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RESEARCH REVIEW

Global ecological impacts of invasive species in aquatic ecosystems

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Abstract

The introduction of invasive species, which often differ functionally from the components of the recipient community, generates ecological impacts that propagate along the food web. This review aims to determine how consistent the impacts of aquatic invasions are across taxa and habitats. To that end, we present a global meta-analysis from 151 publications (733 cases), covering a wide range of invaders (primary producers, filter collectors, omnivores and predators), resident aquatic community components (macrophytes, phytoplankton, zooplankton, benthic invertebrates and fish) and habitats (rivers, lakes and estuaries). Our synthesis suggests a strong negative influence of invasive species on the abundance of aquatic communities, particularly macrophytes, zooplankton and fish. In contrast, there was no general evidence for a decrease in species diversity in invaded habitats, suggesting a time lag between rapid abundance changes and local extinctions. Invaded habitats showed increased water turbidity, nitrogen and organic matter concentration, which are related to the capacity of invaders to transform habitats and increase eutrophication. The expansion of invasive macrophytes caused the largest decrease in fish abundance, the filtering activity of filter collectors depleted planktonic communities, omnivores (including both facultative and obligate herbivores) were responsible for the greatest decline in macrophyte abundance, and benthic invertebrates were most negatively affected by the introduction of new predators. These impacts were relatively consistent across habitats and experimental approaches. Based on our results, we propose a framework of positive and negative links between invasive species at four trophic positions and the five different components of recipient communities. This framework incorporates both direct biotic interactions (predation, competition, grazing) and indirect changes to the water physicochemical conditions mediated by invaders (habitat alteration). Considering the strong trophic links that characterize aquatic ecosystems, this framework is relevant to anticipate the far-reaching consequences of biological invasions on the structure and functionality of aquatic ecosystems.

Keywords: biological invasions, bottom-up effects, ecosystem engineers, effect size, exotic species, food web, habitat alteration, meta-analysis, top-down effects, trophic cascade

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Introduction

The introduction of invasive species, which often constitute new functional components in the recipient community, generates ecological impacts that can propagate along the food web triggering trophic cascades (Moyle & Light, 1996; Strayer, 2010). Impacts can be caused by direct biotic interaction with the resident community (e.g. competition, predation) and also by indirect changes in habitat conditions (e.g. turbidity, habitat structure) (Crooks, 2002). However, evidence of the ecological impacts of invasive species is scattered across multiple local studies, making it difficult to determine whether and to which extent are they consistent across habitats and taxa (Simberloff *et al.*, 2013). Aquatic environments are ideal model ecosystems to test the direct and indirect ecological impacts of invasive species because aquatic organisms are characterized by strong trophic links that can be profoundly disturbed by the loss or the introduction of species (Carpenter *et al.*, 1985; Strong, 1992; Pace *et al.*, 1999).

According to the trophic position hypothesis (Thomsen *et al.*, 2014), we can expect invasive species to trigger distinct changes depending on their position in the food web. If the invasive species is introduced at the upper levels of the trophic web, 'top-down' control of the food web is expected to promote opposite negative and positive changes in the abundance and biomass of lower trophic levels (Pace *et al.*, 1999). In contrast, changes in either primary producers or the input of limiting nutrients by invasive species affect the total energy available to the ecosystem, with 'bottom-up' control propagating changes up the trophic ladder

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(Heath *et al.*, 2014). For example, the introduction of zooplanktivorous fish (*Rutilus rutilus* and *Alburnus alburnus*) into Spanish reservoirs caused a strong decrease in the abundance and richness of large-bodied zooplankton, which in turn released phytoplankton from its grazing pressure (Ordóñez *et al.*, 2010). As opposed to predators, filter feeders like the zebra mussel (*Dreissena polymorpha*) are able to considerably reduce the abundance of phytoplankton (and also small zooplankton), with foreseeable negative consequences upon higher trophic levels (Ward & Ricciardi, 2007).

Ecological impacts in aquatic ecosystems can be further modulated by habitat changes mediated by 'ecosystem engineer' species, which are able to substantially affect other species through large-scale and widespread changes in, for instance, water clarity, nutrients and organic matter concentration (Jones *et al.*, 1996). By increasing sediment resuspension, invasive omnivores like the common carp (*Cyprinus carpio*) or the red swamp crayfish (*Procambarus clarkii*), can lead to abrupt shifts from macrophyte-dominated clear water state to a phytoplankton-dominated turbid state in lakes (Matsuzaki *et al.*, 2009). Invasive molluscs like the zebra mussel have the opposite effect: their filtering activity increases water clarity fostering aquatic macrophytes, whereas the new habitat formed by the shells provides food and shelter to aquatic macroinvertebrates (Ward & Ricciardi, 2007). The overgrowth of macrophytes such as cordgrass (*Spartina* spp.) and common reed (*Phragmites australis*) can substantially change the hydrology, sedimentation, clarity and nutrient state of lakes, reducing the habitat available for other species positioned higher in the trophic web such as invertebrates and fish (see examples in Crooks, 2002). Habitat-mediated impacts do not necessarily have the same direction as those produced by direct biotic interaction, and thus, the outcome of invasion largely depends on the intensity of both processes. Such complexity explains the lack of a unified theoretical framework to anticipate the ecological impacts of aquatic invasions.

