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Research Article

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Abstract

Global databases have contributed to our understanding of alien, naturalised and invasive plant species distributions. Still, the role of species invasions in habitats, specifically in aquatic habitats, remains underexplored at the global scale. Accordingly, a comprehensive global synthesis of the status of plant invasions in aquatic habitats has been missing. Here, we focus on macroecological patterns of naturalised non-invasive and invasive plants in aquatic habitats using the recently built SynHab database. Amongst all the plant records compiled in SynHab, 592 are assigned to aquatic habitats, of which 183 are unique plant taxa (further termed 'species') belonging to 49 families. Of the total number of records, 462 refer to taxa with naturalised non-invasive occurrences and 130 to invasive occurrences. The species pool analysed here refers to 78 regions distributed across all botanical continents as defined by the World Geographical Scheme for Recording Plant Distributions. The number of naturalised non-invasive aquatic species is similar across different continents and biomes, but Tropical Asia had more and the Mediterranean zonobiome had fewer invasive species than expected. Tropical Asia, Temperate Asia and Africa have the highest proportions of naturalised species that have become invasive, while across continents, invasive proportions were highest for tropical and subtropical zonobiomes. New Zealand, Italy and California contained disproportionately more naturalised species than expected, given the area covered by aquatic habitat in those regions, whereas South Sudan, Papua New Guinea and Kyrgyzstan had disproportionately fewer species. In pairwise dissimilarity comparisons, all continents had distinct species compositions (from 0.73 to 0.92 of the Jaccard dissimilarity index) and so did zonobiomes (0.69 to 1.00). The high proportion of invasive species in Tropical Asia in comparison with terrestrial invasions in this region, indicates a greater susceptibility of warmer regions to aquatic plant invasions. This may be exacerbated by further naturalisations in the future, as data from temperate regions suggest a larger pool of available species.

Key words: Macrophyte invasion, plant invasion patterns, SynHab database

Introduction

Aquatic habitats are particularly prone to invasion by alien species due to several factors, including natural disturbance regimes (e.g. river flow variation and lake water level fluctuations), high levels of connectivity and anthropogenic activities (e.g. damming for hydropower and water extraction for agriculture) (Richardson et al. 2007). High levels of connectivity, both natural and anthropogenic (such as raw water transfer schemes and canals), make monitoring and managing pathways of invasion in aquatic habitats difficult (Waine et al. 2025). Invasive aquatic plants (macrophytes) often act as autogenic engineers and primary producers (Ricciardi and MacIsaac 2010), i.e. they transform freshwater systems, change habitat structure (Valley and Bremigan 2002; Ceschin et al. 2020) and reduce water quality by altering flow and primary productivity (Perna and Burrows 2005; Gallardo et al. 2016; South et al. 2016), resulting in changes in local native diversity (Schooler et al. 2006). In addition, projected accumulations of naturalised alien plant species suggest faster increases in aquatic systems than in terrestrial habitats (Seebens et al. 2021), indicating that future impacts are likely to intensify. The severity of impacts caused by alien plants is magnified because aquatic habitats are extremely diverse relative to the area they occupy, compared to other habitats (Román-Palacios et al. 2022).

The ecological impacts of invasive alien plant species and management efforts impose substantial economic costs. From 1975 to 2040, the documented global costs of invasive macrophytes are projected to reach US$ 32.8 billion (in 2017 dollars, Macêdo et al. 2024). However, this figure likely represents a significant underestimation due to data limitations and geographical gaps in current research

(Macêdo et al. 2024), crucially concerning the underestimated costs of invasive plants (Novoa et al. 2021). This raises additional concerns about the extent to which the economic costs of invasive plants in aquatic habitats may be reliably captured. As such, updated knowledge of regional levels of invasion is crucial for a better understanding of impacts and cost estimates.

The World's 100 worst invaders list (Lowe et al. 2000) provides examples of the harmful effects that plant invasions can have on aquatic habitats. One of the globally most prominent invaders is water hyacinth (*Pontederia crassipes* Mart., synonym *Eichhornia crassipes* (Mart.) Solms), which is native to South America and has spread to over 70 countries (Gezie et al. 2018). *Pontederia crassipes* is a fast-growing floating macrophyte that forms dense mats on the water surface, alters habitat structure and disrupts the ecological functioning of aquatic ecosystems (Tobias et al. 2019). This species also has direct socioeconomic impacts, including reduced navigability and recreational quality, restricted water supply for agriculture due to damaged pipe systems and reduced access to fishing grounds and boating (Kateregga and Sterner 2009; Villamagna and Murphy 2010). Similarly, *Azolla filiculoides* Lam., often found alongside *Pontederia crassipes* and *Pistia stratiotes* L., is a small (< 25 mm) floating macrophyte that impacts physical and chemical water features, reduces the richness and biomass of macrophytes, alters zooplankton composition and reduces the survival of amphibian larvae (Pinero-Rodríguez et al. 2021). *Lagarosiphon major* (Ridl.) Moss is a submerged macrophyte (Howard-Williams and Davies 1988) that forms dense underwater beds, outcompeting native macrophytes in the range it has invaded (Martin et al. 2018).

