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REVIEW

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Quantifying the ecological impacts of alien aquatic macrophytes: A global meta-analysis of effects on fish, macroinvertebrate and macrophyte assemblages

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Abstract

1. Biological invasions constitute a pervasive and growing threat to the biodiversity and functioning of freshwater ecosystems. Macrophytes are key primary producers and ecosystem engineers in freshwaters, meaning that alien macrophyte invasions have the capacity to alter the structure and function of recipient aquatic ecosystems profoundly. Although prevailing wisdom holds that alien macrophyte invasions tend to compromise freshwater ecosystem structure and function, the ecological impacts of alien macrophyte invasion have not been quantitatively reviewed to date.
2. Here we present a global meta-analysis of 202 cases from 53 research articles, exploring the impacts of alien macrophyte invasion on the abundance and diversity of three ubiquitous and ecologically important focal groups, which together comprise the bulk of non-microbial freshwater biodiversity: resident macrophytes, macroinvertebrates and fish. Our synthesis includes data from all continents except Antarctica and Asia, covering 25 alien macrophyte species, but reveals considerable taxonomic and geographical biases in knowledge.
3. Meta-analysis results reveal that invasion by alien macrophytes has an overall negative impact on taxonomic diversity of the three focal groups, but no consistent effect on abundance. At a finer resolution, we detect a strong negative effect of alien macrophyte invasion on resident macrophyte abundance and diversity, and a significant but smaller positive effect of submerged alien macrophyte invasion on macroinvertebrates. Effects on fish appear inconsistent.
4. Our findings emphasise the importance of context- and taxon-specific ecological research in informing appropriate and proportionate management of alien macrophyte invasions, since alien macrophyte impacts are not consistently negative. We also identify significant geographical and taxonomic limitations in existing studies, quantitative data being lacking for many alien taxa.

KEYWORDS
abundance, aquatic plants, biological invasions, diversity, invasive species

1 | INTRODUCTION

In the Anthropocene, alien species have become near-ubiquitous components of biological assemblages across the world (Keller et al., 2011; Lewis & Maslin, 2015). Invasion by alien species can disrupt ecosystem composition and function, with knock-on effects for the provision of ecosystem services and the resilience of the system to subsequent environmental change (Hershner & Havens, 2008; Pejchar & Mooney, 2009; Strayer et al., 2006). Losses and expenditures associated with biological invasions are estimated to have cost the global economy US$1.288 trillion since 1970, and continue to mount (Diagne et al., 2021). Biological invasions often act synergistically with other anthropogenic stressors, replacing geographically restricted species with a small number of globally successful invaders and homogenising regional biotas (McKinney & Lockwood, 1999; Olden et al., 2018; Petsch et al., 2022). Such biotic homogenisation may be accelerated by *invasional meltdown*, wherein invasion by one alien species facilitates the invasion of other non-natives (Simberloff & Von Holle, 1999). Alien invasions are the driver most frequently associated with amphibian, reptile, and mammal extinctions on the IUCN Red List, and the second- and fourth-most frequent driver of bird and plant extinctions respectively (Bellard et al., 2016).

The deleterious impacts of a handful of particularly problematic invaders may, however, overshadow the relatively benign nature of most alien species, skewing the perspective of conservation biologists and land managers (Davis et al., 2011; Schlaepfer et al., 2011). In some instances, aliens may not themselves be agents of degradation, but rather ride on the coat-tails of more insidious stressors (e.g. nutrient enrichment, habitat destruction) (Didham et al., 2005; Macdougall & Turkington, 2005). Therefore, whilst complete protection of near-pristine areas should clearly remain a priority, it is unfeasible, and perhaps even counter-productive, to apply this approach to the heavily modified ecosystems now covering much of the Earth (Dudgeon, 2020). Conservationists and land managers must instead develop proportionate and cost-effective strategies for the conditional management of alien species, accounting objectively for the risks posed by a given invader. In this respect, quantitative meta-analysis of primary ecological research represents a powerful tool, reaching beyond potential bias to assess the typical impacts of alien species, as well as gaps in our current knowledge (Gurevitch et al., 2018; Vilà et al., 2011).

Freshwaters are arguably more invasible than most terrestrial ecosystems, owing in part to high propagule pressure from uniquely aquatic vectors (e.g. the ornamental aquatics trade; the release of ballast water), the comparative ease of dispersal through interconnected drainage systems (Moorhouse & Macdonald, 2015) and the anthropogenic depletion of pre-existing biota, all of which facilitate the spread of invaders (Dudgeon, 2020; Strayer, 2010; Tilman, 2004). Freshwaters are also disproportionately diverse, hosting almost 10% of all described non-microbial species despite covering less than 1% of the Earth's surface (Dudgeon, 2020). The insular, island-like nature of freshwater systems, with high endemism and high species turnover between basins, means that many freshwater taxa are disproportionately vulnerable to extinction. The impact of invasive species is considered a key driver in many such extinctions (Dudgeon, 2020; Moorhouse & Macdonald, 2015; Strayer & Dudgeon, 2010).

Alien macrophyte invasion may drive particularly drastic shifts in freshwater ecosystem composition and function, since macrophytes—photosynthetic aquatic organisms visible with the naked eye (Chambers et al., 2007)—are key primary producers (Lodge, 1991; Newman, 1991) and ecosystem engineers (Carpenter & Lodge, 1986; Thomaz & Cunha, 2010; Warfe & Barmuta, 2006). Physicochemical microhabitats with distinct light, temperature, and dissolved oxygen and nutrient concentrations are maintained within macrophyte beds, and attenuated water movement promotes the deposition of fine sediment and retention of detritus (Carpenter & Lodge, 1986; Carter et al., 1991; Miranda et al., 2000; Ondok et al., 1984). Decaying macrophytes leach dissolved organic carbon, phosphorus, and nitrogen into the water column, whilst microbial decomposition of macrophyte detritus may lead to localised oxygen depletion (Carpenter & Lodge, 1986; Carter et al., 1991; Landers, 1982; Miranda et al., 2000; Ondok et al., 1984). Alongside these physicochemical effects, macrophytes are key to an array of biotic interactions. They are colonised by diverse epiphytic assemblages which often make a contribution to productivity and nutrient exchange comparable to that of the macrophyte itself (Allen, 1971; Cattaneo & Kalff, 1980; Sheldon & Boylen, 1975). In addition, protection from predators and abundant food (e.g. epiphyton, live macrophyte tissue, detritus, animal prey) within macrophyte beds attracts macroinvertebrates and fish in higher densities than are found in adjacent unvegetated habitats (Hatzenbeler et al., 2000; Killgore et al., 1989; Schramm & Jirka, 1989; Strayer et al., 2003; Thorp et al., 1997).

Schultz and Dibble (2012) qualitatively reviewed alien macrophyte impacts, identifying changes to habitat structure, oxygen depletion, the release of allelopathic compounds, and facilitation of other alien species as major drivers of ecosystem change following invasion. Habitat structure may be altered dramatically by alien macrophyte invasion due to the tendency of many alien species to form dense, monotypic stands. Where such stands increase plant biomass and structural complexity, macroinvertebrate density may increase (Kuehne et al., 2016), whilst the foraging efficiency of larger predators is compromised (Theel & Dibble, 2008). Dense alien macrophyte canopies may also decrease atmospheric exchange with water, reducing dissolved oxygen concentrations and further impairing predator foraging efficiency (Caraco & Cole, 2002; Troutman et al., 2007). Allelochemicals exuded by alien macrophytes have been demonstrated to reduce lepidopteran larval growth and feeding (*Elodea nuttallii*: Erhard et al., 2007), stickleback larval foraging (*Myriophyllum spicatum*: Lindén & Lehtiniemi, 2005), and the germination and growth of native macrophyte competitors (*Ludwigia* spp.: Dandelot et al., 2008; Thiébaut et al., 2018). Alien macrophytes have also been demonstrated to facilitate the invasion of non-native species, including mussels (Michelan et al., 2014; Wegner et al., 2019), crayfish (Thouvenot et al., 2017), and other macrophytes (Monks et al., 2019). Many of these impacts are contingent on the growth form of the alien

macrophyte in question. For instance, floating-leaved and free-floating macrophytes are most likely to form hypoxia-inducing closed canopies (Caraco & Cole, 2002), whereas, due to a relatively higher proportion of biomass suspended in the water column, submerged macrophytes might be expected to have the greatest effect on aquatic habitat complexity post-invasion (Kuehne et al., 2016). The growth form of an alien macrophyte also determines to a great extent which habitats it is able to invade, although many invasive aliens exhibit growth form plasticity, enabling successful invasion of suboptimal habitats (Hussner et al., 2021).

Although prevailing wisdom holds that alien macrophyte invasions tend to compromise freshwater ecosystem structure and function (Brundu, 2014; Dudgeon, 2020; Fleming & Dibble, 2015), there is considerable variability in the impacts of alien macrophyte invasion, with some invasions having a negligible or even apparently beneficial effect on recipient native taxa. Despite selection bias arising from disproportionate focus on the most problematic non-native taxa (Evangelista et al., 2014), alien macrophyte invasions have been associated variously with elevated native macrophyte diversity (Kuehne et al., 2016) and the promotion of rare native plant taxa (Smith & Buckley, 2015); elevated invertebrate density (Hogsden et al., 2007; Toft et al., 2003) and diversity (Kuehne et al., 2016), and increased fish biomass (Barrientos & Allen, 2008; Bickel & Closs, 2008). Clearly, the impacts of alien macrophyte invasion are not consistently negative, and warrant thorough quantitative review.

A recent meta-analysis by Gallardo et al. (2016) reviewing the impacts of aquatic biological invasions found that invasion by alien primary producers significantly reduced macrophyte diversity and fish and macroinvertebrate abundance. Due to the inclusion of non-macrophyte taxa (e.g. microalgae) and brackish-water systems in their analyses, the typical impacts of alien macrophyte invasion in freshwaters remain unclear, however. In addition, these authors did not explore the differential effect of alien growth form on native assemblages. Here, we present a focused meta-analysis of primary research investigating the effects of alien aquatic macrophyte invasion on three well-studied freshwater focal taxa: resident macrophytes, macroinvertebrates, and fish. Our analyses also investigate the influence of growth form (submerged, emergent, or floating) on the ecological impacts of alien macrophytes, and the specific impacts of the best-studied alien macrophyte taxa. We explore the taxonomic and geographical coverage of studies in our database to contextualise our results and investigate the biogeography of alien macrophyte invasions and the generalisability (and potential limitations) of work conducted to date.