Using quantitative meta-analyses, this study aims to determine the consistency of the ecological impacts of invasive species across taxa and habitats. To ensure the generality of our findings, we covered a wide range of invaders (primary producers, filter collectors, omnivores and predators), resident aquatic functional groups (macrophytes, phytoplankton, zooplankton, benthic invertebrates and fish) and habitat types (rivers, lakes and estuaries). In this study, ecological impacts encompass changes in the abundance or diversity of resident communities produced either by direct biotic interaction with the invader, or as a result of habitat alterations. Thus, the introduction of invasive species is expected to trigger changes through four major mechanisms: (i) competition between species within the same trophic level; (ii) predation causing top-down changes after the introduction of predators or omnivores; (iii) grazing by herbivores or filter collectors that may scale up in bottom-up cascades; (iv) habitat alteration by ecosystem engineer species. By analysing changes not only in resident aquatic communities but also in the physicochemical conditions of invaded habitats, this study helps unravelling the direct and indirect consequences of biological invasions. Finally, the impacts of invasive species vary widely spatially and are highly context-dependent (Ricciardi *et al.*, 2013). We therefore compared the impacts of the invasive species across types of invaded habitats (lake vs. river vs. estuary) and between different study approaches (observational vs. manipulative vs. mesocosm). Ultimately, this review combines characteristics of the invader (trophic position) and the invaded ecosystem (functional group and habitat) to draw broad generalizations regarding the ecological impacts of aquatic invasions.

Methodology

Literature search and study selection criteria

We conducted a literature search on Scopus (http://www.scopus.com/) for the terms: (invas* OR alien OR non-native OR exotic) AND (lake OR river OR estuary OR wetland OR reservoir) AND (impact OR effect). We included all published records up until 24 February 2014 within the subject areas of agriculture, and biological and environmental sciences, which generated 2118 hits. After an initial screening of reference titles and relevant cross-linked references, approximately 400 articles were individually assessed. The criteria for further inclusion were as follows:

1. Type of invasive species. The invaders considered in this study included aquatic species across all taxa, from phytoplankton to fish. We selected studies with a clear focus on the impact of a single species rather than that of multi-species assemblages. Each species was classified by its trophic position into four major groups: primary producers, filter collectors, omnivores and predators (see a list of species in Table S1). Most filter-collector organisms (92%) were filterers (e.g. the bivalves *D. polymorpha* and *Corbicula fluminea*), but also included some deposit feeders (e.g. the gastropod *Batillaria australis* and the bivalve *Nuttalia obscurata*) and scrapers (e.g. the gastropods *Bellamya chinensis* and *Potamopyrgus antipodarum*). Some taxa were over represented in the literature (e.g. *D. polymorpha, C. carpio*), with the 10 most studied taxa accounting for >50% of the cases analysed (see Fig. S1). In contrast, under-represented groups of invaders in the literature included herbivores able to substantially affect the abundance of aquatic plants and algae. Only one herbivore (*Pomacea canaliculata*) was

included and thus incorporated in the omnivores group. Such under-representation of impact studies with invasive herbivores was already noted by Thomsen *et al.* (2014).

2 Response variables. The community response variables included the abundance (comprising density, biomass and coverage metrics) and diversity (encompassing richness and diversity measures such as the Shannon and the Simpson index) of five aquatic functional components, defined as groups of organisms that share similarities in terms of life history, body size and feeding behaviour: macrophytes, phytoplankton, zooplankton, benthic invertebrates and fish. To avoid potential biases introduced by the inclusion of different abundance and diversity metrics, we compared the observed effect sizes between metrics prior to meta-analysis (see 'Effect size calculation'). In terms of physicochemical responses, the variables included water turbidity, organic matter, nitrogen (including total nitrogen, nitrate, ammonia and organic nitrogen) and phosphorous (total phosphorus and phosphate) compounds.

Data on the sample size, the mean and the standard deviation of response variables in invaded (treatment) and uninvaded (control) sites were extracted either from tables and the text of the published papers, or using the program DATATHIEF (http://datathief.org/) when data were only available in figures (roughly 60% of cases). Only replicated studies (sample size >1 in treatment and control sites) incorporating data on the standard deviation or standard error of measures were selected.