Specific inherent biological attributes (such as functional traits) determine the invasiveness of species and increase their potential to become invasive (Gioria et al. 2023) by interacting with native biota and the environment (Pyšek et al. 2020). Additionally, one of the most important factors explaining the success of plant invasions is propagule pressure (e.g. Von Holle and Simberloff 2005; Colautti et al. 2006; Cassey et al. 2018), which also applies to invasive macrophytes (Chadwell and Engelhardt 2008; Xie et al. 2013). High levels of connectivity can facilitate the spread of propagules, increasing dispersal distances for invasive plants within and between waterbodies in aquatic habitats (Richardson et al. 2007; Leuven et al. 2009). For example, natural flood events accelerate the dispersal process by facilitating the movement of propagules within catchments (Gurnell et al. 2008; Čuda et al. 2017). Climate-related changes to the flow regime further facilitate the spread of propagules by increasing the frequency of extreme floods (Pattison et al. 2017). In addition, dams create lentic habitats with slow-moving waters, which are preferred by *Azolla*, *Pistia* and *Pontederia* species. Given the expected increase in dam construction to mitigate climate-driven rainfall reductions, this may result in enhanced proliferation of these macrophytes. Raw water transfer schemes (water diversions) move large volumes of freshwater between catchments via complex infrastructure networks, facilitating the long-distance spread of invasive species (Waine et al. 2024a, b).

Research on plant invasions in aquatic habitats is under-represented compared to terrestrial habitats, particularly in the Tropics (Evangelista et al. 2014; Havel et al. 2015; McKnight et al. 2017), with certain species or taxonomic groups dominating the literature (Stevenson et al. 2023). Here, we utilise the newly-developed SynHab database (https://www.synhab.com/the-project), which contains information on plant naturalisations and invasions in specific habitat types worldwide (Pyšek et al. 2022; Dawson et al. 2025), to achieve a more balanced perspective of the overall diversity of naturalised plants in aquatic habitats. We address this knowledge gap by asking the following questions: (i) Which continents and biogeographical regions (zonobiomes) have the highest levels of naturalisation and invasion of plants in aquatic habitats? (ii) Which aquatic naturalised non-invasive and invasive plants are most widely distributed? (iii) Does the vulnerability of aquatic habitats to naturalisations and invasions of plants differ in temperate vs. tropical regions? (iv) Which regions (regions or states) harbour more naturalised plant species in aquatic habitats than expected? (v) Which regions are more similar in terms of naturalised plant species composition in aquatic habitats? (vi) Which naturalised aquatic plant species are indicative of continents and zonobiomes?

Materials and methods

Habitat classification and macrophyte definition

Habitat classification, adapted from Hejda et al. (2015) for the SynHab database, resulted in 14 categories (Pyšek et al. 2022). The aquatic habitat is a category defined as "waterbodies and streams with submerged and floating plant species". Macrophytes can be defined in several ways, with some definitions including macroalgae (e.g. Chambers et al. 2008); however, here we restrict our focus to aquatic vascular plants. Species were assigned to the aquatic habitat if they exhibited growth in water as submerged or floating, including littoral species that can cope with long-term flooding, with roots anchored below the water level. Some species, such as *Iris pseudacorus* L., *Eleocharis palustris* (L.) Roem. & Schult., *Juncus effusus* L. and *Jacobaea aquatica* (Hill) G.Gaertn., B.Mey. & Scherb., can grow in the littoral zones of freshwater or brackish waterbodies, as well as in mud. In such cases, they were assigned to both aquatic and wetland habitats in SynHab, of which only the former is dealt with in the present paper. Species inhabiting mud, but intolerant to prolonged flooding, such as *Lysimachia nummularia* L. were excluded. Dimorphic species, such as *Alternanthera philoxeroides* (Mart.) Griseb., exhibiting mud-dwelling and littoral forms, were also affiliated with both aquatic habitats and wetlands. In such cases, species were assigned to the aquatic habitat if the habitat descriptions explicitly confirmed growth in a submerged environment of freshwater lakes, rivers, running waters, coastal basins or streams. Species that grow along rivers, but not in the water were not included. We thus included also aquatic vascular plants that are not exclusively aquatic, but that are important invaders in the aquatic habitat.

Data acquisition

The data on habitat affiliations for the SynHab database were extracted from literature sources (regional checklists of alien floras), where the verbal description of habitats allowed unequivocal assignment of a given species (see Suppl. material 1: table S1 for the complete references). If published sources lacked information on habitat affiliations, we invited the authors of original publications to collaborate and provide habitat affiliations for SynHab. The SynHab project leaders (PP, MH, AK) assessed the received information to harmonise the habitat classification with other datasets and then the final habitat affiliations were agreed upon in collaboration with data providers. In total, 78 regions (countries or states) from all continents were included (Suppl. material 1: table S1).