2 | METHODS

2.1 | Literature search

2.1.1 | Identification of relevant literature

We conducted a literature search for research investigating the effects of alien macrophyte invasion on macrophyte, macroinvertebrate, and fish assemblages. A search conducted on Scopus (Elsevier Co.) for titles, abstracts or keywords containing the terms "inva* OR alien OR 'non native' OR exotic OR introduc* PRE/2 macrophyte OR plant OR weed AND freshwater OR aquatic OR stream OR river OR wetland OR pond OR lake OR reservoir AND abundance OR cover OR density OR biomass OR richness OR diversity" yielded 1,672 results. We included all published records up to 31 December 2020 within the subject areas of environmental/agricultural and biological sciences. After screening of search results (titles/abstracts) and supplementary searching of the bibliographies of retrieved articles, 192 articles (published 1982–2020) were individually assessed against our criteria for inclusion.

2.1.2 | Criteria for inclusion

To meet the criteria for inclusion, articles were required to report the impact of alien aquatic macrophyte invasion on the abundance and/or taxonomic diversity of one or more focal taxa (resident macrophytes, macroinvertebrates, fish) in freshwaters. Invasive native species were excluded, except where a non-native lineage had been implicated in the invasion, e.g. *Typha x glauca* and *Phragmites australis* in North America (Saltonstall, 2002; Travis et al., 2010). Articles were also required to report the mean and standard error/standard deviation of effect size and number of invaded and control sites (>1), in tabular or graphical form. Where summary statistics were only available in graphical form (>50% of articles), we used WebPlotDigitizer v4.4 (Rohatgi, 2020) to extract the necessary data.

2.1.3 | Database collation

The resulting database collates results from 53 articles representing 202 cases of ecological impact (Table S4). Studies span 25 species of alien macrophyte (Table 1), encompassing 116 effects on macroinvertebrates, 56 effects on macrophytes and 30 effects on fish. Most of the studies in our database were conducted in North America (141 cases).

In addition to recording summary statistics, we classified studies according to:

- Alien macrophyte growth form: submerged, floating (sediment-rooted with floating leaves and/or free-floating), emergent.
- Habitat: lotic (rivers, streams); lentic (ponds, lakes, backwaters, reservoirs); wetland (defined as the boundary area between open water and dry land).
- Climate: subtropical, temperate, tropical.
- Study type: observational (field studies); manipulative (field experiments); mesocosm (experiments in aquaria/outdoor tubs).
- Control type: analogous uninvaded site; before–after invasion; treated plot (wherein alien is subjected to control or eradication technique); native vegetation; no vegetation.

Following Gallardo et al. (2016), we considered each treatment: control comparison as a separate case in our database where data

TABLE 1 Alien macrophyte species of each growth form included in the complete dataset

Submerged		Floating		Emergent	
Myriophyllum spicatum	40, 7	*Eichhornia crassipes*	14, 3	*Typha* spp.	32, 14
Hydrilla verticillata	39, 10	*Hydrocharis morsus-ranae*	6, 1	*Phragmites australis*	13, 5
Lagarosiphon major	7, 2	*Trapa natans*	4, 2	*Hymenachne amplexicaulis*	9, 1
Cabomba caroliniana	4, 1	*Pistia stratiotes*	3, 1	*Urochloa mutica*	8, 1
Elodea canadensis	3, 1	*Azolla filiculoides*	2, 1	*Myriophyllum aquaticum*	6, 3
Ranunculus fluitans	3, 1	*Ceratopteris thalictroides*	1, 1	*Lythrum salicaria*	2, 2
Egeria densa	1, 1	*Hydrocotyle ranunculoides*	1, 1	*Ludwigia grandiflora*	1, 1
		Lemna minuta	1, 1		
Total	99, 23	Total	32, 11	Total	71, 27

Note: Values *a*, *b* correspond to: (*a*) the number of cases of ecological impact recorded for each macrophyte species; (*b*) the number of articles from which these cases were sourced.

from multiple control groups (e.g. both native vegetation and no vegetation) were reported in an article. Where multiple treatment groups of varying alien density were reported, we used only data from the highest alien-density treatment, and where multiple sampling dates were reported, we used only data from the last available date.

2.2 | Data analysis

2.2.1 | Coverage

We explored the coverage of our database by study region, climate, habitat type, study type, and alien species identity to assess the generalisability of our findings across taxa, habitats, and regions and to investigate gaps in knowledge of alien macrophyte invasions.

2.2.2 | Effect size calculation and preliminary analyses

For each case of alien macrophyte impact, we calculated effect sizes using Hedge's g, a measure of standardised mean difference (SMD) that is not biased by small sample sizes (Hedges, 1981; Lüdecke, 2019; R Core Team, 2020):

$$\text{Hedge's } g = \frac{\text{treatment mean} - \text{control mean}}{\text{pooled standard error}} \times \text{weighting factor (based on no. of replicates)}$$

Hedge's *g* is unitless and ranges from −∞ to +∞, with the value's magnitude and sign corresponding respectively to the size and direction of the effect.

In the literature, the effects of alien macrophyte invasion were often reported using different measures of abundance (density, biomass, cover, catch-per-unit-effort) and diversity (taxa richness, Simpson's index, Shannon's index). Since resulting effect sizes were not significantly different (Table S1), metrics were pooled under abundance and diversity, respectively.

2.2.3 | Meta-analysis

Using restricted maximum likelihood estimation, we ran multi-level random-effects (MLRE) models in R-package *metafor* (Viechtbauer, 2020) to assess the impact of alien macrophyte invasion on our three focal taxa: resident macrophytes, macroinvertebrates and fish. A multi-level structure (with cases nested within articles) was employed in these models to account for non-independence arising where multiple effect sizes were extracted from the same study (Cheung, 2019; Habeck & Schultz, 2015; Harrer et al., 2019a, 2019b).

Preliminary analyses revealed contrasting effects of alien macrophyte invasion on resident macrophytes, macroinvertebrates and fish. Therefore, we proceeded to analyse each focal taxon independently, alongside all-taxon *grand mean* analysis.

We ran an additional set of MLRE models to test the effects of growth form on the ecological impacts of alien macrophytes, and another set to examine the ecological impacts of the specific alien macrophyte taxa most highly represented in our database: *Typha* spp. (*Typha angustifolia*, *T. x glauca* [Typhaceae]), *P. australis* (Poaceae), *M. spicatum* (Haloragaceae), and *Hydrilla verticillata* (Hydrocharitaceae) and submerged macrophytes excl. *M. spicatum*/*H. verticillata*. To maintain statistical power for these subgroup analyses, we aggregated abundance and diversity results for each focal taxon/growth form (Coetzee et al., 2014; Gallardo et al., 2016). Furthermore, we included only those subgroups with at least 10 effect sizes from at least three articles (Habeck & Schultz, 2015).

Between-study heterogeneity was assessed for each dataset using *Q* and I^2 statistics (Harrer et al., 2019a, 2019b). A significant *Q* value indicates the presence of significant heterogeneity in the dataset,

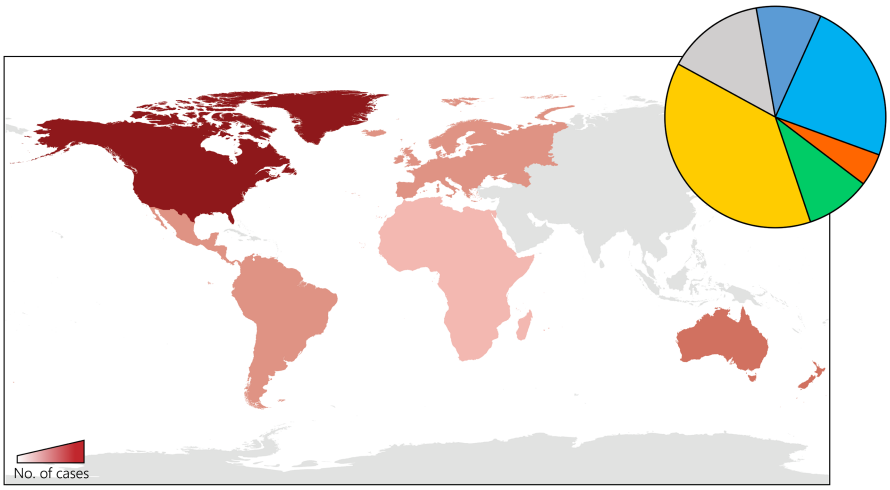

FIGURE 1 Number of cases from each continent included in our meta-analysis, and the biogeographic origins of the alien macrophytes upon which these studies focus: Nearctic (■); Palearctic (■); Oriental (■); Ethiopian (■); Neotropical (■); Cosmopolitan (■).

unaccounted for by the model. I^2 represents the percentage of variability in effect sizes not caused by sampling error. An I^2 value exceeding 75% indicates substantial heterogeneity (Higgins et al., 2003), but it is worth noting that I^2 values are typically higher than 75% in most ecological and evolutionary meta-analyses due to the intrinsic variability of the study systems (Senior et al., 2016). In an attempt to explain residual heterogeneity, we ran duplicate MLRE models separately incorporating the following moderators: control type nested within study type; habitat; climate; alien species identity. The addition of these covariates did not consistently increase the explanatory power of our models (likelihood ratio test, $p > 0.05$; Table S2), however, so we proceeded using the original (reduced) MLRE models wherein cases were nested within articles, with no additional covariates.