3 Type of study. Regarding the experimental approach, we classified studies within three groups. The majority of studies were observational (*N* = 113 articles, 446 cases), which included: (i) invaded-reference studies: field studies comparing a number of water bodies that have been invaded (treatment) with water bodies that remained 'uninvaded' (control); and (ii) before–after invasion studies: temporal studies where 'before invasion' conditions corresponded to control and 'after invasion' to treatment. The second group was manipulative studies (*N* = 40 articles, 223 cases) and included (i) field studies that manipulated the habitat to investigate the effect of the target invasive species, frequently removing the invasive species, or using enclosures to prevent the entrance of the invasive species, the native species or else both; and (ii) before–after eradication settings where the study investigates the recovery of the natural communities after the eradication of the invader. In this case, 'before eradication' was considered the treatment and 'after eradication' the control. The third group incorporated indoor mesocosm studies (*N* = 13 articles, 64 cases) that included replicated treatments with and without a particular invasive species. The control in this type of study consists on the effect of a 'native species' or 'no species' at all.

One may argue that observational and experimental studies (including both manipulative and mesocosm studies) differ systematically in variance and cannot be considered in a single meta-analysis (Hurlbert & Lombardi, 2003). For instance, experimental studies are a simplification of natural ecosystems and usually have a short duration, which reduces the variability of the response variables in comparison with observational studies. However, Hillebrand & Gurevitch (2014) recently demonstrated that such differences in data variation between field and experimental studies are generally small and unlikely to affect the outcomes of the meta-analysis.

4 Habitat. For all studies, the habitat was classified as lake (encompassing different types of stagnant waters, such as wetlands, lakes, ponds and reservoirs), river (flowing waters, such as rivers and streams) and estuary (brackish waters, including bays and coastal wetlands). Meta-analysis reporting impacts in purely marine habitats and not covered in this study can be found in Thomsen *et al.* (2014) and Maggi *et al.* (2015).

5 Nonindependence of study cases. When the study incorporated information on more than one control (e.g. native species and no species), experimental treatment (e.g. several invasive species, BACI designs, nested designs), resident functional group (e.g. phytoplankton and zooplankton) or physicochemical variables (e.g. turbidity and organic matter), we considered each of these separately as they represent different cases of ecological impact. However, when multiple invasion density treatments were reported, we used data from the highest invasion density treatment. Likewise, when data from multiple sampling dates (e.g. sampling at different seasons or years) were available, we used the last available sampling date. While this can represent a form of pseudoreplication in the meta-analysis, the same approach has previously been used in meta-analysis (e.g. Rey-Benayas *et al.*, 2009; Vilà *et al.*, 2011). The influence of pseudoreplication was nevertheless tested with a randomly selected single effect size per article (see 'Effect size calculation').

The final database contains information from 166 articles from which we retrieved 733 cases that assessed the impact of aquatic invasive species on several aquatic functional groups and water physicochemical variables (see a full list of references in Table S2, and find the full database in Table S3). The database covered a total 67 invasive species with a broad representation of fish (24 species), plants (22 species), molluscs (11 species) and crustaceans (7 species). Most of the studies incorporated in our database were conducted in North America (89 articles, 420 cases) and dealt with invasive species from Europe (68 articles, 313 cases) (Fig. S2).

Data analysis

We examined the response of aquatic communities to biological invasions using standard meta-analytical models. First, meta-regression models were used to investigate the overall effects of invasive species, without attending to the type of invader, on (i) the overall abundance and diversity of aquatic communities, (ii) the abundance and diversity of five different functional groups and (iii) four physicochemical variables. Afterwards, a new set of meta-regression models were implemented subdividing the database by the trophic position of the invader.

Effect size calculation. Meta-analyses were based on differences in the 'effect size' between invaded (i) and control (c) treatments. Amongst different measures of effect size, the standardized mean difference (SMD, equivalent to Hedge's *d*, Hedges, 1981) was selected and calculated as:

$$\mathrm{SMD} = \frac{\bar{X}_\mathrm{i} - \bar{X}_\mathrm{c}}{S} g,$$

where $\bar{X}$ denotes the mean value of the response variable being abundance, diversity or physicochemical characteristics in treatment and control groups; S is the pooled standard deviation of the two groups; and g is a weighting factor based on the number of replicates in the treatment (N_i) and control groups (N_c), calculated as follows:

$$g = \left(1 - \frac{3}{4(N_\mathrm{i} + N_\mathrm{c}) - 9}\right).$$

The SMD is unitless and ranges from $-\infty$ to $+\infty$. The interpretation of the magnitude of effect sizes that is used throughout this study follows Cohen (2013): 0.2 is considered a small effect, 0.5 is medium in magnitude, 0.8 is large, and any effect >1.0 would be considered very large. A negative effect size in our study indicates that the variable of interest (abundance, diversity or physicochemical characteristics) decreases in the presence of the invader, while a positive effect indicates the opposite. Thus, we should emphasize that positive and negative effects imply no judgement of the costs or benefits of biological invasion.