Each plant species was assigned the invasion status as 'naturalised' or 'invasive' in the region, following the definitions of Richardson et al. (2000) and Blackburn et al. (2011) ca; note that the species' invasion status can vary across different regions. Invasion status was assigned, based on information in the GloNAF (Global Naturalized Alien Flora) database (van Kleunen et al. 2015, 2019; Pyšek et al. 2017; Davis et al. 2025) or inferred from the description in the original source or provided by data contributors for their regions. In the context of the analyses described below, the term 'naturalised' refers to all naturalised taxa and is composed of two separate subsets: 'naturalised non-invasive' and 'invasive.'

Each taxon name, as given in the original source, was standardised according to The World Checklist of Vascular Plants (WCVP) database (https://powo.science.kew.org/about-wcvp; Govaerts et al. 2021) using the *rWCVP* package for R (Brown et al. 2023). Accepted names of the species were used in the analyses to enable species comparisons amongst regions. Four taxa were identified at the subspecies level, but were merged with the corresponding species level for analyses.

Habitat area

To quantify the area of aquatic habitats within each region, gridded global land-cover data, with a spatial resolution of 300 m, were acquired from Defourny et al. (2023). These data comprised 37 land-cover classes, conforming to the United Nations Land Cover Classification System (UN-LCCS) (Di Gregorio and Jansen 2005). We converted the year 2019 raster to a shapefile and intersected it with SynHab regions for further analysis. We excluded permanent snow and ice classes, which resulted in 35 classes included in the analyses. Water surface area of classes was summed for use in analyses.

Biogeographical variables: continents and zonobiomes

Each of the 78 regions for which data on naturalised plant species in aquatic habitats were available was assigned to a continent and a state or country (levels 1 and 4, respectively, of the TDWG World Geographic Scheme for Recording Plant Distributions; Brummitt 2001): Northern America (data available for n = 13 regions); Southern America, n = 11; Africa, n = 16; Europe, n = 16; Temperate Asia, n = 9; Tropical Asia, n = 11; and Australasia, n = 2. Only one record was sampled in the Pacific, which was not considered in the analyses. Further, regions were assigned to one of the following zonobiomes: I. Tropical (equatorial), n = 18 regions; II. Tropical (savannah), n = 15; III. Subtropical (arid), n = 7; IV. Mediterranean, n = 8; VI. Temperate (nemoral), n = 17 regions; VII. Arid temperate (continental), n = 4; VIII. Cold temperate (boreal), n = 1; and n = 8 regions were assigned as "multiple" zonobiomes (Chile, China, Flores, Faial and Santa Maria, Azores, Florida, New South Wales, Russia Kostroma, Russia Middle Volga and Russia Novosibirsk based on Walter and Breckle (1991). While some regions, categorised as 'multiple', may encompass the V. Warm Temperate Zonobiome, no regions were exclusively assigned to it.

Statistical analyses

To test whether naturalisation and invasion in aquatic habitats differ amongst continents and zonobiomes, we used generalised linear models (GLM) with Poisson distribution. Using standardized residuals from generalised linear models (GLMs), we determined if observed species richness was significantly higher or lower than expected across zonobiomes and continents. Statistical significance was assessed by comparing these residuals to critical values corresponding to $P < 0.05$ (± 1.96), $P < 0.01$ (± 2.58) and $P < 0.001$ (± 3.29). Positive values indicate higher and negative values indicate lower naturalised species richness than expected by chance.

The species-area relationship was calculated by fitting a linear model to the number of all naturalised species recorded and the area of aquatic habitat in each region on a log-log scale. To compare the dissimilarity of the regions in terms of their naturalised species composition in aquatic habitats, we calculated the Jaccard dissimilarity index using the "betapart" package (Baselga and Orme 2012; Baselga et al. 2023). To identify which species were significant indicators of each continent and zonobiome, we used the "multipatt" function of the indicator value analysis (IndVal) in the R package "indicspecies" (Dufrêne and Legendre 1997; De Cáceres and Legendre 2009), calculated considering groups of regions within each continent or zonobiome. Complementary to the species composition analysis, the indicator value analysis determines groups of indicator species by measuring their association with each group (continent or zonobiome) or combination of groups and it does not explicitly consider climate, local environment or introduction history.

All statistical analyses were performed in R version 4.4.1 (R Core Team 2024).

Results

Naturalised and invasive species numbers

Of the 585 records in aquatic habitats, 458 referred to naturalised, non-invasive occurrences and 127 to invasive occurrences. The same species can be naturalised, non-invasive in one region and invasive in another; thus, the focus was on the number of occurrences rather than the number of species. In total, we recorded 183 naturalised plant taxa (further referred to as 'species' for simplicity) belonging to 46 families and 88 genera; of these 183, there were 52 classified as invasive in at least one region. The 10 families with the largest number of species were Hydrocharitaceae, Plantaginaceae, Cyperaceae, Poaceae, Araceae, Alismataceae, Onagraceae, Nymphaeaceae, Pontederiaceae and Salviniaceae.

