some examples on ecological and economical effects of species introductions with special emphasis in the Azores.

The introduction of predators (fishes) on the Azores lakes had marked effects on the trophic dynamics and ecological state of formerly fishless lakes. Particularly evident was the negative effect of *C. auratus* and *C. carpio* both of which have altered the trophic dynamics and the relative importance of benthic and pelagic production, contributing to the increase of turbidity, leading to a change in oxygen conditions of the hypolimnion of the deep lakes, and increasing the eutrophication processes in the lakes (Skov et al., 2010; Raposeiro et al., 2017). Additionally, direct predation has caused the disappearance of several native macroinvertebrate and zooplankton species (Skov et al., 2010; Buchaca et al., 2011; Raposeiro et al., 2017).

In the Azores, the introduction of Lymnaeidae snails [e.g., *G. truncatula* and *Radix peregra* (Müller, 1774) vectors of *Fasciola hepatica* Linnaeus, 1758] have contributed to significant revenue losses in livestock farms in São Miguel (Frias Martins, 1991), which highlights the importance to consider health and ecosystem services aspects in locally accessing introductions' impacts.

Economic impacts are also associated with landscape deterioration due to the decline and impoverishment of ecosystem services (Fei et al., 2014). The introduction of non-indigenous cyanobacteria and plants such as *Egeria densa* Planch. has decreased water quality and increased turbidity of Azorean lakes, negatively impacting leisure recreational activities undertaken both by tourists and the local population (Santos et al., 2012; Cruz et al., 2015; Cordeiro et al., 2020). Moreover, climate changes may promote the spread of non-indigenous species that act as hosts of parasites and transmit human illness.

Despite the high number of non-indigenous species that may negatively affect ecology and economy, the introduction of some species may also have had socio-economic benefits like enhanced recreational fishing in Azorean lakes by fish stocking (Hunt et al., 2017).

Cyanobacteria, Diatoms, Desmids, and Synurophytes

Little is known about the distribution of freshwater cyanobacteria, desmids, synurophytes, and diatom species in the Azores (Jorgen Kristiansen, 1996; Foissner and Hawksworth, 2009). Nevertheless, cyanobacterial blooms were recorded for the first time in Azorean lakes, namely Sete Cidades and Furnas (e.g., Santos et al., 2005; Gonçalves, 2008; Cruz et al., 2015) during the late 1980s. Several well-known bloom-forming species associated with eutrophication, such as *D. scheremetieviae, M. aeruginosa, M. flosaquae* were not only recorded for the Azores between 1989 and 1991, but became dominant in several lakes. When these microorganisms become invasive, they contribute to the eutrophication of aquatic ecosystems (Hillebrand and Sommer, 2000), altering the structure of native communities significantly and leading to loss of biodiversity (Chapin et al., 2000; Korneva, 2014).

In general, invasions by microorganisms are poorly understood and, until recently, their impact on the environment has been underestimated (Foissner and Hawksworth, 2009; Kaštovský et al., 2010).Many species of cyanobacteria can produce toxins harmful to the ecosystem, and when present in drinking or recreational waters might lead to human health problems (Christoffersen and Kaas, 2000; Funari and Testai, 2008; Oscoz et al., 2010) that can vary from psychological effects, discomfort, nuisance, and phobias, to skin irritations, allergies, poisoning, disease and even death (Bayliss et al., 2017; Peyton et al., 2019). Examples of the latter can be posed by the invasive species *Microcystis aeruginosa* (Kützing) Kützing, *Microcystis flosaquae* (Wittrock) Kirchner, *Aphanizomenon flos-aquae* Ralfs ex Bornet & Flahault, *Aphanizomenon gracile* Lemmermann and *Dolichospermum scheremetieviae* (Elenkin) Wacklin, L. Hoffmann & Komárek, found in many lakes in the archipelago, often with high abundance (Santos et al., 2005; Cordeiro et al., 2020; Luz et al., 2020).