Some studies reported data on more than one treatment, control or resident functional group. To investigate the potential effects of pseudoreplication, we compared effect sizes calculated for the complete data set, with those observed for a randomly selected single effect size per study (reduced data set). Observed effect sizes in the complete and reduced data sets were not significantly different (ANOVA, $F_{1,395} = 3.93$, $P > 0.05$) (Fig. S3). As a consequence, we felt confident to include all the data in our analyses (as in Vilà *et al.*, 2011).

Likewise, because effect sizes reported by studies using different measures of abundance (density, biomass and coverage) and diversity (number of taxa, Shannon and Simpson diversity) were not significantly different (Abundance: ANOVA $F_{3,27} = 2.22$, $P > 0.05$; Diversity: ANOVA, $F_{2,168} = 0.52$, $P > 0.05$), we decided to pool together the three abundance and diversity metrics.

Meta-regression models. Meta-regression models were used to examine the influence of the trophic position of the invader and study-level covariates on the observed effects of invasion. Meta-regression analysis is a quantitative method of conducting literature meta-analysis that is more effective than other classical analyses of variance or standard meta-analytic techniques (Viechtbauer, 2010). Effect sizes across all cases are combined by meta-regression models to provide the overall effect size estimate (μ) and confidence interval (CI), where the weight of each individual effect size is the inverse of its variance. If the confidence interval for a given effect excluded zero, we considered the effect significant at the 0.05 level. Wide confidence intervals generally indicate large unexplained variation in the main effects, while narrow intervals suggest that the effect does not vary across studies.

To define the variation in effect sizes that can be ascribed to differences between our five functional groups (macrophytes, phytoplankton, zooplankton, benthic invertebrates and fish), the model treats the effect of functional group as a 'moderator' and adds a random effects variance component that represents the variability within each of the groups. For each meta-regression, the total heterogeneity in the data can be partitioned into heterogeneity attributed to moderators (Q_M) and unexplained or residual heterogeneity (Q_E). Thus, the null hypothesis tested by Q_M is that no difference in invasive species impact exists among the five functional groups. A significant value of residual heterogeneity (Q_E) indicates that there is still significant heterogeneity unaccounted for by the model.

Differences in the habitat, type of study and control may introduce variability among the true effects. One way to solve this problem is to include random effect components in the model that may account for at least part of the variability in the true effects. In our case, we included three random covariables: habitat (three levels: lake, river and estuary), type of study (three levels: observational, manipulative and mesocosm) and type of control (five levels: native species, no species, low invader abundance, before–after and uninvaded, see types of studies and corresponding controls in Literature search and study selection criteria).

The restricted maximum-likelihood estimation was used for estimating the amount of residual heterogeneity (τ^2) and between-study variance (Higgins' I^2) of meta-regression models (Viechtbauer, 2010). The I^2 statistic estimates how much of the total variability in the effect size estimates can be attributed to between-study variation ($\tau^2 = 0$, therefore, implies $I^2 = 0\%$). The remaining variability in effect sizes can be ascribed to sampling error variance.

Publication bias. Meta-analysis results may be distorted by publication bias, that is the selective publication of articles finding significant effects over those that find nonsignificant effects (Rothstein *et al.*, 2006). In our case, this bias in publication can lead to an overestimate of the effects of invasion in aquatic ecosystems. Thus, three methods were used to assess the validity of meta-analyses. We started from the premise that accuracy in estimating the true effects of invasion will increase as the sample size increases. In a funnel plot representing effect sizes against the sample size of all individual cases incorporated in the meta-analysis, the results from small studies will scatter at the bottom of the graph, with the spread narrowing among larger studies. In the absence of bias, the plot will resemble a symmetrical inverted funnel. Conversely, if there is bias, funnel plots will be skewed and asymmetrical. Egger's test is used to quantitatively evaluate the asymmetry of the funnel plot (Egger *et al.*, 1997).

Our second approach was to use a 'trim and fill' method, which provides an estimate of the number of hypothetically 'missing' studies based on asymmetry in the funnel plot (Duval & Tweedie, 2000). Simply put, this method 'trims' off the asymmetric part of the funnel plot, then uses the remainder to 'fill' missing studies symmetrically around the centre of the plot and then recalculates the overall mean estimate and confidence interval. If results from this recalculation are not different from the initial (supposedly biased) analysis, we can conclude that the missing studies do not significantly affect the outcome of the meta-analysis.