Naturalised aquatic species occurred in 78 regions on all continents (Suppl. material 1: table S1). Of the sampled regions, 34 (i.e. 43.6%) contained information on invasive species. New Zealand had the largest number of naturalised species (n = 37), followed by California and Italy (n = 29 each), France (n = 27), Florida (n = 23), Chile and Virginia (n = 20). Species recorded as naturalised in at least one region were native to Temperate Asia (n = 94), Northern America (n = 87), Tropical Asia (n = 81), Africa (n = 79), Southern America (n = 77), Europe (n = 58), Australasia (n = 45) and the Pacific (n = 21). The most widespread invader, occurring in 55.7% of the sampled regions (n = 43), was *Pontederia crassipes* (this species was considered invasive in 15 of the 43 regions), followed by *Pistia stratiotes* and *Elodea canadensis* Michx., *Azolla filiculoides*, *Elodea densa* (Planch.) Casp. and *Myriophyllum aquaticum* (Vell.) Verdc., all occurring in at least 25% of the sampled regions (Table 1). In contrast, 105 species (56.6% of all sampled species) were found in only one region.

Table 1. The top 21 aquatic species recorded in the largest number of SynHab regions presented by invasion status. These represent 11.3% of species recorded and 50.3% of all records. Am-S = Southern America, Am-N = Northern America, EU = Europe, AUS = Australasia, AS-temp = Temperate Asia, AS-trop = Tropical Asia, AF = Africa; I = number of records as invasive, N = number of records as naturalised non-invasive.

Species	I	N	Total	Continent of origin
Pontederia crassipes	15	28	43	Am-S
Pistia stratiotes	7	16	23	AF, Am-N, Am-S
Elodea canadensis	7	15	22	Am-N
Azolla filiculoides	7	14	21	Am-N, Am-S, Antarctica
Elodea densa	5	15	20	Am-S
Myriophyllum aquaticum	6	14	20	Am-S
Nasturtium officinale	2	17	19	AF, AS-temp, AS-trop, EU
Salvinia molesta	10	7	17	Am-S
Hydrilla verticillata	5	11	16	EU, AF, AS-temp, AS-trop, AUS
Alternanthera philoxeroides	6	7	13	Am-S
Potamogeton crispus	1	9	10	EU, AF, AS-temp, AS-trop, AUS
Myriophyllum spicatum	3	7	10	EU, AF, AS-temp, AS-trop, Am-N
Pontederia vaginalis	1	8	9	AS-temp, AS-trop, AUS
Elodea nuttallii	2	6	8	Am-N
Lemna minuta	2	7	9	Am-N, Am-S
Veronica anagallis-aquatica		8	8	AF, AS-temp, AS-trop, EU
Nymphoides peltata	1	6	7	AF, AS-temp, AS-trop, EU
Acorus calamus		7	7	AS-temp, AS-trop, Am-N
Typha angustifolia	1	5	6	EU, AF, AS-temp, AS-trop, Am-N
Nelumbo nucifera		6	6	EU, AS-temp, AS-trop, AUS
Sagittaria latifolia		6	6	Am-N, Am-S

Biogeographical patterns

The numbers of naturalised aquatic species (considering naturalised non-invasive and invasive species together) per continent and zonobiome were not significantly different from the values expected by chance. However, a different pattern was evident for invasive species. Aquatic habitats in Tropical Asia harboured more invasive species than expected; the opposite was found for the Mediterranean zonobiome, where invasive aquatic species were under-represented (Table 2). Using the proportion of naturalised species that have become invasive as a measure, Tropical Asia, Africa and Tropical Asia ranked the highest amongst continents, with 58.6%, 42.3% and 40.7%, respectively (Fig. 1). Tropical zonobiomes, both Savannah (44.4%) and Equatorial (43.5%) and the Subtropical Arid zonobiome (38.7%) had the greatest proportions of naturalised species recorded as invasive (Fig. 1). No species were sampled in the Warm Temperate zonobiome.

A continental-scale comparison of naturalised species richness in aquatic versus terrestrial habitats, using a combined dataset of all naturalised species, demonstrated that in Africa and Temperate Asia, the observed proportion of aquatic naturalised species was significantly lower than expected by chance (Table 3). For zonobiomes, the aquatic habitats in the Mediterranean harboured disproportionally more and Warm Temperate fewer (none) naturalised species than terrestrial habitats in this region (Table 3, Fig. 2).

For invasive species, the number of aquatic compared to terrestrial was higher than expected by chance in Tropical Asia and Northern America and lower in Temperate Asia (Table 3). Regarding zonobiomes, the representation

Table 2. Number of naturalised non-invasive and invasive aquatic species in continents and zonobiomes. Light orange cells indicate more and blue fewer alien species than expected by chance based on the generalised linear models. Significance indicated by asterisks (* $P < 0.05$).