In addition to the predominance of cyanobacteria in most eutrophic lakes, which manifests the most significant degradation of these ecosystems' biological quality, non-indigenous diatoms can also cause considerable damage to the environment. The invasive *A. formosa* and non-indigenous *F. crotonensis*, are widely distributed species whose populations have been increasing in numerous lakes worldwide (Gonçalves, 2008; Sivarajah et al., 2016). The species *A. formosa* has at times been the most abundant diatom in several Azorean lakes (Gonçalves, 2008). The synurophyte *Synura petersenii* Korshikov and the desmid *Micrasterias papilifera* Brébisson ex Ralfs are also considered non-indigenous and were recently found in one lake in São Miguel and Terceira islands, respectively.

Plants

Among the 41 plant species (see **Supplementary Material 1**), free-floating macrophytes such as the water hyacinth *E. crassipes* interfere with water utilization resources (Cook, 1990; Vereecken et al., 2006). Water hyacinth has invaded freshwater systems on five continents, and it is expected to expand in consequence of global warming (Kriticos and Brunel, 2016). In Portugal, the possession and sale of water hyacinth were prohibited by Law Decree no 165/74 (1974). Its mats with complex radicular structures prevent light penetration and water oxygenation with severe consequences to the autochthonous fauna and flora. Despite its presence on several islands of the archipelago (currently present in five of the nine islands), it has only been found in water tanks and ponds as ornamental, or on temporally waterlogged areas in Sete Cidades lakes (São Miguel Island). The local containment of this species is essential as it may constitute a threat for many small lakes in the Azores (Kriticos and Brunel, 2016).

The non-indigenous duckweeds *Landoltia punctata* (G. Meyer) D. H. Les & D. and *Lemna minor* L. can be aggressive invaders in aquatic ecosystems, whose colonies cover the surface of the water, causing oxygen depletion (Landolt, 1986). These plants should be controlled before they cover the entire water surface. Although they have a high dispersal capacity, populations in the archipelago are small and sparse.

Two species of Hydrocharitaceae recently introduced to the archipelago also stand out, *Egeria densa* and *Elodea canadensis* Michx. The first is disseminated worldwide and is capable of high-speed growth (Oliveira et al., 2005) due to fragmentation and posterior vegetative reproduction. *E. densa* is a very resistant species and tolerates an extensive range of nutrient, oxygen, carbon dioxide, and pH conditions (Matthews et al., 2014). In the Azores, it is present in three islands, but problems have been mainly reported in Sete Cidades and Furnas lakes (São Miguel Island) where the eutrophic conditions have been enhancing its growth. *E. canadensis* was first reported in 1970 for São Miguel island (Santos et al., 2005). These species introductions have been related to escapes from aquaria or deliberate ornamental plantations in natural ponds and subsequent dispersion by fragments through water flow or associated with human activities. Their impacts include restrictions on recreational activities, rising flooding risk, and interfering with some infrastructure such as turbines (Oliveira et al., 2005; Matthews et al., 2014).

A number of non-indigenous dicotyledonous helophytes develop on temporarily flooded soils, such as *Apium nodiflorum* (L.) Rchb.fil., *Nasturtium officinale* W.T.Aiton, *Persicaria hydropiper* (L.) Spach and Poaceae *Glyceria fluitans* R.Br. and are common species inhabiting small watercourses. Similarly, the emergent and submergent macrophytes (helophytes) can flourish in fens and temporarily or permanently flooded areas (Rivas-Martínez et al., 2001). In the Azores, these macrophyte communities, mainly composed of non-indigenous species, are favored by removing forest cover and the abusive use of water resources for both humans and livestock (Rodrigues et al., 2004). This ecotone has been extended in many aquatic margins where livestock access creates disturbed areas that facilitate invasive species spreading, such as *Cyperus* spp. and *Typha* spp.

Certain herbaceous invasive species, non-strictly aquatic, prefer wetland habitats, such as *Ranunculus* spp., *Mentha* spp. and *Tradescantia fluminensis* Vell., and form dense populations in moist and shady areas. With a short reproductive maturation and high levels of seed dispersal, these species are common on most islands. These reproductive strategies constitute a competitive advantage over native flora that inhabit similar environments.