Finally, we examined how robust the results are to the effects of publication bias using Rosenberg's fail-safe number (Rosenberg, 2005). A fail-safe number indicates the number of nonsignificant unpublished (or missing) studies that would need to be added to a meta-analysis to reduce the observed significance level to $P \geq 0.05$. Fail-safe numbers are often considered robust if they are greater than $5N + 10$, where N is the original number of cases (Rosenberg, 2005).

Context dependency of impacts

To test for context dependency in the outcomes of invasion, we investigated whether the size and direction of any effect is consistent under different habitat and experimental conditions. To this end, for each of our study covariables (habitat, experimental approach and type of control used), we averaged the effect sizes for invasive species at different trophic positions: for example the average effect of primary producers upon fish abundance in lakes, in rivers and in estuaries, respectively. We then tested the correlation between effects paired by habitats (e.g. effect size in rivers vs. effect size in lakes), experimental approach (e.g. effect size in observational vs. effect size in experimental studies) or type of control (e.g. effect size using native controls vs. effect size using no species as control). A significant and positive slope would indicate that, in spite of individual case study singularities, impacts are consistent between habitats and/or between experimental approaches. In contrast, lack of significance would be interpreted as a lack of consistency in impacts across categories. This analysis differs from the meta-analysis described above in that all effects (on the abundance and diversity of resident aquatic communities, and on physicochemical variables) are considered together, but paired by type of habitat or experimental setting.

Because all variables are in this case independent (i.e. none of them can be considered a response or explanatory), we used type II linear regression models following Legendre & Legendre (2012) recommendations: (i) we first confirmed that the random variation of variables was approximately similar, (ii) we then transformed the variables to render them normal, and (iii) finally, we used the major axis (MA) method to build linear models, which produces unbiased slope estimates and accurate confidence intervals (Jolicoeur, 1990). The variance explained by the models (R^2) will further indicate the agreement in effect sizes between habitats and experimental approaches.

Meta-analyses were run using the package 'METAFOR' (Viechtbauer, 2010), whereas the 'LMODEL2' package (Legendre, 2014) was used to fit type II regression models, both of them in R v.3.1.1 (R Core Team, 2014).

Results

Overall effects of invasive species on aquatic ecosystems

Invasive species caused a strong decrease in the overall diversity (mean estimate = −0.40; confidence interval: −0.69, −0.11; $P < 0.001$, $I^2 = 95.61\%$) and abundance (estimate = −0.34; CI: −0.57, −0.11; $P < 0.001$; $I^2 = 93.15\%$) of aquatic communities. However, a significant asymmetry was detected in the funnel plot (Egger's regression test, $P < 0.01$ both for aquatic abundance and diversity) (see Table S4). Furthermore, the trim and fill analysis suggested 55 ± 12 cases missing on the right side of the funnel plot for abundance and 19 ± 8 for diversity, evidencing a certain publication bias towards studies showing the negative impacts of invasion (Table S4). Nonetheless, after the potential effects of publication bias were accounted for by the trim and fill method, the decrease in species diversity and abundance after invasion remained significantly negative. Moreover, large fail-safe numbers (Table S4) suggest that we can be confident in our conclusion that invasive species generally cause a decrease in resident species diversity and abundance.

The five aquatic functional groups investigated showed varying responses to invasion, with a very large significant decrease in the abundance and diversity of macrophytes, and in the abundances of zooplankton and fish (Fig. 1a,b). For the other groups examined (phytoplankton and benthic invertebrates), the trend in the responses was also negative, but the confidence interval of the effect size overlapped with zero due to large variation among studies. Despite the detection of certain publication biases, particularly for phytoplankton and fish (Table S4), fail-safe numbers indicated that a very large number of nonsignificant studies would be needed to reduce the significance of our results.

In terms of physicochemical changes, there was a general tendency towards increased turbidity, organic matter and nitrogen concentration in invaded sites, although the confidence interval of the effect sizes overlapped zero (Fig. 1c). A significant asymmetry in the funnel plot was noticed for turbidity, whereas no publication bias was detected for the other three physicochemical variables (Table S4).