Continent	Naturalised non-invasive	Invasive
Africa	20	11
Temperate Asia	18	11
Tropical Asia	21	17*
Australasia	39	6
Europe	67	14
Northern America	61	15
Southern America	45	10
Zonobiome		
Boreal	3	0
Continental	8	1
Mediterranean	69	10*
Multiple	50	18
Nemoral	79	19
Subtropical Arid	22	12
Tropical Equatorial	33	17
Tropical Savannah	27	16
Warm Temperate	0	0

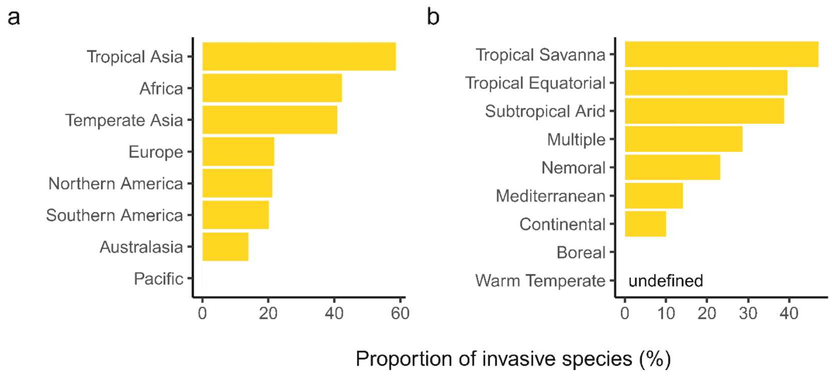

Figure 1. Proportion of invasive species amongst naturalised species in continents (**a**) and in zonobiomes (**b**).

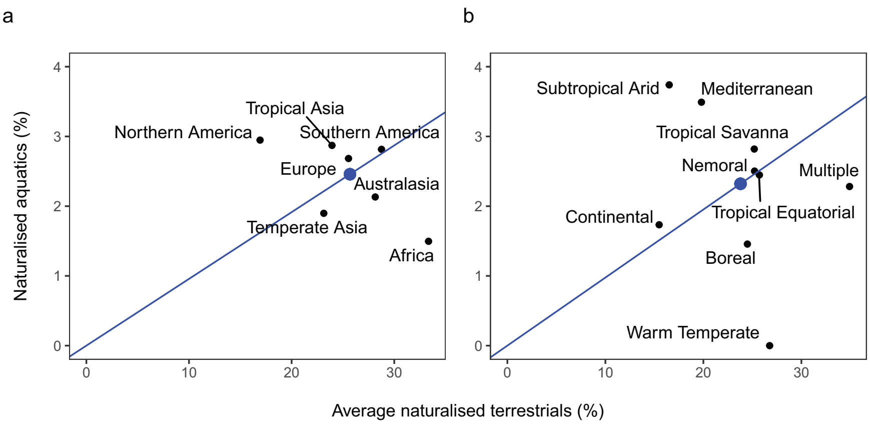

Figure 2. Naturalisation in aquatic habitat compared to terrestrial habitats (mean for all other habitats) by continent (**a**) and zonobiome (**b**). The blue line shows the theoretical linear increase in mean naturalisation in both aquatic habitat and terrestrial habitats, connecting zero and mean naturalisation in each habitat (marked by a blue point).

Table 3. Number of naturalised and invasive species in different habitat types (aquatic, terrestrial) by continents and zonobiomes. Significance is indicated by asterisks (** $P < 0.001$, * $P < 0.05$) and direction by colours: light orange cells show more and blue fewer species than expected by chance, based on the generalised linear models.

Continent	Naturalised aquatic	Naturalised terrestrial	Invasive aquatic	Invasive terrestrial
Africa	20**	1,729	11	319
Temperate Asia	18*	1,420	11*	468
Tropical Asia	21	1,008	17*	208
Australasia	39	2,000	6	183
Europe	67	2,548	14	319
Northern America	64	2,384	15*	196
Southern America	45	1,774	10	313
Zonobiome				
Boreal	3	204	0	5
Continental	9	571	1	98
Mediterranean	70**	2,017	10	231
Multiple	50	2,748	18	520
Nemoral	79	3,243	19	342
Subtropical Arid	22	819	12	146
Tropical Equatorial	33	1,747	17	482
Tropical Savannah	27	1,202	16	217
Warm Temperate	0*	139	0**	90

of invasive species in aquatic compared to terrestrial habitats was lower than expected in Warm Temperate areas, where no invasive aquatic species were recorded in our dataset (Table 3).

Species-area relationships

The species-area relationship highlights that specific regions contain disproportionately more naturalised species than would be expected, based on the area of aquatic habitat in each region. This was most pronounced in New Zealand, Italy, and California. Other regions that fall below this expectation include South Sudan, Papua New Guinea and Kyrgyzstan (Fig. 3).

Species composition

Overall, species composition differed across continents and zonobiomes. All pairs of continents exhibited a high dissimilarity, as revealed by the Jaccard dissimilarity index ranging from 0.73 to 0.92 (Fig. 4a). Tropical Asia and Temperate Asia had the lowest mutual dissimilarity (0.73), followed by Europe and Northern America (0.78), Tropical Asia and Southern America (0.80) and Temperate Asia and Europe (0.81). The most distinct pair of continents was Africa and Australasia (0.92).