Invertebrates

Non-indigenous invertebrate species that may cause ecological and socioeconomic impacts in Azorean freshwaters are represented by Platyhelminthes, Cnidaria, Annelida, Mollusca, and Arthropoda (**Table 1**). The species that have the most serious negative effects in freshwater ecosystems are described in detail.

Craspedacusta sowerbii Lankester, 1880 (Cnidaria, Hydrozoa) native from China (Jankowski, 2001), shows a cosmopolitan distribution due to its introduction in many freshwater habitats (Jankowski et al., 2008) on all continents except Antarctica (Rayner, 1988). Most of these introductions have been accidental and associated with fauna trade or ornamental plants (Jakovčev-Todorović et al., 2010). In 2010 some individuals were found in Congro lake, São Miguel Island (Raposeiro et al., 2011c). Recently, *C. sowerbii* has been discovered on other islands. *C. sowerbii* feeds on zooplankton (Smith and Alexander, 2008; Moreno-Leon and Ortega-Rubio, 2009) and may impact aquatic food webs by removal of a significant part of the zooplankton population, leading to changes in the structure of plankton community (Smith and Alexander, 2008) and cascading effects on primary producers (Brooks and Dodson, 1965; Carpenter and Kitchell, 1984; Williamson et al., 1989). Moreover, blooms of *C. sowerbii*, that often occur under eutrophic conditions and high temperatures, may trigger severe impact on the ecosystem (Davis, 1955; Jakovčev-Todorović et al., 2010).

Ferrissia fragilis (Mollusca, Gastropoda) is a native from North America and was probably introduced to the Azores by aquarists and/or associated with ornamental plants ("Transport-contaminant" pathway). This species was first observed on São Miguel Island in Sete Cidades Lake in 2004 (Raposeiro et al., 2011b). Since then, it has been found on Santa Maria, Graciosa, and Pico islands. Freshwater habitats where *F. fragilis* are present are usually characterized by high nutrient concentrations where these snails are typically found on submerged leaves of the introduced plant *E. densa* in shallow littoral shores. *F. fragilis* can also be found in submersed periphyton-covered stones or on plant detritus in weak flow areas (Raposeiro et al., 2013). The impact of this species is not clear (Raposeiro et al., 2011b). The impact in the Azores is probably masked by other introduced freshwater gastropods (Backhuys, 1975; Frias Martins, 1991; Raposeiro et al., 2012).

Galba truncatula (Mollusca, Gastropoda) introduction to the archipelago is possibly associated with imported sheep from mainland Portugal or aquarium trade (Duggan, 2010). Its introduction may have also been mediated by Nearctic birds or insects (Raposeiro et al., 2011a). The invasive potential of

Lymnaeids species may be related to marked resistance to desiccation which increases their survival probability (Chapuis and Ferdy, 2012). When released in new environments, even a single individuals can develop a population as Lymnaeids can be self-fertilized (Escobar et al., 2011; Lounnas et al., 2018). Snails belonging to the Lymnaeidae family (Hurtrez-Boussès et al., 2001; Mas-Coma et al., 2005), such as *G. truncatula* and *R. peregra,* both introduced in the archipelago, are intermediary hosts for the Trematoda F. *hepatica* that contaminates part of São Miguel, Flores, and Santa Maria islands causing significant socioeconomic losses associated with damage to dairy livestock (Barbosa et al., 2019).

Procambarus clarkii, a crayfish native from North America and Mexico, is considered globally one of the most invasive aquatic species (Meineri et al., 2014; Arce and Diéguez-Uribeondo, 2015). In Portugal, it is forbidden under the Law Decree no 565/99 (1999) to keep and rear this species. *P. clarkii* was reported for the first time in São Miguel Island in 1994 (Correia and Costa, 1994; Costa et al., 1997), and it has since spread to Terceira Island. Its introduction in the Azores may be related to the aquarium trade, with an escape or release from a private aquarium or tank. This crayfish can actively disperse by land (Gherardi et al., 2000; Ramalho and Anastácio, 2014) and spread by passive vectors such as vehicles and animals (Águas et al., 2014; Anastácio et al., 2014). Its short life cycle, rapid growth, digging activity, and high populational densities facilitate its establishment (Gherardi and Acquistapace, 2007). In lakes in São Miguel island, *P. clarkii* is associated with the invasive species *E. densa* contributing actively to this plant fragmentation and dispersion. The presence of the red swamp crayfish in the archipelago is restricted to highly impacted systems, making its impact evaluation difficult, but it is probably lower than on the mainland. Interestingly, *P. clarkii* is now absent from Lagoa do Peixe, the small lake where its presence was first detected in São Miguel island, which seems to be a first record for a population extinction of this species.