Impacts of invasive species from different trophic positions

Meta-regression models performed separately by trophic position of the invader further revealed distinctive impacts on aquatic ecosystems (Table 1 and Fig. 2). Primary producers significantly reduced the abundance

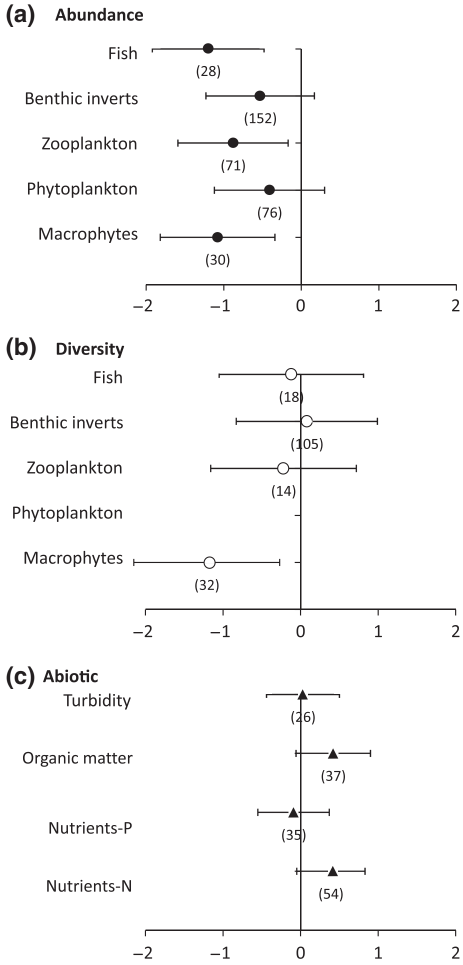

Fig. 1 Overall effects of invasive species on the abundance (a) and diversity (b) of five different functional groups of aquatic ecosystems and four environmental characteristics (c). In parentheses, the number of effect sizes considered in each case. Error bars represent 95% confidence intervals and are only displayed when the number of effect sizes analysed was ≥ 5. A significant effect of invasion is found when error bars do not overlap zero.

of fish and benthic invertebrates and produced a notable increase in the abundance of macrophytes and phytoplankton (Fig. 2a). Filter collectors produced a very large increase in the abundance and diversity of benthic invertebrates and a large increase in the abundance of macrophytes, while greatly reducing the abundance of planktonic communities (Fig. 2b, Table 1). This is congruent with the observed changes in environmental conditions, registering a medium-to-large reduction of turbidity and phosphorous, and a very large increase in organic matter content (Fig. 2f). Omnivores led to a very large reduction in the abundance and diversity of macrophytes, and a smaller decrease in the abundance of benthic invertebrates (Fig. 2c). Turbidity and nutrient concentration considerably increased after omnivore invasion, whereas the content of deposited organic matter decreased (Fig. 2g). Predators caused a medium decrease in the abundance of two potential groups of prey (benthic invertebrates and zooplankton) while driving an increase in phytoplankton abundance and nitrogen concentration (Fig. 2d,h). When impacts were analysed by type of predator, further significant impacts emerged (Fig. 3): piscivores led to a large decline in fish and benthic invertebrates, whereas zooplanktonic communities were negatively affected by benthivores and to a lesser extent planktivores. Full statistics of meta-regression models (including model fit statistics and heterogeneity indicators) can be consulted in Tables S5 and S6.

Context dependency of impacts

According to the information compiled in this study, the overall effects of biological invasions do not significantly change across the three types of habitats investigated (ANOVA, $F_{2,87} = 1.20$, $P > 0.05$). Yet, particular differences could be observed across habitats, mostly in the concentration of nutrients (Table 2).

Type II regression models indicated a high agreement of effect sizes between lakes and estuaries, and to a lesser extent between rivers and lakes, but there was no relationship between effects observed in rivers and estuaries, which may be explained by the low sample size (Table S7 and Fig. 4). The impact of invasive species also showed a high agreement among experimental settings, especially between the two types of experimental approaches: manipulative and mesocosm (Table S7). In accordance, the differences in mean effects were not statistically significant (ANOVA $F_{2,92} = 0.09$, $P > 0.05$). However, differences arose when investigating the type of control used as reference (Table S7). In particular, effect sizes reported in studies utilizing native species as controls (mostly mesocosm studies) were uncorrelated with those using more complex uninvaded conditions as reference (e.g. before–after and invaded–uninvaded studies).