In relation to zonobiomes, the dissimilarity ranged from 0.68 to 1.00. The lowest dissimilarity was found between Mediterranean and Nemoral (0.68), followed by Subtropical Arid and Tropical Savannah (0.75) and Nemoral and Tropical Equatorial (0.77). Boreal and Continental, as well as Boreal and Tropical Equatorial zonobiomes differed most from other zonobiomes in their species composition (Fig. 4b).

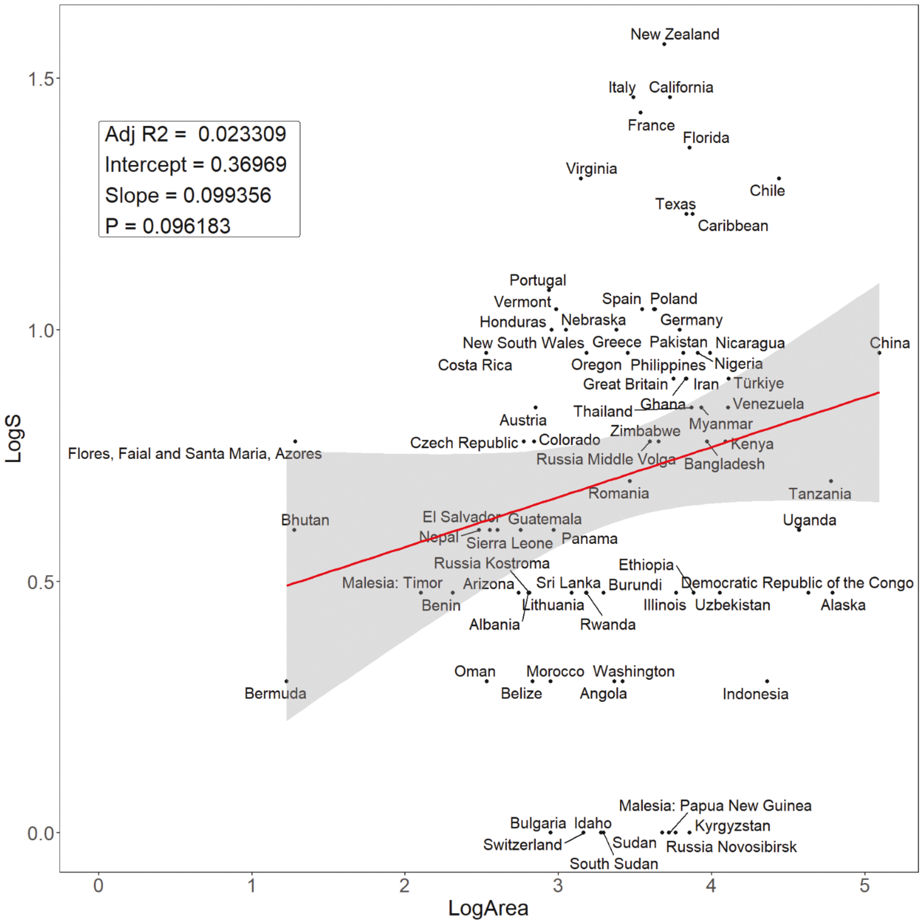

Figure 3. Species-area relationships of aquatic habitats. LogS represents the decadic logarithm of the number of species sampled, while LogArea represents the decadic logarithm of the aquatic habitat area (in km^2) for each region. Grey area denotes 95% confidence interval and the red line represents the regression line.

Indicator species

The most widespread invaders (Table 1, Fig. 5) occurred in at least 25% of the sampled regions. Indicator species analysis identified indicative species of some continents and zonobiomes, as well as certain widespread species that are typical of a combination of two or more continents and zonobiomes. Australasia had the largest number of indicator species (n = 30), while *Ludwigia palustris* (L.) Elliott and *Lagarosiphon major* had the highest significance values. In Europe, *Lemna minuta* Kunth and *Elodea nuttallii* (Planch.) H.St.John were selected as indicator species and, in Northern America, they were *Myriophyllum spicatum* L., *Veronica anagallis-aquatica* L. and *Typha angustifolia* L. (Suppl. material 1: table S2). A single species, *Juncus effusus*, was selected as an indicator of the Boreal zonobiome (Suppl. material 1: table S3). *Elodea canadensis* was selected for the groups of two or more zonobiomes: Mediterranean, Nemoral and for the “Multiple” category, whereas the most widespread species, *Pontederia crassipes*, was indicative of all zonobiomes, except Boreal and Nemoral.