Other non-indigenous species categorized as invasive in Azores freshwaters are the platyhelminth *Dugesia tigrina* (Girard, 1850); the annelids *B. sowerbyi* and *Eiseniella tetraedra* (Savigny, 1826); the gastropod *P. acuta*; the crustacean *Argulus foliaceus* (Linnaeus, 1758); and diptera considered urban and agricultural pests, as *Culex pipiens* Linnaeus, 1758 and *T. oleracea*.

Vertebrates

Non-indigenous amphibians in the Azores include, the frog *P. perezi*, introduced in 1820 and scattered on all the islands and by the crested newt *Triturus cristatus carnifex* (Laurenti, 1768) already present in 1922 on São Miguel (Svenberg, 1975), and both considered as invasive in the region. Due to the Azores' oceanic geography, fishless lakes were common before human settlement, and the only native freshwater fish is *A. anguilla*, a common inhabitant of Azorean streams. In Azorean lakes, fishes' introduction had a strong effect on macroinvertebrates communities, mainly due to the absence of native predators, with direct impacts on the diversity and abundance of prey populations (e.g., native invertebrates) (Skov et al., 2010; Raposeiro et al., 2017). Among the non-indigenous fishes introduced in the Azores (**Supplementary Material 1**), we mention the most abundant species with a negative impact on Azorean freshwaters.

Cyprinus carpio is the most abundant fish species in Azorean lakes, and is present on Flores, Pico and São Miguel islands (Gonçalves et al., 2006; Bio et al., 2008; Raposeiro et al., 2017). The first record of introduction dates from 1890 in São Miguel Island (Chaves, 1911). Recent introductions of fishes in the Azores have been for recreational fishing purposes (Anastácio et al., 2019), and dispersion among aquatic systems and islands is due to human action either by introductions from breeding facilities (e.g., trout) or by anglers' translocations. *C. carpio* has a detritivorous bottom-feeding strategy consuming benthic invertebrates, removing sediments from the bottom, uprooting the macrophytes leading to the increase of water turbidity (Parkos et al., 2003; Miller and Crowl, 2006) and consequently, contributing to decrease water quality and habitat degradation (Lougheed et al., 1998; Buchaca et al., 2011). Moreover, *C. carpio* has a substantial impact on benthic communities by releasing nutrients from sediments thus and indirectly promoting algae blooms (Ribeiro et al., 2009; Raposeiro et al., 2017). *C. carpio* may also have socio-economic impacts through decreasing high value fish species by outcompeting with them and reducing recreational activities' attractiveness. Increasing nutrient availability through sediment disturbance and excretion by fish may directly affect primary producers (quantity and diversity) and subsequent bottom–up consequences on food webs (Skov et al., 2010; Buchaca et al., 2011; Raposeiro et al., 2017).

Micropterus salmoides is a piscivorous species introduced in 1898 for fishing purposes. Nowadays, it is well distributed in Pico, São Miguel, Flores, and Corvo Island (unpublished data). This species may impact the ichthyofauna and amphibians, causing top-down consequences in trophic webs (Takamura, 2007).

Perca fluviatilis is planktivorous fish introduced for angling in São Miguel's lakes in 1898, an activity long fomented by Forestry Services. Thus, anglers can act as dispersion vectors for some non-indigenous species, fishes, and accompanying species. *P. fluviatilis,* as a zooplanktivorous fish, may promote the decrease of native zooplankton densities, lowering grazing pressure on phytoplankton with resulting increased chlorophyll-a concentration, reduced water clarity, and enhanced eutrophication in Azorean lakes (Skov et al., 2010; Buchaca et al., 2011).