Discussion

Overall effects of invasive species on aquatic ecosystems

Our global quantitative synthesis consistently suggests that aquatic invaders produce a generalized decrease in the abundance and diversity of aquatic communities. Among different functional groups of the recipient community, the meta-analysis revealed large-to-very large decreases in the abundance of fish, zooplankton and macrophytes in invaded habitats, whereas the impacts of invaders on the abundance of benthic

Table 1 Meta-regressions of the impacts of invasive species at different trophic positions on the diversity of resident aquatic communities. Q_M and the associated P-value provide a test for the effect of functional grouping on the mean effect size, while Q_E provides a test of residual heterogeneity, estimated by τ^2. Measures of between-study variation (I^2) and the amount of variance ($\sigma > 0$) attributed to three random variables are also included. Results are only shown for functional groups examined by more than one study in the database. Graphical outputs can be consulted in Fig. S4

Trophic position (invader)	Functional group (resident community)	Mean effect	95% CI	P	Model statistics	Random variables (σ)
Primary Producers	Benthic invertebrates	−0.53	−1.65, 0.59	ns	$Q_E = 431.3$, df = 68, $P < 0.01$	Habitat = 0.26
	Macrophytes	−1.79	−2.96, −0.62	**	$Q_M = 34.3$, df = 2, $P < 0.01$	Type study = 0.14
					$\tau^2 = 2.54 \pm 0.54$, $I^2 = 91.6\%$	Type control = 0.63
Filter Collector	Benthic invertebrates	1.02	0.40, 1.63	**	$Q_E = 225.3$, df = 37, $P < 0.01$	Habitat = 0.09
					$\tau^2 = 1.53 \pm 0.47$, $I^2 = 94.62\%$	Type control = 0.16
Omnivores	Fish	−0.06	−0.32, 0.21	ns	$Q_E = 84.0$, df = 14, $P < 0.01$	
	Benthic invertebrates	−0.48	−0.76, −0.19	**	$Q_M = 22.4$, df = 3, $P < 0.01$	
	Macrophytes	−1.72	−2.70, −0.6673	***	$\tau^2 = 0.53 \pm 0.29$, $I^2 = 75.36\%$	
Predators	Fish	−0.76	−2.52, 1.01	ns	$Q_E = 164.2$, df = 42, $P < 0.01$	Habitat = 0.71
	Benthic invertebrates	−1.80	−3.59, −0.02	*	$Q_M = 42.7$, df = 4, $P < 0.01$	Type study = 0.88
	Phytoplankton	0.57	−1.66, 2.80	ns	$\tau^2 = 0.98 \pm 0.3$, $I^2 = 85.34\%$	Type control = 0.30
	Zooplankton	−0.08	−1.71, 1.86	ns		

ns, not significant. *Significant at $P \leq 0.05$, **Significant at $P \leq 0.01$, ***Significant at $P \leq 0.001$.

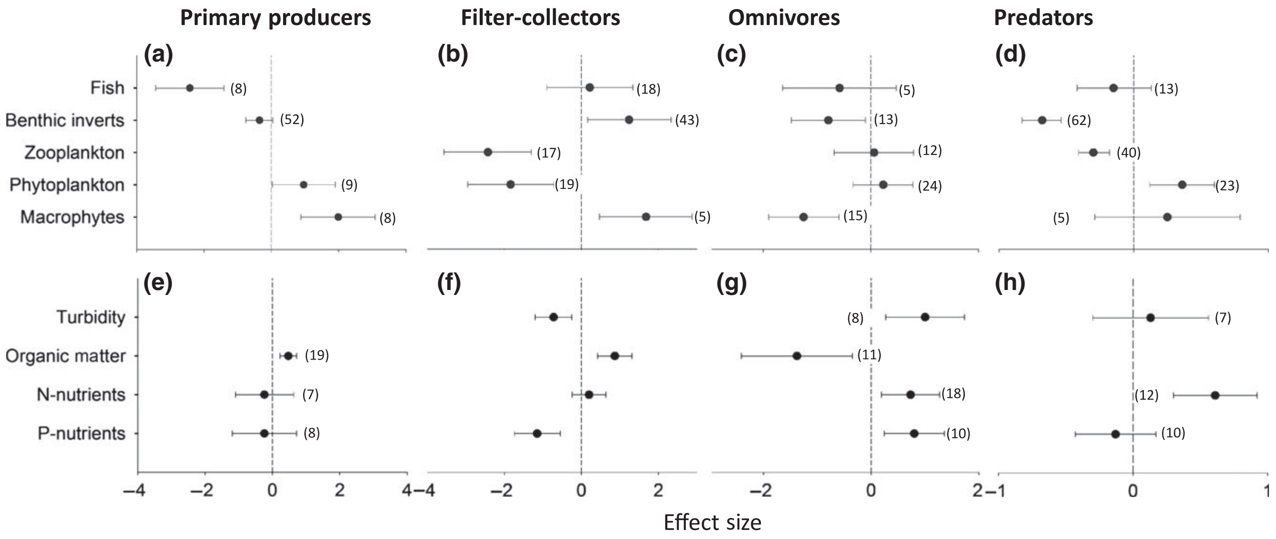

Fig. 2 Impacts of invasive species on the abundance of resident aquatic communities as determined by the trophic position of the invader. In parentheses, the number of cases considered. Error bars represent 95% confidence intervals and are only displayed when the number of effect sizes analysed was ≥5. A significant effect of invasion is found when error bars do not overlap zero. Consult full meta-regression statistics in Tables S5 and S6.

invertebrates and phytoplankton were generally variable and overall nonsignificant.