Discussion

Our research sheds light on global patterns of naturalised and invasive plants in aquatic habitats. A considerable number of naturalised non-invasive and invasive species were recorded in tropical regions, raising a concern highlighted

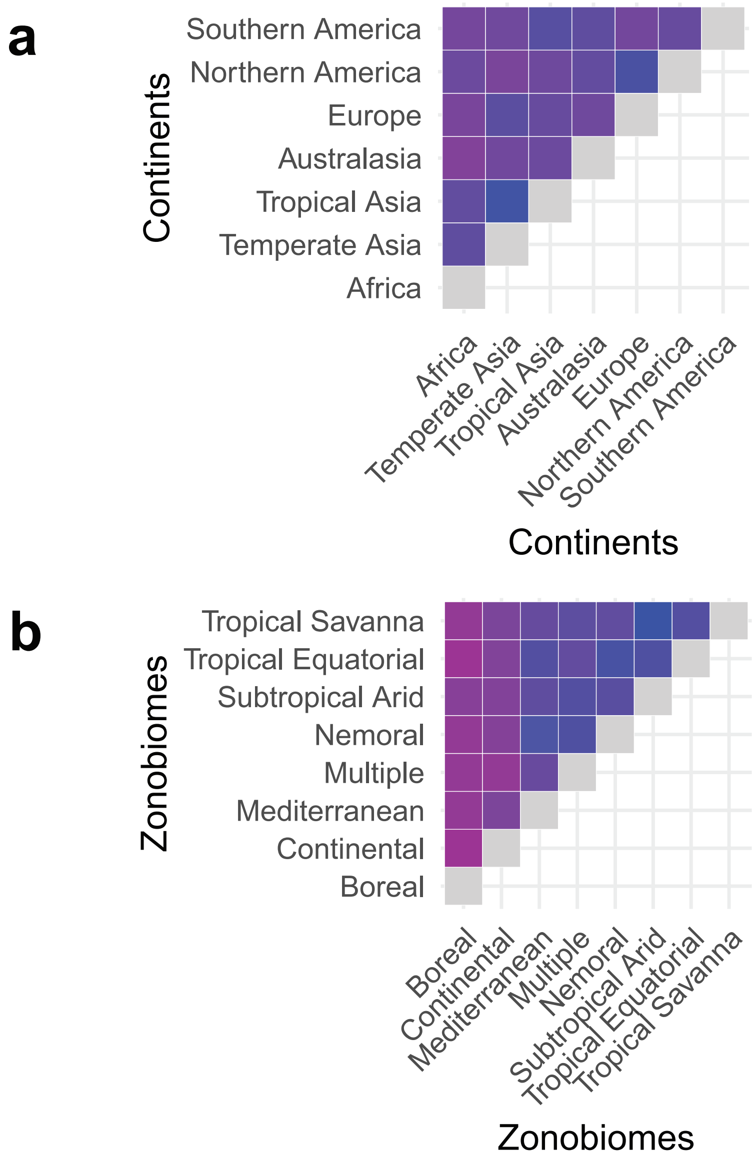

Figure 4. Jaccard dissimilarity of naturalised aquatic species composition. Grey shades represent higher similarity (= lower dissimilarity) amongst sites and purple shows the lowest similarity (= complete dissimilarity) amongst continents (**a**) and zonobiomes (**b**).

by the higher proportion of invasive species within naturalised flora in tropical zonobiomes (Fig. 1). Furthermore, aquatic habitats harbour more invasive species than expected, particularly in Tropical Asia (Table 3), which is consistent with previous findings linking higher numbers of introduced macrophyte species to an increase in both higher annual temperature and higher longitude (Murphy et al. 2019; Lobato-de Magalhães et al. 2023). Moreover, the high number of alien aquatic plants in Tropical Asia is likely a result of a combination of suitable environmental conditions: warm climate, high nutrients and numerous intentional and accidental introductions, combined with a large human influence and deforestation in the area (Wu and Ding 2019).

However, data on global aquatic naturalised flora in the SynHab database remains incomplete. SynHab was not designed exclusively for aquatic habitats and data available in the database do not allow us to distinguish the role of specific

Figure 5. Invasion by *Pontederia crassipes* in Hawaii (**a**) and in the canal in Bayou Chevreuil, Louisiana, USA (**b**); *Pistia stratiotes* in its native range, Argentina (**c**) and in Panama (**d**). Photos by MH and JČ.

finer habitats, such as lakes, rivers and ponds. The aim of SynHab was to collect data on the distribution of naturalised species in habitats worldwide, enabling comparisons amongst them. Therefore, only regions for which there was comprehensive information on affiliations to all habitat types were considered. Thus, data is lacking from many regions of the world. Still, our dataset provides a reasonably thorough account of what is known about naturalised alien species globally, despite the relatively low research effort in aquatic compared to terrestrial habitats (Evangelista et al. 2014; Havel et al. 2015; McKnight et al. 2017). According to the most comprehensive assessment of the world's naturalised flora (Pyšek et al. 2017), aquatic species comprised only 0.9% of the total species reported. The first edition of the GloNAF database (van Kleunen et al. 2019) included 147 taxa, whereas our updated dataset has 183 taxa.