Management and Conservation Actions

Climate change and the increasing magnitude and frequency of introductions of species across geographic barriers resulting from international trade (see Hulme, 2009) are likely to change their establishment, spread, abundance, physiology, or phenology, potentially altering humans' health impacts (Bayliss et al., 2017). Many non-indigenous species will likely benefit from climate change as some of their ecological traits provide high plasticity and adaptation abilities to cope with changing conditions (Hellmann et al., 2008). Global change may lead to new public health concerns as globalization increases the likelihood of disease vectors' movement and facilitates the transmission of tropical and subtropical pathogens to higher latitudes and other Atlantic archipelagos (Seixas et al., 2019). Trade plays a vital role in the spread of invasive species and has arguably contributed to the recent acceleration of biological invasions (Seebens et al., 2015). The magnitude of merchandise imports is a determinant of the number of invasive species (Hulme, 2009), evidenced by correlations between invasive species richness and economic indicators (Dalmazzone, 2013). This has been proved stronger for islands than for continents, reflecting the more significant proportion of imports and higher establishment of invasive species (Hulme, 2009). Considering the observed trends in international trading, importations, and enhanced connectivity of the Azores archipelago as a result of the increasing number of flights and shipping (Vieira et al., 2019), unintentional introductions may accelerate beyond control if some preventive measures are not enforced (Howeth et al., 2016) due to enhanced propagule pressure. Higher connectivity among islands (**Figure 1**) is likely to improve non-indigenous freshwater species' dispersal within the archipelago as accidental transportation seems to be an essential pathway for the non-indigenous freshwater species present in the Azores.

An important focus should be developing a biosecurity program addressing different sorts of species importation, improving the existing legislation and customs controls, and public campaigns to ensure good practices for watersheds users. For example, the "Clean Drain" movements, applied in the United States, New Zealand, and the United Kingdom, empowered recreational and other water users to promote biosecurity best practice to reduce the risk of accidental introduction and spread of aquatic IAS, encouraging people to check, clean and dry all equipment and clothing thoroughly (Beyer et al., 2011; Anderson et al., 2015). A relevant problem to address is the introduction of ornamental species. The ornamental plant industry needs "new" varieties of plants to offer to the public. Still, at the same time, there must be mechanisms to prevent non-indigenous species' entry with high invasive potential. The large number of species coming from aquariums is worrying, and strict control of importation for business purposes must be put in place, and information and prevention campaigns should be carried out among the general public and anglers. The awareness-raising campaign could also include citizen science initiatives directed at key species that should be included in an early warning monitoring program. It is widely accepted that citizen science can play a significant role in public engagement. Their observations are crucial to informing policy on biodiversity conservation from government decisions to those made by local conservation managers (Theobald et al., 2015; Anderson et al., 2017). This is particularly relevant in restricting and preventing biological invasions (Theobald et al., 2015; Anderson et al., 2017; Chandler et al., 2017). A wealth of species occurrence data generated by citizen scientists enables surveillance of emerging and established invaders at larger spatial extents. Strictly regulating – or even prohibiting – the trade of species highly likely to become invasive, together with early alert and rapid response systems, is generally considered the most successful management strategy (Leung et al., 2002).

In parallel, monitoring of aquatic ecosystems would allow early detection of new species. To do this effectively, it is necessary to provide high quality and up-to-date information. Monitoring staff must be well trained in species identification to avoid confusion as occurred in the past, such as the case of clover fern *Marsilea azorica* Launert & J. Paiva (Schaefer et al., 2011). This species was described in 1983 and included as 'critically endangered' on the IUCN red list and as 'strictly protected' species by the Bern Convention and the European Union's habitats directive, but was later identified by Schaefer et al. (2011) as *Marsilea hirsuta* R.Br., a non-indigenous species in the archipelago. A similar problem arose with *Potamogeton lucens* Nolte, subsequently determined by Kaplan and Zdenek (2005) as *Potamogeton schweinfurthii* A.Benn.