Meta-analyses may be distorted by the *file-drawer problem*, a form of publication bias wherein non-significant results (particularly those resulting from studies with small sample sizes) are less likely to reach publication. To assess whether the file drawer problem affected our meta-analyses, we evaluated plots using Egger's test (Egger et al., 1997) by modifying models to include the variance of the effect sizes as a moderator. Analyses were considered biased where the intercept of this model differed significantly from zero ($p < 0.1$). Meta-analyses may also be distorted by a handful of highly influential cases. To evaluate whether pooled results were skewed by the presence of influential cases, we conducted leave-one-out analyses, iteratively removing one case at a time and recalculating the pooled effect size in its absence. We defined influential cases as those with DFBETAs (differences in β values) above 1 (Viechtbauer & Cheung, 2010). Where a case exceeded this cut-off, we conducted a sensitivity analysis, running the relevant MLRE model again with the case in question removed.

3 | RESULTS

3.1 | Geographical, taxonomic, and methodological coverage

The invasions included in our meta-analyses occur largely in North America (70% of cases; Figure 1), although Central and South America are also well represented. Palaeotropical coverage is poor, reflecting the comparative dearth of published quantitative ecological research on alien macrophyte invasions in these regions. Studies focus mostly on shallow wetlands and lentic ecosystems such as lakes and river backwaters, leaving lotic systems underrepresented (12% of cases). Only five cases in our database are drawn from invasions of small waterbodies such as ponds and streams (Table S3). Manipulative field experiments and mesocosm trials make up only 24% of cases in our database, with the remaining three-quarters drawn from observational studies.

Although our database includes 25 species of alien macrophyte, *Typha* spp., *H. verticillata*, and *M. spicatum* together contribute more than half of the cases included (Table 1). Other well-studied aliens include *P. australis* and *Eichhornia crassipes* (Pontederiaceae). Alien macrophyte taxa in our database mostly originate in the tropics, particularly the Neotropical region (eight species). Only eight species in our database originate from the Holarctic.

3.2 | Meta-analyses

We found a significant negative overall effect of alien macrophyte invasion on all-taxon diversity, whilst the effect on all-taxon abundance was non-significant. Alien macrophytes caused significant reductions to resident macrophyte abundance and diversity, but had no significant pooled effect on macroinvertebrate abundance, macroinvertebrate diversity, fish abundance, or fish diversity (Figure 2; Table 2). Influence analyses indicated the presence of influential outlying cases in macroinvertebrate diversity and fish abundance meta-regressions. Following the removal of these cases (1 from each dataset), models were recalculated to assess the robustness of our initial findings. Whilst the effect of alien macrophyte invasion on macroinvertebrate diversity remained non-significant (mean estimate = 0.37; 95% CI = −0.1, 0.83; $p > 0.05$), fish abundance became negatively correlated with alien macrophyte invasion (mean estimate = −0.4; 95% CI = −0.73, −0.08; $p < 0.05$). We detected evidence of publication bias (*file-drawer problem*) in the datasets evaluating overall diversity ($p = 0.009$) and macroinvertebrate diversity ($p = 0.06$). A significant amount of residual heterogeneity remained unexplained for all models (Table 2).

When split by growth form, emergent alien macrophyte invasion had a strong negative impact on resident macrophytes (aggregated abundance and diversity), whilst submerged alien macrophyte invasion had a smaller positive effect on macroinvertebrates (Figure 3, Table 3). To determine whether this positive effect was an artefact of comparison with unvegetated control sites, we repeated the model including only those results wherein the macroinvertebrates amongst alien vegetation were compared to those amongst native vegetation (55 of 65 cases), finding a similarly positive effect (mean estimate = 0.46; 95% CI 0.09, 0.89, $p < 0.05$). Submerged alien macrophyte invasion had no significant effect on resident macrophytes nor fish. Floating and emergent alien macrophytes had no significant effect on macroinvertebrates ($p > 0.05$). We excluded effects of emergent alien macrophytes on fish, effects of floating alien macrophytes on fish and effects of floating alien macrophytes on macrophytes from these subgroup analyses due to insufficient data (see Methods). We detected no evidence of influential outlying cases nor publication bias in these analyses. A significant amount of residual heterogeneity remained unexplained for all models, however (Table 3).

When split by alien species identity, invasion by emergent *Typha* spp. caused strong resident macrophyte declines, whilst *P. australis* caused weaker but still significant resident macrophyte declines (aggregated abundance and diversity). Invasion by submergent *M. spicatum* and *H. verticillata* had significant (but somewhat weaker) positive effects on macroinvertebrates. Invasion by *H. verticillata* had a non-significant impact on fish. With *M. spicatum* and *H. verticillata* removed from the subgroup, remaining submerged macrophytes had no significant impact on macroinvertebrates (Figure 4, Table 4). We could not analyse the effects of *Typha* spp. or *P. australis* on fish and macroinvertebrates, the effects of *M. spicatum* on fish and macrophytes or the effects of *H. verticillata* on macrophytes in these subgroup analyses due to insufficient data. We found evidence of publication bias in the other submerged aliens: macroinvertebrates dataset. We also detected two influential outlying cases in the *H. verticillata*: macroinvertebrates dataset. Following removal of these influential cases, the impact of *H. verticillata* invasion on macroinvertebrates remained significantly positive (mean estimate = 0.43; 95% CI = 0.03, 0.83; $p < 0.05$). A significant amount of residual heterogeneity remained unexplained for all models (Table 4).

4 | DISCUSSION

Alien macrophyte invasions are often perceived as wholly negative for native freshwater assemblages (Brundu, 2014; Fleming & Dibble, 2015; Hussner et al., 2017), and indeed, our meta-analyses demonstrate that, in the literature we review, alien macrophytes have an overall negative impact on the taxonomic diversity of invaded assemblages (although impacts on abundance are inconsistent). At a finer resolution, however, our meta-analyses reveal a more nuanced picture. We detected a significant negative relationship between alien macrophyte invasion and resident macrophyte abundance and diversity, but found no significant, consistent effect on fish or macroinvertebrate abundance or diversity. Split by alien macrophyte growth form, we found a strong negative effect of emergent alien macrophytes on resident macrophytes, but a significant positive effect of submerged alien macrophytes on macroinvertebrates. Split by alien species identity, *Typha* spp. and *P. australis* had significant negative effects on macrophytes, whilst *M. spicatum* and *H. verticillata* had significant positive impacts on macroinvertebrates. The consistently high residual heterogeneity of our meta-regression models illustrates the prevalence of context-dependent variation in the responses of freshwater biota

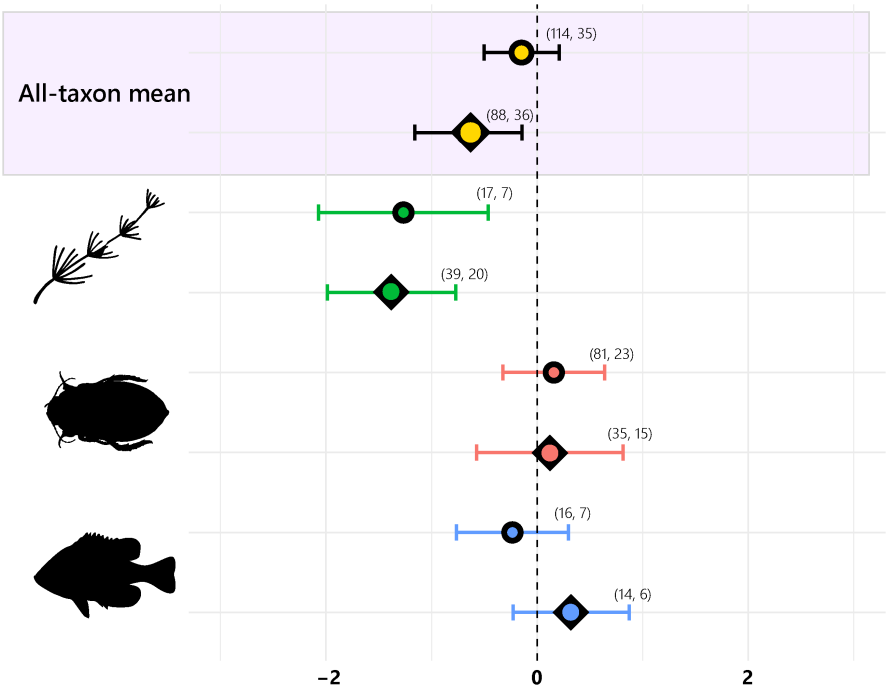

FIGURE 2 Effects of invasive alien macrophytes on the abundance (●) and diversity (◆) of macrophyte, macroinvertebrate and fish assemblages. Means are taken from standardised mean difference (Hedge's g) of treatment and control groups. Error bars represent 95% confidence intervals. Values in parentheses (*a*, *b*) represent: (*a*) the number of effect sizes used in the model; (*b*) the number of articles from which the effect sizes were sourced. Credit to Maxime Dahirel (https://creativecommons.org/licenses/by/3.0/) and Sergio A. Muñoz-Gómez (https://creativecommons.org/licenses/by-nc-sa/3.0/) for taxa illustrations.