Our SynHab-based analysis reveals that the highest numbers of naturalised aquatic species were recorded in New Zealand, Italy, California and France, i.e. regions with high Gross Domestic Product (GDP), a warm climate and a long history of plant introductions. Research on biological invasions in New Zealand is extensive and a remarkable number of introduced macrophyte species have been previously reported (Lobato-de Magalhães et al. 2023). Hussner (2012) suggested that Italy and France have the highest number of alien aquatic plant species in Europe (34 species each). These two countries are known gateways for alien aquatic species introductions in Europe, especially through aquaculture (Nunes et al. 2014). In addition, France and Italy practise extensive rice cultivation (in the Camargue and the Po Valley, respectively) and species introduced into rice fields can subsequently colonise other aquatic habitats. According to Hussner et al. (2010), the number of alien aquatic plant species has increased rapidly in recent decades, doubling in Germany from 12 to 24 between 1980 and 2009. This has been attributed to an increase in the movement of ship ballast water and the continued popularity of the aquarium trade over the last 50 years, whilst improved monitoring and reporting may also contribute to this observed increase.

The global pattern of aquatic macrophyte distribution suggests that most species have a limited range across the world's ecozones (Murphy et al. 2019, 2020; Lobato-de Magalhães et al. 2023). Our study also reveals, despite the data limitations in SynHab, that naturalised species tend to be region-specific, exhibiting high dissimilarity between continents and zonobiomes (Fig. 4). More specifically, we identified distinct species indicative of specific continents and zonobiomes (Suppl. material 1: tables S2, S3). Some indicator species occur in similar environments that match those in their native range, such as *Juncus effusus*, invading in the boreal zonobiome and native to temperate regions. However, a subset of ~ 1.2% of the total macrophyte species have broad ranges (Murphy et al. 2019). For instance, *Pontederia crassipes* was sampled in 36.8% of the world's 238 grid cells 10 × 10° (latitude × longitude) in size covering the aquatic habitat area (Lobato-de Magalhães et al. 2023). Our results show that certain species serve as indicators for invaded regions that are climatically different from their native ranges, which is expected, as aquatic species may be less limited by climatic conditions than terrestrial species. *Pontederia crassipes*, the most widespread species in our dataset, is native to southern tropical America and primarily grows in the wet tropical biome. However, *P. crassipes* has been assigned as indicative not only of Tropical Equatorial and Tropical Savannah, as expected, but also of Continental, Mediterranean, Multiple and Subtropical Arid zonobiomes. *Pistia stratiotes*, native to the Tropics and Subtropics and primarily also growing in the wet tropical biome, is an indicator of Tropical Savannah and has expanded into Subtropical Arid and Continental zonobiomes. *Elodea canadensis*, native to southern Canada and the United States, mostly in the Temperate zonobiome, is indicative of Nemoral and Mediterranean, and zonobiomes classified as Multiple.

Invasive alien macrophytes are considered more successful than native macrophytes due to the absence of natural enemies or competitors, higher tolerance to eutrophication and altered hydrology (Coetzee and Hill 2012). Moreover, higher temperatures are expected to increase the invasibility of temperate habitats by tropical macrophytes (Adebayo et al. 2011). An increase in temperature, CO_2 and nutrients can potentially benefit emergent and floating macrophytes (Lind et al. 2022). Indeed, *P. crassipes* and *P. stratiotes* (both floating macrophytes) are more widely distributed than other species and disperse easily. The distribution patterns of these species, as revealed in our study, suggest variation in the plasticity of their invasiveness. Lind et al. (2022) suggested that submerged macrophytes may be negatively affected by climate change and other anthropogenic pressures. However, in our study, the submerged macrophyte *E. canadensis* was reported across multiple zonobiomes, suggesting we should not underestimate the capacity of submerged macrophytes to respond positively to global change.

Projected climate change impacts pose future challenges, notably the emergence of invasion hotspots, particularly in the United States, north-eastern Europe, southwest Australia and New Zealand (Bellard et al. 2013; Gillard et al. 2017). Conversely, Indonesia, Pacific islands, central Africa and southern Brazil are predicted to be less affected (Bellard et al. 2013). This projected pattern suggests a greater increase in invasive species in the Northern Hemisphere compared to the Southern Hemisphere, with tropical regions potentially exhibiting lower invasibility (Bellard et al. 2013). While Bellard et al. (2013) focused on a limited number of aquatic species, more recent work modelling future invasive macrophyte distributions has indicated suitable habitat expansion in Europe and North America (Gillard et al. 2017), specifically for three aquatic plant taxa (*Elodea densa*, *Myriophyllum aquaticum* and *Ludwigia* spp.). Our results highlight the presence of invasive species in tropical aquatic habitats. Further efforts to document naturalised species, especially in tropical regions, are essential to disentangle the risk of invasion in the Tropics by alien species.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Use of AI

No use of AI was reported.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Complete results of the indicator species analysis

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Data type: docx

Explanation note: **table S1.** List of regions with data (region, continent, type of data extraction = literature/collaboration; data sources; data provider in case of collaboration). **table S2.** Indicator species selected for a continent or a group of continents. **table S3.** Indicator species selected for a zonobiome or a group of zonobiomes.

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