In the Azores case, the moderate climate without large annual fluctuations makes it possible for many species to potentially acclimatize (Walther et al., 2009; March-Salas and Pertierra, 2020), which would be more difficult elsewhere. Despite its oceanic isolation, the archipelago is halfway between the Americas and Europe, doubling the possible routes of entry for invasive species that can rapidly spread in the islands. Therefore, regarding the flora, most non-indigenous aquatic plants in the Azores should have monitoring plans due to the risk of rapid dispersal in lakes and water courses, and eradication should be advised for newly established species with limited distribution (Sharov, 2004). This should be considered, for instance, for controlling the water hyacinth *E. crassipes* in the Azores. The percentage of non-indigenous plants (69%) in the Azorean flora is relatively high (Silva and Smith, 2004). Some of these such as the terrestrial *Hedychium gardnerianum* Ker Gawl., *Clethra arborea* Vent., or *Hydrangea macrophylla* Thunb. although not strictly aquatic plants, strongly influence the Azorean freshwater ecosystems' ecotone zones. Their presence at the margins of water courses, transport of rhizome fragments, deliberate introduction (hedges) allied with their aggressive nature, and strong presence in the archipelago will create severe problems in the structure, native status, and succession of these ecosystems. This complete alteration of riparian phytocenosis is of paramount importance since it provides the habitat and food for many organisms and influences aquatic microbial community composition (Ferreira et al., 2017).

Eutrophication is a slow natural process that has been dramatically accelerated by human activities, such as the runoff of excess fertilizer or sewage effluent in the Azores. Anthropogenic eutrophication is typically associated with higher primary productivity, higher oxygen demand, lower species richness, and species abundance changes (Engelhardt, 2011). One of the leading causes of this eutrophication in the Azores is the agricultural and livestock use of the territory, mainly focused on cattle. The alterations caused by livestock in the riparian areas are mostly three: physical destruction of the habitat by trampling, selective grazing of the vegetation, and excess supply of nutrients and seeds of non-indigenous species by excrements. This complex interaction of factors can lead over time to the complete alteration of delicate aquatic ecosystems by favoring invasion of non-indigenous plants in the riparian galleries and their proliferation in the water, as is the case of *E. densa* and non-indigenous cyanobacteria blooms.

Management actions against freshwater weeds were applied in some Azorean lakes (e.g., Sete Cidades lakes) using mechanical harvesting. Although large amounts of weed biomass were removed from the lakes (Santos et al., 2012) no ecological improvement was detected in these lakes. Mechanical approaches to control *E. densa* are known to be ineffective and can even enhance its dispersal and spread (Pennington, 2009). Massive removal of lake macrophytes can also resuspend lake sediments and release sediment-sequestered nutrients, favoring phytoplankton growth (Sayer et al., 2010; Quilliam et al., 2015) and enhancing eutrophication. Therefore, the removal of large stands of weeds in water bodies with massive proliferation is not recommended. However, removing non-indigenous macrophytes should be prioritized in recently invaded water bodies to contain or even eliminate them in the early invasion stages.

Another important factor contributing to eutrophication is the internal recycling of nutrients (Sondergaard et al., 2001). Fishes play an essential role in this process (Horppila et al., 1998; Buchaca et al., 2011), especially in ecosystems where they were naturally absent, as is the case of Azorean lakes (Skov et al., 2010; Raposeiro et al., 2017). Efforts were made in one lake (Lake Furnas, São Miguel Island) to reduce fish abundance to minimize eutrophication, and increase water quality (Bio et al., 2008). Despite the promising results of the first attempt to control fish populations in Azorean lakes, this approach was only applied for a short period (Bio et al., 2008). However, habitat restoration and implementation of land-use changes and more sustainable livestock and agriculture practices within some watersheds can not only fight the eutrophication problem but could also help manage the invasive species that benefit from nutrient-enriched conditions and impaired habitats. Some efforts have been put in place, e.g., on São Miguel, through watershed management plans, to tackle this problem (Cruz et al., 2015), but more robust measures have to be enforced to control of the freshwater invasive species spread.