TABLE 2 Multilevel random effects models assessing the impacts of alien macrophyte invasion on abundance and diversity of macrophyte, macroinvertebrate, and fish assemblages

Focal taxon	Response variable	Mean effect	95% CI	*p*	Heterogeneity statistics
All-taxon	Abundance	−0.15	−0.50, 0.21	ns	$Q = 873.03$, $df = 113$, $p < 0.0001$; $I^2 = 90.31\%$
	Diversity	−0.65	−1.16, −0.14	*	$Q = 710.34$, $df = 87$, $p < 0.0001$; $I^2 = 92.85\%$
Macrophytes	Abundance	−1.27	−2.07, −0.46	**	$Q = 91.48$, $df = 16$, $p < 0.0001$; $I^2 = 88.55\%$
	Diversity	−1.38	−1.99, −0.77	***	$Q = 322.26$, $df = 38$, $p < 0.0001$; $I^2 = 91.02\%$
Macroinvertebrates	Abundance	0.16	−0.32, 0.64	ns	$Q = 628.25$, $df = 80$, $p < 0.0001$; $I^2 = 89.56\%$
	Diversity	0.12	−0.57, 0.82	ns	$Q = 124.35$, $df = 34$, $p < 0.0001$; $I^2 = 84.57\%$
Fish	Abundance	−0.23	−0.76, 0.30	ns	$Q = 56.41$, $df = 15$, $p < 0.0001$; $I^2 = 85.84\%$
	Diversity	0.32	−0.23, 0.87	ns	$Q = 73.78$, $df = 13$, $p < 0.0001$; $I^2 = 84.93\%$

Note: *Q* (and its associated *p*-value) and I^2 provide estimates of residual heterogeneity. An I^2 value exceeding 75% indicates substantial residual heterogeneity.
$^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

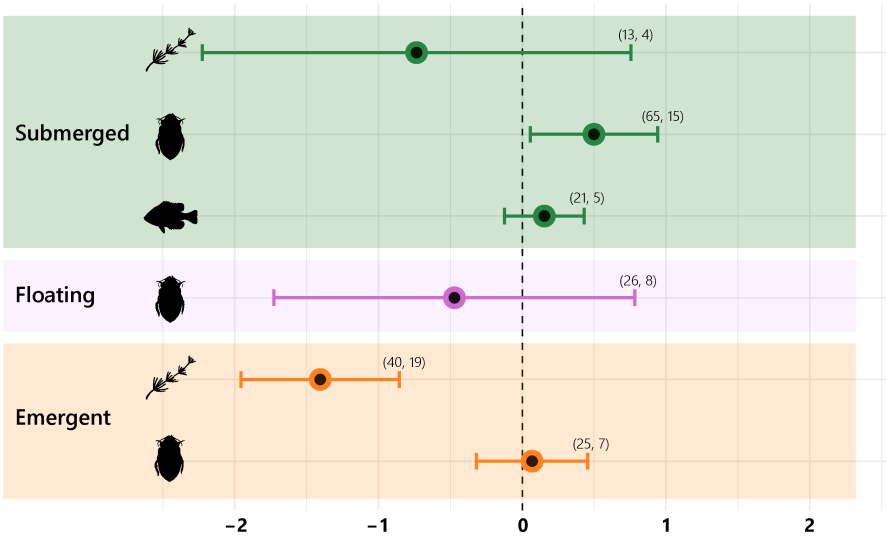

FIGURE 3 Response of resident macrophyte, macroinvertebrate and fish assemblages to submerged (■), floating (■), and emergent (■) alien macrophytes. Error bars represent 95% confidence intervals. Values in parentheses (*a*, *b*) represent: (*a*) the number of effect sizes used in the model; (*b*) the number of articles from which the effect sizes were sourced. Abundance and diversity results are pooled for each subgroup.

to alien macrophyte invasion. Some of this heterogeneity may also arise due to lags between alien macrophyte arrival and the onset of invasive proliferation, with consequent delayed impacts on resident biota (Crooks, 2005). Our findings challenge the notion that alien macrophyte impacts are consistently negative (Goodenough, 2010), and reiterate the need to consider environmental context, growth form and species identity in assessments of alien macrophyte threat.

Most of the invasions included here occurred in North America. This is chiefly a reflection of the comparative dearth of quantitative studies meeting our criteria that have been conducted elsewhere. Most of the alien macrophyte species included in our meta-analyses originate in the tropics, particularly the Neotropical realm—a macrophyte diversity hotspot (Murphy et al., 2019).

4.1 | Macrophytes

Despite considerable heterogeneity in the response of resident macrophytes to aliens, we detected a strong association between alien macrophyte invasion and the degradation of macrophyte assemblages. This effect, however, is chiefly driven by emergent

TABLE 3 Multilevel random effects models assessing the influence of growth form on the ecological impacts of alien macrophyte invasion

Focal taxon	Alien growth form	Mean effect	95% CI	*p*	Heterogeneity statistics
Macrophytes	Submerged	−0.74	−2.23, 0.76	ns	$Q = 142.84$, $df = 12$, $p < 0.0001$; $I^2 = 94.31\%$
	Emergent	−1.41	−1.96, −0.85	***	$Q = 258.24$, $df = 39$, $p < 0.0001$; $I^2 = 89.24\%$
Macroinvertebrates	Submerged	0.5	0.06, 0.94	*	$Q = 430.51$, $df = 64$, $p < 0.0001$; $I^2 = 87\%$
	Floating	−0.47	−1.73, 0.78	ns	$Q = 226.50$, $df = 25$, $p < 0.0001$; $I^2 = 91.57\%$
	Emergent	0.07	−0.32, 0.46	ns	$Q = 62.09$, $df = 24$, $p < 0.0001$; $I^2 = 57.43\%$
Fish	Submerged	0.15	−0.12, 0.43	ns	$Q = 53.87$, $df = 20$, $p < 0.0001$; $I^2 = 62.54\%$

Note: Q and I^2 provide estimates of residual heterogeneity. An I^2 value exceeding 75% indicates substantial residual heterogeneity. Abundance and diversity results are pooled for each subgroup.
$^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

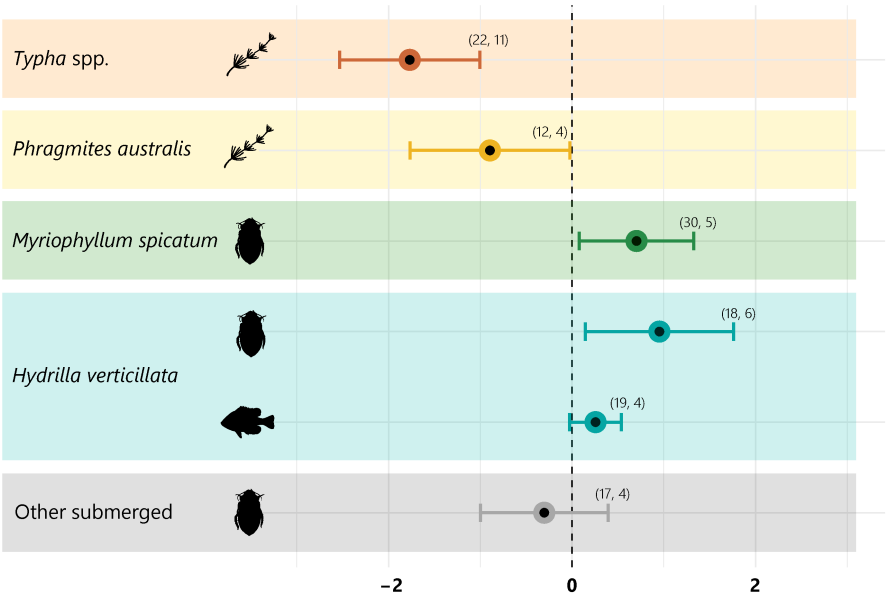

FIGURE 4 Effects of the alien macrophytes *Typha* spp. (■), *Phragmites australis* (■), *Myriophyllum spicatum* (■), *Hydrilla verticillata* (■), and submerged alien macrophytes excl. *M. spicatum*/*H. verticillata* (■) on macrophyte, macroinvertebrate and fish assemblages. Error bars represent 95% confidence intervals. Values in parentheses (*a*, *b*) represent: (*a*) the number of effect sizes used in the model; (*b*) the number of articles from which the effect sizes were sourced. Abundance and diversity results are pooled for each subgroup.

macrophytes, notably *P. australis* and the North American *Typha* species complex. Emergent invaders (e.g. *T. x glauca*, *Phalaris arundinacea*) are typically equipped with a suite of characters (tall, fast-growing, capable of clonal integration), which readily facilitate the competitive exclusion of native macrophytes via superior resource acquisition (Galatowitsch et al., 1999; Hussner et al., 2021; Michelan et al., 2018; Zedler & Kercher, 2004). In addition, the fibrous litter produced by many invasive emergent taxa indirectly displaces native macrophytes through nutrient enrichment and light reduction (Farrer & Goldberg, 2009; Holdredge & Bertness, 2011; Larkin et al., 2012; Vaccaro et al., 2009). Floating and submerged invasive macrophytes may also displace native vegetation (Boylen et al., 1999; Houston & Duivenvoorden, 2002; Pinero-Rodríguez et al., 2021; Silveira et al., 2018), probably via superior resource acquisition (Madsen, 1998) and/or phenotypic plasticity (Fleming & Dibble, 2015; Riis et al., 2012). Displacement of native macrophytes by aliens may also be promoted by the production of plant secondary metabolites which defend the invader from herbivores (Erhard et al., 2007; Grutters et al., 2017) or inhibit the growth of native macrophyte competitors (Dandelot et al., 2008; Thiébaut et al., 2018). Although responsibility for the replacement of native vegetation is often ascribed to the alien invader itself, the competitive dominance of invasive alien macrophytes does not arise in a vacuum. Rather, competitive interactions are often mediated by extraneous factors such as climate change (Calvo et al., 2019; Hussner et al., 2014; You et al., 2014) and anthropogenic nutrient/contaminant loading (Chase & Knight, 2006; Galatowitsch et al., 1999; Richburg et al., 2001; van der Loop et al., 2020; You et al., 2014; Zedler & Kercher, 2004). For example, eutrophication has been demonstrated to facilitate the replacement of native macrophytes by *M. spicatum* (Chase & Knight, 2006) and promote colonisation of bare soil by *Crassula helmsii* (van der Loop et al., 2020), whilst eutrophication and warming interactively promote the growth and clonal propagation of *E. crassipes* (You et al., 2014). In such instances, invaders might be better considered as passengers, rather than drivers, of environmental change.

TABLE 4 Multilevel random effects models assessing the effects of the alien macrophytes *Typha* spp., *Myriophyllum spicatum*, *Hydrilla verticillata* (and other submerged alien macrophytes, excl. *M. spicatum*/*H. verticillata*) on macrophyte, macroinvertebrate and fish assemblages

Alien macrophyte	Focal taxon	Mean effect	95% CI	*p*	Heterogeneity statistics
Typha spp.	Macrophytes	−1.77	−2.53, −1.01	***	$Q = 165.30$, $df = 21$, $p < 0.0001$; $I^2 = 89.98\%$
Phragmites australis	Macrophytes	−0.89	−1.77, −0.02	*	$Q = 62.31$, $df = 11$, $p < 0.0001$ $I^2 = 84.18\%$
M. spicatum	Macroinvertebrates	0.7	0.08, 1.33	*	$Q = 117.69$, $df = 29$, $p < 0.0001$; $I^2 = 78.6\%$
H. verticillata	Macroinvertebrates	0.95	0.14, 1.76	*	$Q = 71.60$, $df = 17$, $p < 0.0001$; $I^2 = 86.92\%$
	Fish	0.26	−0.03, 0.54	ns	$Q = 42.11$, $df = 18$, $p = 0.0011$; $I^2 = 54.58\%$
Other submerged alien macrophytes	Macroinvertebrates	−0.3	−1, 0.39	ns	$Q = 156.66$, $df = 16$, $p < 0.0001$ $I^2 = 89.43$

Note: Q and I^2 provide estimates of residual heterogeneity. An I^2 value exceeding 75% indicates substantial residual heterogeneity. Abundance and diversity results are pooled for each subgroup.
$^*p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$.