A very positive point of Portuguese legislation in force on invasive species (Law Decree no 92/2019, 2019) is that investment is made in preventive culture. Monitoring, early detection, and rapid reaction mechanisms are put in place to contain the spread of invasive species. Despite including more invasive species than the previous law (Law Decree no 565/99, 1999), many species appear in this document as invasive only for the autonomous region of Madeira, leaving out the Azores, as it is the case of *Adiantum raddianum* C.Presl, *Adiantum hispidulum* Sw., *Colocasia esculenta* (L.) Schott, *Holcus lanatus* L., *Z. aethiopica and Crocosmia x crocosmiiflora.* The Regional Legislative Decree n.o 15/2012/A (2012) aims to regulate the import, holding, and introduction into the territory of the Autonomous Region of the Azores of non-indigenous species, in annex XI (Animal specimens whose introduction is permitted in the Autonomous Region of the Azores). However this decree concerning pets allows the entry into the islands of two groups of animals whose dispersion in the aquatic systems of the archipelago is problematic: "(e) Turtles (reptiles of the Chelidae family) and (f) Freshwater aquarium fish when produced in captivity." Another point to note is the absence in Annex IX (List of species of fauna and flora invasive or at known ecological risk) of a fish list, which does appear in national law (Regional Legislative Decree n.o 15/2012/A, 2012). Moreover, in recent years, efforts have been made to reinforce controls at border levels by customs in local airports and ports.

River basin management plans implemented in the framework of WFD should also be an instrument for invasive species control. Even though non-indigenous species are not explicitly referred in the WFD, the directive aims to restore pristine communities in European water bodies, which implies that invasive species must be removed from or controlled within these ecosystems. Unfortunately, most European countries do not include invasive species in WFD assessments, and many do not take them into account in the status classification (Boon et al., 2020). Although in the Azores invasive species are not used for the ecological status classification, they negatively impact water bodies, and measures to control invasive plants in transitional waters were proposed in the Azores river basin management plan (AHA-DRA, 2015). Due to their impact on native communities and ecological quality, invasive species can preclude the achievement of WFD environmental objectives of good water status in water bodies. Therefore, more actions to control invasive species must be considered in future river basin management plans.

FINAL REMARKS

In island freshwater ecosystems, it is challenging to predict vulnerability to non-indigenous species. Still, it is crucial to compile a detailed list of species, distribution, and associated environmental and historical information. Using this information combined with alternative approaches, like paleolimnological reconstruction, a comparative analysis of past introductions could be a significant step to understand the consequence of invasive species on insular freshwater systems. Detailed and general knowledge of the principal pathways and efforts to enhance environmental conditions would minimize invaders' success within fragile insular ecosystems. Also, control measures such as checking the consignment both by air and sea for non-indigenous species would prevent new species' entrance. In contrast, a more conscious and educated behavior from all users (e.g., tourists, anglers, and aquariologists) and management measures to improve water quality will prevent the spread of present invasions. Furthermore, systematic monitoring of these habitats and biota should be carried out to provide additional information that is essential for improving freshwater management, sustainable development, and ensuring the functioning and services of freshwater ecosystems.

Managing non-indigenous species on remote oceanic islands requires a well-coordinated strategy among all stakeholders. In the future, we must take into account that expanding international trade, tourism, transport, and climate change will probably facilitate the entry, spread, and establishment of non-native species through new pathways. Future actions such as political awareness and compromise and public awareness and education concerning species introductions are needed to tackle this problem.

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/s.

AUTHOR CONTRIBUTIONS

AC and PR contributed to the conception and design of this study. All the authors contributed to the manuscript with essential inputs from AB (fauna species lists and data compilation), PR (data treatment), and SS (microalgae and cyanobacteria data compilation), largely contributed to the manuscript writing, and approved the submitted version. VG contributed microalgae, cyanobacteria and management, and ecosystem data analysis. MS contributed plants and management sections.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.631214/full#supplementary-material

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