4.2 | Macroinvertebrates

The considerable residual heterogeneity in our macroinvertebrate abundance and diversity meta-regressions indicates strong context-dependent variation in the effects of alien macrophyte invasion on macroinvertebrates, and whilst the pooled effects of invasion on macroinvertebrate abundance and diversity were non-significant, invasion by submerged alien macrophytes had a significant positive effect on macroinvertebrates. In this context, it is important to remember that the physical structure provided by vegetation may be of greater importance to most macroinvertebrates than macrophyte species identity (McAbendroth et al., 2005; Thomaz et al., 2008). Due to the strong role played by physical structure in governing the response of macroinvertebrates to alien macrophyte invasion, macroinvertebrate abundance and diversity can increase even where a diverse native macrophyte mosaic is replaced by monotypic alien macrophyte stands, provided that structural complexity is increased (Hogsden et al., 2007; Kelly & Hawes, 2005). The positive impacts of invasion by architecturally complex *H. verticillata* and *M. spicatum* drive the positive effect of submerged alien macrophytes on macroinvertebrate abundance/diversity we observe in our meta-analysis, with the effect disappearing once *H. verticillata*/*M.spicatum* are removed from the subgroup. Whilst structural change is likely to be the most common determinant of the impacts of alien macrophyte invasion on macroinvertebrates, alteration of hydrochemistry might in some instances drive equally strong shifts in macroinvertebrate assemblage structure. Dense mats formed by floating alien macrophytes can reduce atmospheric exchange of oxygen, leading to declines in the abundance of hypoxia-sensitive macroinvertebrate taxa (Ceschin et al., 2020, but see Kornijów et al., 2010), whilst the allelopathic exudates of alien macrophytes may alter community composition and diversity via the mortality of sensitive taxa or the deterrence of herbivores (Erhard et al., 2007; Lindén & Lehtiniemi, 2005). In general, the effects of alien macrophyte invasion may differ for oligophagous herbivorous macroinvertebrates, since shifts in macrophyte assemblage composition impact directly on their nutrition (Erhard et al., 2007; Grutters et al., 2017). Similarly, alien macrophyte invasion may alter autochthonous detritus production and retention, impacting on the nutrition of detritivorous macroinvertebrates (Cuassolo et al., 2020). As with resident macrophytes, alien taxon identity and context are important determinants of the outcomes of alien macrophyte invasion for macroinvertebrates.

4.3 | Fishes

Due to the comparatively large spatial scale of habitat use by many fishes, the extent to which alien macrophyte invasion affects a fish assemblage may often be dictated by the invasion's scale (Keast, 1984). As well as potentially impacting individual movement and refuge, the impacts of alien macrophyte invasion on fishes are expected to depend strongly on the effects of that invasion on prey taxa abundance and availability (Bickel & Closs, 2008; Carniatto et al., 2020; Dibble & Harrel, 1997). Alien macrophyte invasion may also affect fish assemblage structure by altering interspecific interactions between fishes (Schultz & Dibble, 2012). For instance, increased structural complexity following alien macrophyte invasion may impair foraging by piscivorous fishes by enhancing availability of refugia for prey taxa (Collingsworth & Kohler, 2010), whilst secondary metabolites produced by alien macrophytes may alter the behaviour of predator or prey (Lindén & Lehtiniemi, 2005). A number of studies have detected elevated abundance of non-native fishes in alien macrophyte beds (Houston & Duivenvoorden, 2002; Kuehne et al., 2016), suggesting that alien macrophytes may facilitate alien

fishes. Whilst we found no consistent effect of alien macrophyte invasion on fish abundance or diversity, we caution that a general trend in the impacts of alien macrophyte invasion on fish might remain undetected by our meta-analysis, given the relatively small number of fish articles that met the criteria for inclusion.

5 | CONCLUSION

We found a significant negative impact of alien macrophyte invasion on all-taxon diversity, but considerable variation in impacts at a finer resolution. Our meta-analyses should therefore serve to emphasise that, whilst growth form appears to be a major determinant of alien macrophyte impact, the effects of alien aquatic plant invasions depend strongly on species identity and ecological context. We suggest that context- and taxon-specific ecological research is an irreplaceable prerequisite to the development of proportionate and cost-effective alien macrophyte management, and should be pursued wherever possible. Currently there is a notable bias (Evangelista et al., 2014) towards the study of a handful of widely distributed, well-established invasive plants (e.g. *M. spicatum*, *T. x glauca*, *H. verticillata*), reflected in the articles included in our meta-analyses. Past work has often relied on qualitative assessment of ecological impacts, and published quantitative data (suitable for meta-analysis) is lacking for a number of widespread and problematic invasive macrophytes (e.g. *C. helmsii*, *Alternanthera philoxeroides*). The publication of quantitative ecological research on such plants will better serve the evidence-based management of alien macrophytes.

Beyond abundance and diversity, the potential impacts of alien macrophyte invasion on recipient communities are, of course, unexamined by our meta-analysis. Changing community composition following alien macrophyte invasion is a pressing concern, given the threat of biotic homogenisation posed by widespread alien invaders (Olden et al., 2004). Whilst the metrics included in our meta-analysis tend to correlate positively with other measures of diversity (e.g. functional diversity, β-diversity) (Pool et al., 2014; Stevens & Tello, 2014; Strecker et al., 2011), positive effects of alien macrophyte invasion on the site-scale abundance and taxonomic α-diversity of pre-existing assemblages may mask degradation of other dimensions of biodiversity (Devictor et al., 2010; Strecker et al., 2011), or the degradation of biodiversity at a landscape or global scale. In biotic homogenisation, for instance, macroinvertebrate diversity could potentially increase at the site-scale due to the facilitation of widespread eurytopic species, whilst global diversity is compromised by the loss of geographically restricted endemic taxa (McKinney & Lockwood, 1999; Olden et al., 2004).

As noted above, the impacts of alien macrophytes on fish remain particularly poorly studied (Evangelista et al., 2014). Lotic systems are also understudied, despite their significance as invasion corridors (Čuda et al., 2017; Johansson et al., 1996). Additionally, we note that ponds and other small waterbodies are under-represented in the primary literature we reviewed, despite their disproportionate contribution to freshwater biodiversity and their intrinsic vulnerability to invasion (Davies et al., 2008; Stiers et al., 2011; Williams et al., 2004). Clearly, these subjects warrant further attention.

AUTHOR CONTRIBUTIONS

Conceptualisation, developing methods, data analysis, data interpretation, writing: S.T., D.B., A.F. Conducting the research, preparation figures and tables: S.T.

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DATA AVAILABILITY STATEMENT

The database and R script used in our meta-analyses are available via the Dryad Digital Repository (https://datadryad.org/).

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REFERENCES

Allen, H. L. (1971). Primary productivity, chemo-organotrophy, and nutritional interactions of epiphytic algae and bacteria on macrophytes in the littoral of a lake. *Ecological Monographs*, *41*, 97–127. https://doi.org/10.2307/1942387

Barrientos, C. A., & Allen, M. S. (2008). Fish abundance and community composition in native and non-native plants following hydrilla colonisation at Lake Izabal, Guatemala. *Fisheries Management and Ecology*, *15*, 99–106. https://doi.org/10.1111/j.1365-2400.2007.00588.x

Bellard, C., Cassey, P., & Blackburn, T. M. (2016). Alien species as a driver of recent extinctions. *Biology Letters*, *12*, 20150623. https://doi.org/10.1098/rsbl.2015.0623

Bickel, T. O., & Closs, G. P. (2008). Fish distribution and diet in relation to the invasive macrophyte *Lagarosiphon major* in the littoral zone of Lake Dunstan, New Zealand. *Ecology of Freshwater Fish*, *17*, 10–19. https://doi.org/10.1111/j.1600-0633.2007.00249.x

Boylen, C. W., Eichler, L. W., & Madsen, J. D. (1999). Loss of native aquatic plant species in a community dominated by Eurasian watermilfoil. *Hydrobiologia*, *415*, 207–211. https://doi.org/10.1023/A:1003804612998

Brundu, G. (2014). Plant invaders in European and Mediterranean inland waters: Profiles, distribution, and threats. *Hydrobiologia*, *746*, 61–79. https://doi.org/10.1007/S10750-014-1910-9

Calvo, C., Mormul, R. P., Figueiredo, B. R. S., Cunha, E. R., Thomaz, S. M., & Meerhoff, M. (2019). Herbivory can mitigate, but not counteract, the positive effects of warming on the establishment of the invasive macrophyte *Hydrilla verticillata*. *Biological Invasions*, *21*, 59–66. https://doi.org/10.1007/s10530-018-1803-3

Caraco, N. F., & Cole, J. J. (2002). Contrasting impacts of a native and alien macrophyte on dissolved oxygen in a large river. *Ecological Applications*, *12*, 1496–1509. https://doi.org/10.2307/3099987

Carniatto, N., Cunha, E. R., Thomaz, S. M., Quirino, B. A., & Fugi, R. (2020). Feeding of fish inhabiting native and non-native macrophyte stands in a Neotropical reservoir. *Hydrobiologia*, *847*, 1553–1563. https://doi.org/10.1007/s10750-020-04212-2

Carpenter, S. R., & Lodge, D. M. (1986). Effects of submersed macrophytes on ecosystem processes. *Aquatic Botany*, *26*, 341–370. https://doi.org/10.1016/0304-3770(86)90031-8

Carter, V., Rybicki, N. B., & Hammerschlag, R. (1991). Effects of submersed macrophytes on dissolved oxygen, pH, and temperature under different conditions of wind, tide, and bed structure. *Journal of Freshwater Ecology*, *6*, 121–133. https://doi.org/10.1080/02705060.1991.9665286

Cattaneo, A., & Kalff, J. (1980). The relative contribution of aquatic macrophytes and their epiphytes to the production of macrophyte beds. *Limnology and Oceanography*, *25*, 280–289. https://doi.org/10.4319/lo.1980.25.2.0280

Ceschin, S., Ferrante, G., Mariani, F., Traversetti, L., & Ellwood, N. T. W. (2020). Habitat change and alteration of plant and invertebrate communities in waterbodies dominated by the invasive alien macrophyte *Lemna minuta*. *Biological Invasions*, *22*, 1325–1337. https://doi.org/10.1007/s10530-019-02185-5

Chambers, P. A., Lacoul, P., Murphy, K. J., & Thomaz, S. M. (2007). Global diversity of aquatic macrophytes in freshwater. In *Freshwater animal diversity assessment* (pp. 9–26). Springer, Dordrecht. https://doi.org/10.1007/978-1-4020-8259-7_2

Chase, J. M., & Knight, T. M. (2006). Effects of eutrophication and snails on Eurasian watermilfoil (*Myriophyllum spicatum*) invasion. *Biological Invasions*, *8*, 1643–1649. https://doi.org/10.1007/s10530-005-3933-7

Cheung, M. W. L. (2019). A guide to conducting a meta-analysis with non-independent effect sizes. *Neuropsychology Review*, *29*, 387–396. https://doi.org/10.1007/s11065-019-09415-6

Coetzee, B. W. T., Gaston, K. J., & Chown, S. L. (2014). Local scale comparisons of biodiversity as a test for global protected area ecological performance: A meta-analysis. *PLoS One*, *9*, e105824. https://doi.org/10.1371/journal.pone.0105824

Collingsworth, P. D., & Kohler, C. C. (2010). Abundance and habitat use of juvenile sunfish among different macrophyte stands. *Lake and Reservoir Management*, *26*, 35–42. https://doi.org/10.1080/07370651003634380

Crooks, J. A. (2005). Lag times and exotic species: The ecology and management of biological invasions in slow-motion. *Ecoscience*, *12*, 316–329. https://doi.org/10.2980/i1195-6860-12-3-316.1

Cuassolo, F., Díaz Villanueva, V., & Modenutti, B. (2020). Litter decomposition of the invasive *Potentilla anserina* in an invaded and non-invaded freshwater environment of North Patagonia. *Biological Invasions*, *22*, 1055–1065. https://doi.org/10.1007/s10530-019-02155-x

Čuda, J., Rumlerová, Z., Brůna, J., Skálová, H., & Pyšek, P. (2017). Floods affect the abundance of invasive *Impatiens glandulifera* and its spread from river corridors. *Diversity and Distributions*, *23*, 342–354. https://doi.org/10.1111/DDI.12524

Dandelot, S., Robles, C., Pech, N., Cazaubon, A., & Verlaque, R. (2008). Allelopathic potential of two invasive alien *Ludwigia* spp. *Aquatic Botany*, *88*, 311–316. https://doi.org/10.1016/J.AQUABOT.2007.12.004

Davies, B., Biggs, J., Williams, P., Whitfield, M., Nicolet, P., Sear, D., Bray, S., & Maund, S. (2008). Comparative biodiversity of aquatic habitats in the European agricultural landscape. *Agriculture, Ecosystems and Environment*, *125*, 1–8. https://doi.org/10.1016/j.agee.2007.10.006

Davis, M. A., Chew, M. K., Hobbs, R. J., Lugo, A. E., Ewel, J. J., Vermeij, G. J., Brown, J. H., Rosenzweig, M. L., Gardener, M. R., Carroll, S. P., Thompson, K., Pickett, S. T. A., Stromberg, J. C., Tredici, P. D., Suding, K. N., Ehrenfeld, J. G., Grime, J. P., Mascaro, J., & Briggs, J. C. (2011). Don't judge species on their origins. *Nature*, *474*, 153–154. https://doi.org/10.1038/474153a

Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., & Mouquet, N. (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: The need for integrative conservation strategies in a changing world. *Ecology Letters*, *13*, 1030–1040. https://doi.org/10.1111/j.1461-0248.2010.01493.x

Diagne, C., Leroy, B., Vaissière, A.-C., Gozlan, R. E., Roiz, D., Jarić, I., Salles, J.-M., Bradshaw, C. J. A., & Courchamp, F. (2021). High and rising economic costs of biological invasions worldwide. *Nature*, *592*, 1–6. https://doi.org/10.1038/s41586-021-03405-6

Dibble, E. D., & Harrel, S. L. (1997). Largemouth bass diets in two aquatic plant communities. *Journal of Aquatic Plant Management*, *35*, 74–78.

Didham, R. K., Tylianakis, J. M., Hutchison, M. A., Ewers, R. M., & Gemmell, N. J. (2005). Are invasive species the drivers of ecological change? *Trends in Ecology & Evolution*, *20*, 470–474. https://doi.org/10.1016/J.TREE.2005.07.006

Dudgeon, D. (2020). *Freshwater Biodiversity: status, threats and conservation*. Cambridge University Press, Cambridge. https://doi.org/10.1017/9781139032759

Egger, M., Smith, G. D., Schneider, M., & Minder, C. (1997). Bias in meta-analysis detected by a simple, graphical test. *British Medical Journal*, *315*, 629–634. https://doi.org/10.1136/bmj.315.7109.629

Erhard, D., Pohnert, G., & Gross, E. M. (2007). Chemical defense in *Elodea nuttallii* reduces feeding and growth of aquatic herbivorous Lepidoptera. *Journal of Chemical Ecology*, *33*, 1646–1661. https://doi.org/10.1007/s10886-007-9307-0

Evangelista, H. B. A., Magela Thomaz, S., & Umetsu, C. A. (2014). An analysis of publications on invasive macrophytes in aquatic ecosystems. *Aquatic Invasions*, *9*, 521–528. https://doi.org/10.3391/ai.2014.9.4.10

Farrer, E. C., & Goldberg, D. E. (2009). Litter drives ecosystem and plant community changes in cattail invasion. *Ecological Applications*, *19*, 398–412. https://doi.org/10.1890/08-0485.1

Fleming, J. P., & Dibble, E. D. (2015). Ecological mechanisms of invasion success in aquatic macrophytes. *Hydrobiologia*, *746*, 23–37. https://doi.org/10.1007/s10750-014-2026-y

Galatowitsch, S. M., Anderson, N. O., & Ascher, P. D. (1999). Invasiveness in wetland plants in temperate North America. *Wetlands*, *19*, 733–755. https://doi.org/10.1007/BF03161781

Gallardo, B., Clavero, M., Sánchez, M. I., & Vilà, M. (2016). Global ecological impacts of invasive species in aquatic ecosystems. *Global Change Biology*, *22*, 151–163. https://doi.org/10.1111/gcb.13004

Goodenough, A. (2010). Are the ecological impacts of alien species misrepresented? A review of the "native good, alien bad" philosophy. *Community Ecology*, *11*, 13–21. https://doi.org/10.1556/ComEc.11.2010.1.3

Grutters, B. M. C., Roijendijk, Y. O. A., Verberk, W. C. E. P., & Bakker, E. S. (2017). Plant traits and plant biogeography control the biotic resistance provided by generalist herbivores. *Functional Ecology*, *31*, 1184–1192. https://doi.org/10.1111/1365-2435.12835

Gurevitch, J., Koricheva, J., Nakagawa, S., & Stewart, G. (2018). Meta-analysis and the science of research synthesis. *Nature*, *555*, 175–182. https://doi.org/10.1038/nature25753

Habeck, C. W., & Schultz, A. K. (2015). Community-level impacts of white-tailed deer on understorey plants in North American forests: A meta-analysis. *AoB Plants*, *7*, plv119. https://doi.org/10.1093/aobpla/plv119

Harrer, M., Cuijpers, P., Furukawa, T., & Ebert, D. D. (2019a). *Doing meta-analysis in R: A hands-on guide*. https://doi.org/10.5281/zenodo.2551803

Harrer, M., Cuijpers, P., Furukawa, T., & Ebert, D. D. (2019b). *dmetar: Companion R Package For The Guide "Doing Meta-Analysis in R."* http://dmetar.protectlab.org/

Hatzenbeler, G. R., Bozek, M. A., Jennings, M. J., & Emmons, E. E. (2000). Seasonal variation in fish assemblage structure and habitat structure in the nearshore littoral zone of Wisconsin Lakes. *North American Journal of Fisheries Management*, *20*, 360–368. https://doi.org/10.1577/1548-8675(2000)020<0360:svifas>2.3.co;2

Hedges, L. V. (1981). Distribution theory for glass's estimator of effect size and related estimators. *Journal of Educational Statistics*, *6*, 107–128. https://doi.org/10.2307/1164588

Hershner, C., & Havens, K. J. (2008). Managing invasive aquatic plants in a changing system: Strategic consideration of ecosystem services. *Conservation Biology*, *22*, 544–550. https://doi.org/10.1111/j.1523-1739.2008.00957.x

Higgins, J. P. T., Thompson, S. G., Deeks, J. J., & Altman, D. G. (2003). Measuring inconsistency in meta-analyses. *British Medical Journal*, *327*, 557–560. https://doi.org/10.1136/bmj.327.7414.557

Hogsden, K. L., Sager, E. P. S., & Hutchinson, T. C. (2007). The impacts of the non-native macrophyte *Cabomba caroliniana* on littoral biota of Kasshabog Lake, Ontario. *Journal of Great Lakes Research*, *33*, 497–504. https://doi.org/10.3394/0380-1330(2007)33[497:TIOTNM]2.0.CO;2

Holdredge, C., & Bertness, M. D. (2011). Litter legacy increases the competitive advantage of invasive *Phragmites australis* in New England wetlands. *Biological Invasions*, *13*, 423–433. https://doi.org/10.1007/s10530-010-9836-2

Houston, W. A., & Duivenvoorden, L. J. (2002). Replacement of littoral native vegetation with the ponded pasture grass *Hymenachne amplexicaulis*: Effects on plant, macroinvertebrate and fish biodiversity of backwaters in the Fitzroy River, Central Queensland, Australia. *Marine and Freshwater Research*, *53*, 1235–1244. https://doi.org/10.1071/MF01042

Hussner, A., Heidbüchel, P., Coetzee, J., & Gross, E. M. (2021). From introduction to nuisance growth: A review of traits of alien aquatic plants which contribute to their invasiveness. *Hydrobiologia*, *848*, 2119–2151. https://doi.org/10.1007/S10750-020-04463-Z

Hussner, A., Stiers, I., Verhofstad, M. J. J. M., Bakker, E. S., Grutters, B. M. C., Haury, J., van Valkenburg, J. L. C. H., Brundu, G., Newman, J., Clayton, J. S., Anderson, L. W. J., & Hofstra, D. (2017). Management and control methods of invasive alien freshwater aquatic plants: A review. *Aquatic Botany*, *136*, 112–137. https://doi.org/10.1016/J.AQUABOT.2016.08.002

Hussner, A., Van Dam, H., Vermaat, J. E., & Hilt, S. (2014). Comparison of native and neophytic aquatic macrophyte developments in a geothermally warmed river and thermally normal channels. *Fundamental and Applied Limnology*, *185*, 155–166. https://doi.org/10.1127/fal/2014/0629

Johansson, M. E., Nilsson, C., & Nilsson, E. (1996). Do rivers function as corridors for plant dispersal? *Journal of Vegetation Science*, *7*, 593–598. https://doi.org/10.2307/3236309

Keast, A. (1984). The introduced aquatic macrophyte, *Myriophyllum spicatum*, as habitat for fish and their invertebrate prey. *Canadian Journal of Zoology*, *62*, 1289–1303. https://doi.org/10.1139/z84-186

Keller, R. P., Geist, J., Jeschke, J. M., & Kühn, L. (2011). Invasive species in Europe: Ecology, status, and policy. *Environmental Sciences Europe*, *23*, 1–17. https://doi.org/10.1186/2190-4715-23-23

Kelly, D. J., & Hawes, I. (2005). Effects of invasive macrophytes on littoral-zone productivity and foodweb dynamics in a New Zealand high-country lake. *Journal of the North American Benthological Society*, *24*, 300–320. https://doi.org/10.1899/03-097.1

Killgore, K. J., Morgan, R. P., & Rybicki, N. B. (1989). Distribution and abundance of fishes associated with submersed aquatic plants in the Potomac river. *North American Journal of Fisheries Management*, *9*, 101–111. https://doi.org/10.1577/1548-8675(1989)009<0101:daaofa>2.3.co;2

Kornijów, R., Strayer, D. L., & Caraco, N. F. (2010). Macroinvertebrate communities of hypoxic habitats created by an invasive plant (*Trapa natans*) in the freshwater tidal Hudson River. *Fundamental and Applied Limnology*, *176*, 199–207. https://doi.org/10.1127/1863-9135/2010/0176-0199

Kuehne, L. M., Olden, J. D., & Rubenson, E. S. (2016). Multi-trophic impacts of an invasive aquatic plant. *Freshwater Biology*, *61*, 1846–1861. https://doi.org/10.1111/fwb.12820

Landers, D. H. (1982). Effects of naturally senescing aquatic macrophytes on nutrient chemistry and chlorophyll a of surrounding waters. *Limnology and Oceanography*, *27*, 428–439. https://doi.org/10.4319/lo.1982.27.3.0428

Larkin, D. J., Freyman, M. J., Lishawa, S. C., Geddes, P., & Tuchman, N. C. (2012). Mechanisms of dominance by the invasive hybrid cattail *Typha* × *glauca*. *Biological Invasions*, *14*, 65–77. https://doi.org/10.1007/s10530-011-0059-y

Lewis, S. L., & Maslin, M. A. (2015). Defining the Anthropocene. *Nature*, *519*, 171–180. https://doi.org/10.1038/nature14258

Lindén, E., & Lehtiniemi, M. (2005). The lethal and sublethal effects of the aquatic macrophyte *Myriophyllum spicatum* on Baltic littoral planktivores. *Limnology and Oceanography*, *50*, 405–411. https://doi.org/10.4319/lo.2005.50.2.0405

Lodge, D. M. (1991). Herbivory on freshwater macrophytes. *Aquatic Botany*, *41*, 195–224. https://doi.org/10.1016/0304-3770(91)90044-6

Lüdecke, D. (2019). *esc: Effect Size Computation for Meta Analysis (version 0.5.1)*. https://doi.org/10.5281/zenodo.1249218

Macdougall, A. S., & Turkington, R. (2005). Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology*, *86*, 42–55. https://doi.org/10.2307/3450986

Madsen, J. D. (1998). Predicting invasion success of eurasian watermilfoil. *Journal of Aquatic Plant Management*, *36*, 28–32. https://doi.org/10.21236/ada362305

McAbendroth, L., Ramsay, P. M., Foggo, A., Rundle, S. D., & Bilton, D. T. (2005). Does macrophyte fractal complexity drive invertebrate diversity, biomass and body size distributions? *Oikos*, *111*, 279–290. https://doi.org/10.1111/j.0030-1299.2005.13804.x

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, *14*, 450–453. https://doi.org/10.1016/S0169-5347(99)01679-1

Michelan, T. S., Silveira, M. J., Petsch, D. K., Pinha, G. D., & Thomaz, S. M. (2014). The invasive aquatic macrophyte *Hydrilla verticillata* facilitates the establishment of the invasive mussel *Limnoperna fortunei* in Neotropical reservoirs. *Journal of Limnology*, *73*, 598–602. https://doi.org/10.4081/JLIMNOL.2014.909

Michelan, T. S., Thomaz, S. M., Bando, F. M., & Bini, L. M. (2018). Competitive effects hinder the recolonization of native species in environments densely occupied by one invasive exotic species. *Frontiers in Plant Science*, *9*, 1261. https://doi.org/10.3389/fpls.2018.01261

Miranda, L. E., Driscoll, M. P., & Allen, M. S. (2000). Transient physicochemical microhabitats facilitate fish survival in inhospitable aquatic plant stands. *Freshwater Biology*, *44*, 617–628. https://doi.org/10.1046/J.1365-2427.2000.00606.X

Monks, A. M., Lishawa, S. C., Wellons, K. C., Albert, D. A., Mudrzynski, B., & Wilcox, D. A. (2019). European frogbit (*Hydrocharis morsus-ranae*) invasion facilitated by non-native cattails (*Typha*) in the Laurentian Great Lakes. *Journal of Great Lakes Research*, *45*, 912–920. https://doi.org/10.1016/J.JGLR.2019.07.005

Moorhouse, T. P., & Macdonald, D. W. (2015). Are invasives worse in freshwater than terrestrial ecosystems? *Wiley Interdisciplinary Reviews: Water*, *2*, 1–8. https://doi.org/10.1002/wat2.1059

Murphy, K., Efremov, A., Davidson, T. A., Molina-Navarro, E., Fidanza, K., Crivelari Betiol, T. C., Chambers, P., Grimaldo, J. T., Martins, S. V., Springuel, I., Kennedy, M., Mormul, R. P., Dibble, E., Hofstra, D., Lukács, B. A., Gebler, D., Baastrup-Spohr, L., Urrutia-Estradam, J., & Urrutia-Estrada, J. (2019). World distribution, diversity and endemism of aquatic macrophytes. *Aquatic Botany*, *158*, 103127. https://doi.org/10.1016/J.AQUABOT.2019.06.006

Newman, R. M. (1991). Herbivory and detritivory on freshwater macrophytes by invertebrates: A review. *Journal of the North American Benthological Society*, *10*, 89–114. https://doi.org/10.2307/1467571

Olden, J. D., Comte, L., & Giam, X. (2018). The homogocene: A research prospectus for the study of biotic homogenisation. *NeoBiota*, *37*, 23–36. https://doi.org/10.3897/neobiota.37.22552

Olden, J. D., Poff, N. L. R., Douglas, M. R., Douglas, M. E., & Fausch, K. D. (2004). Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology & Evolution*, *19*, 18–24.

Ondok, J. P., Pokorný, J., & Květ, J. (1984). Model of diurnal changes in oxygen, carbon dioxide and bicarbonate concentrations in a stand of *Elodea canadensis michx*. *Aquatic Botany*, *19*, 293–305. https://doi.org/10.1016/0304-3770(84)90045-7

Pejchar, L., & Mooney, H. A. (2009). Invasive species, ecosystem services and human well-being. *Trends in Ecology and Evolution*, *24*, 497–504. https://doi.org/10.1016/j.tree.2009.03.016

Petsch, D. K., dos S. Bertoncin, A. P., Ortega, J. C. G., & Thomaz, S. M. (2022). Non-native species drive biotic homogenization, but it depends on the realm, beta diversity facet and study design: A meta-analytic systematic review. *Oikos*, *2022*, 1–11. https://doi.org/10.1111/OIK.08768

Pinero-Rodríguez, M. J., Fernández-Zamudio, R., Arribas, R., Gomez-Mestre, I., & Díaz-Paniagua, C. (2021). The invasive aquatic fern *Azolla filiculoides* negatively impacts water quality, aquatic vegetation and amphibian larvae in Mediterranean environments. *Biological Invasions*, *23*, 755–769. https://doi.org/10.1007/s10530-020-02402-6

Pool, T. K., Grenouillet, G., & Villéger, S. (2014). Species contribute differently to the taxonomic, functional, and phylogenetic alpha and beta diversity of freshwater fish communities. *Diversity and Distributions*, *20*, 1235–1244. https://doi.org/10.1111/ddi.12231

R Core Team. (2020). *R: A Language and Environment for Statistical Computing*. R Core Team. https://www.r-project.org/

Richburg, J. A., Patterson, W. A., & Lowenstein, F. (2001). Effects of road salt and *Phragmites australis* invasion on the vegetation of a Western Massachusetts calcareous Lake-Basin fen. *Wetlands*, *21*, 247–255. https://doi.org/10.1672/0277-5212(2001)021[0247:EORSAP]2.0.CO;2

Riis, T., Olesen, B., Clayton, J. S., Lambertini, C., Brix, H., & Sorrell, B. K. (2012). Growth and morphology in relation to temperature and light availability during the establishment of three invasive aquatic plant species. *Aquatic Botany*, *102*, 56–64. https://doi.org/10.1016/J.AQUABOT.2012.05.002

Rohatgi, A. (2020). *WebPlotDigitizer v4.4*. https://automeris.io/WebPlotDigitizer/

Saltonstall, K. (2002). Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. *Proceedings of the National Academy of Sciences of the United States of America*, *99*, 2445–2449. https://doi.org/10.1073/pnas.032477999

Schlaepfer, M. A., Sax, D. F., & Olden, J. D. (2011). The potential conservation value of non-native species. *Conservation Biology*, *25*, 428–437. https://doi.org/10.1111/j.1523-1739.2010.01646.x

Schramm, H. L., & Jirka, K. J. (1989). Effects of aquatic macrophytes on benthic macroinvertebrates in two Florida lakes. *Journal of Freshwater Ecology*, *5*, 1–12. https://doi.org/10.1080/02705060.1989.9665208

Schultz, R., & Dibble, E. (2012). Effects of invasive macrophytes on freshwater fish and macroinvertebrate communities: The role of invasive plant traits. *Hydrobiologia*, *684*, 1–14. https://doi.org/10.1007/s10750-011-0978-8

Senior, A. M., Grueber, C. E., Kamiya, T., Lagisz, M., O'Dwyer, K., Santos, E. S. A., & Nakagawa, S. (2016). Heterogeneity in ecological and evolutionary meta-analyses: Its magnitude and implications. *Ecology*, *97*, 3293–3299. https://doi.org/10.1002/ecy.1591

Sheldon, R. B., & Boylen, C. W. (1975). Factors affecting the contribution by epiphytic algae to the primary productivity of an oligotrophic freshwater lake. *Applied Microbiology*, *30*, 657–667. https://doi.org/10.1128/AM.30.4.657-667.1975

Silveira, M. J., Alves, D. C., & Thomaz, S. M. (2018). Effects of the density of the invasive macrophyte *Hydrilla verticillata* and root competition on growth of one native macrophyte in different sediment fertilities. *Ecological Research*, *33*, 927–934. https://doi.org/10.1007/s11284-018-1602-4

Simberloff, D., & Von Holle, B. (1999). Positive interactions of nonindigenous species: Invasional meltdown? *Biological Invasions*, *1*, 21–32. https://doi.org/10.1023/A:1010086329619

Smith, T., & Buckley, P. (2015). The growth of the non-native *Crassula helmsii* (Crassulaceae) increases the rarity scores of aquatic macrophyte assemblages in southeastern England. *New Journal of Botany*, *5*, 191–198. https://doi.org/10.1080/20423489.2015.1096137

Stevens, R. D., & Tello, J. S. (2014). On the measurement of dimensionality of biodiversity. *Global Ecology and Biogeography*, *23*, 1115–1125. https://doi.org/10.1111/geb.12192

Stiers, I., Crohain, N., Josens, G., & Triest, L. (2011). Impact of three aquatic invasive species on native plants and macroinvertebrates in temperate ponds. *Biological Invasions*, *13*, 2715–2726. https://doi.org/10.1007/s10530-011-9942-9

Strayer, D. L. (2010). Alien species in fresh waters: Ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology*, *55*, 152–174. https://doi.org/10.1111/j.1365-2427.2009.02380.x

Strayer, D. L., & Dudgeon, D. (2010). Freshwater biodiversity conservation: Recent progress and future challenges. *Journal of the North American Benthological Society*, *29*, 344–358. https://doi.org/10.1899/08-171.1

Strayer, D. L., Eviner, V. T., Jeschke, J. M., & Pace, M. L. (2006). Understanding the long-term effects of species invasions. *Trends in Ecology and Evolution*, *21*, 645–651. https://doi.org/10.1016/j.tree.2006.07.007

Strayer, D. L., Lutz, C., Malcom, H. M., Munger, K., & Shaw, W. H. (2003). Invertebrate communities associated with a native (*Vallisneria americana*) and an alien (*Trapa natans*) macrophyte in a large river. *Freshwater Biology*, *48*, 1938–1949. https://doi.org/10.1046/j.1365-2427.2003.01142.x

Strecker, A. L., Olden, J. D., Whittier, J. B., & Paukert, C. P. (2011). Defining conservation priorities for freshwater fishes according to taxonomic, functional, and phylogenetic diversity. *Ecological Applications*, *21*, 3002–3013. https://doi.org/10.1890/11-0599.1

Theel, H. J., & Dibble, E. D. (2008). An experimental simulation of an exotic aquatic macrophyte invasion and its influence on foraging behavior of bluegill. *Journal of Freshwater Ecology*, *23*, 79–89. https://doi.org/10.1080/02705060.2008.9664559

Thiébaut, G., Thouvenot, L., & Rodríguez-Pérez, H. (2018). Allelopathic effect of the invasive *Ludwigia hexapetala* on growth of three macrophyte species. *Frontiers in Plant Science*, *9*, 1835. https://doi.org/10.3389/fpls.2018.01835

Thomaz, S. M., & da Cunha, E. R. (2010). The role of macrophytes in habitat structuring in aquatic ecosystems: Methods of measurement, causes and consequences on animal assemblages' composition and biodiversity. *Acta Limnologica Brasiliensia*, *22*, 218–236. https://doi.org/10.4322/ACTALB.02202011

Thomaz, S. M., Dibble, E. D., Evangelista, L. R., Higuti, J., & Bini, L. M. (2008). Influence of aquatic macrophyte habitat complexity on invertebrate abundance and richness in tropical lagoons. *Freshwater Biology*, *53*, 358–367. https://doi.org/10.1111/j.1365-2427.2007.01898.x

Thorp, A. G., Jones, R. C., & Kelso, D. P. (1997). A comparison of water-column macroinvertebrate communities in beds of differing submersed aquatic vegetation in the tidal freshwater Potomac River. *Estuaries*, *20*, 86–95. https://doi.org/10.2307/1352722

Thouvenot, L., Haury, J., Pottier, G., & Thiébaut, G. (2017). Reciprocal indirect facilitation between an invasive macrophyte and an invasive crayfish. *Aquatic Botany*, *139*, 1–7. https://doi.org/10.1016/j.aquabot.2017.02.002

Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences*

of the United States of America, *101*, 10854–10861. https://doi.org/10.1073/PNAS.0403458101

Toft, J. D., Simenstad, C. A., Cordell, J. R., & Grimaldo, L. F. (2003). The effects of introduced water hyacinth on habitat structure, invertebrate assemblages, and fish diets. *Estuaries*, *26*, 746–758. https://doi.org/10.1007/BF02711985

Travis, S. E., Marburger, J. E., Windels, S., & Kubàtovà, B. (2010). Hybridization dynamics of invasive cattail (Typhaceae) stands in the Western Great Lakes Region of North America: A molecular analysis. *Journal of Ecology*, *98*, 7–16. https://doi.org/10.1111/j.1365-2745.2009.01596.x

Troutman, J. P., Rutherford, D. A., & Kelso, W. E. (2007). Patterns of habitat use among vegetation-dwelling littoral fishes in the Atchafalaya River Basin, Louisiana. *Transactions of the American Fisheries Society*, *136*, 1063–1075. https://doi.org/10.1577/T06-118.1

Vaccaro, L. E., Bedford, B. L., & Johnston, C. A. (2009). Litter accumulation promotes dominance of invasive species of cattails (*Typha* spp.) in Lake Ontario wetlands. *Wetlands*, *29*, 1036–1048. https://doi.org/10.1672/08-28.1

van der Loop, J. M. M., Tjampens, J., Vogels, J. J., van Kleef, H. H., Lamers, L. P. M., & Leuven, R. S. E. W. (2020). Reducing nutrient availability and enhancing biotic resistance limits settlement and growth of the invasive Australian swamp stonecrop (*Crassula helmsii*). *Biological Invasions*, *22*, 3391–3402. https://doi.org/10.1007/s10530-020-02327-0

Viechtbauer, W. (2020). *The metafor reference manual*. https://cran.r-project.org/web/packages/metafor/metafor.pdf

Viechtbauer, W., & Cheung, M. W.-L. (2010). Outlier and influence diagnostics for meta-analysis. *Research Synthesis Methods*, *1*, 112–125. https://doi.org/10.1002/jrsm.11

Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., Pergl, J., Schaffner, U., Sun, Y., & Pyšek, P. (2011). Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, *14*, 702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Warfe, D. M., & Barmuta, L. A. (2006). Habitat structural complexity mediates food web dynamics in a freshwater macrophyte community. *Oecologia*, *150*, 141–154. https://doi.org/10.1007/s00442-006-0505-1

Wegner, B., Kronsbein, A. L., Gillefalk, M., van de Weyer, K., Köhler, J., Funke, E., Monaghan, M. T., & Hilt, S. (2019). Mutual facilitation among invading nuttall's waterweed and quagga mussels. *Frontiers in Plant Science*, *10*, 789. https://doi.org/10.3389/fpls.2019.00789

Williams, P., Whitfield, M., Biggs, J., Bray, S., Fox, G., Nicolet, P., & Sear, D. (2004). Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. *Biological Conservation*, *115*, 329–341. https://doi.org/10.1016/S0006-3207(03)00153-8

You, W., Yu, D., Xie, D., Yu, L., Xiong, W., & Han, C. (2014). Responses of the invasive aquatic plant water hyacinth to altered nutrient levels under experimental warming in China. *Aquatic Botany*, *119*, 51–56. https://doi.org/10.1016/J.AQUABOT.2014.06.004

Zedler, J. B., & Kercher, S. (2004). Causes and consequences of invasive plants in wetlands: Opportunities, opportunists, and outcomes. *Critical Reviews in Plant Sciences*, *23*, 431–452. https://doi.org/10.1080/07352680490514673

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