In contrast, except for a decrease of macrophyte diversity, there was no general evidence that the diversity of different functional groups of resident communities changed in invaded habitats. This finding has two possible explanations. First, invaders may prompt rapid abundance changes, but they may take a long time to produce local extinctions (*sensu* 'extinction debt', Tilman *et al.*, 1994). The relatively short time since invasion in many parts of the world may thus be insufficient to observe the full impact of biological invasions on resident biodiversity (Gilbert & Levine, 2013). Second, the invaded habitat may exhibit changes in assemblage composition due to changes in species dominance that are not necessarily reflected in local diversity. For instance, benthic invertebrate assemblages often shift as a response to the increased

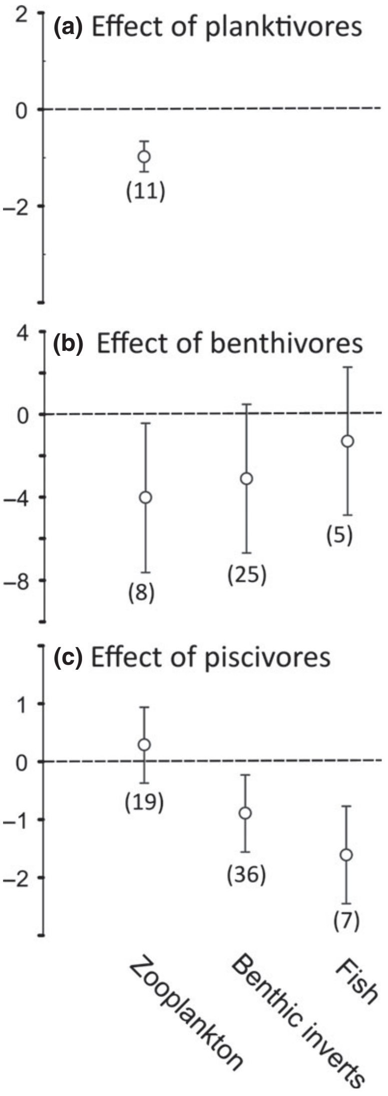

Fig. 3 Impacts of different aquatic predators on three types of prey. In parentheses, the number of studies considered. Error bars represent 95% confidence intervals and are only displayed when the number of effect sizes analysed was ≥5. A significant effect of invasion is found when error bars do not overlap zero.

predatory pressure exerted by invasive species, becoming increasingly dominated by taxa such as Hirudinea, Oligochaeta and Chironomidae (e.g. Crawford *et al.*, 2006; Kadye & Booth, 2012). Likewise, the introduction of planktivorous fish causes the rapid elimination of large-bodied zooplankton and their replacement by small-bodied taxa that may not be reflected in diversity metrics (Ordóñez *et al.*, 2010). Furthermore, because of the strong trophic links established in aquatic communities, the impacts associated to the introduction of invasive species extend beyond simple changes in the abundance of particular functional groups, but can threat species interaction at the community level (Sanders *et al.*, 2003).

Regarding environmental conditions, our analyses suggest increased nitrogen and organic matter concentrations in invaded habitats. Invasive species can certainly increase nutrient loading through dead material (e.g. excretions, 'senescence', Rooth & Stevenson, 2000; Driver *et al.*, 2005; Neira *et al.*, 2006) and changing hydrological conditions (e.g. increasing sedimentation rates, Botts *et al.*, 1996; Stewart *et al.*, 1998), which may deeply affect ecosystem functioning (e.g. nutrient cycles, metabolism, benthic-pelagic coupling, Ward & Ricciardi, 2007; Matsuzaki *et al.*, 2009; Higgins & Zanden, 2010).

Impacts of invasive species from different trophic positions

Based on results from our meta-analysis, we propose a framework linking the impacts of invasive species from four trophic positions to five different functional groups of recipient communities (Fig. 5). As expected, the impacts of invasive species in aquatic ecosystems were the result of direct ecological interactions (i.e. predation, competition, grazing) and indirect impacts mediated by changes in the physicochemical conditions of the habitats. In the following paragraphs, we explain each of the links identified in this study using the most logical mechanism documented in the literature. However, we recognize that the impacts of invasive species are often multifaceted and more complex explanations could be plausible.

Invasive primary producers, such as the common reed (*P. australis*) and the killer algae (*Caulerpa taxifolia*), are capable of changing the environmental conditions of their surroundings through the production of detritus and sediment capture (Rooth & Stevenson, 2000; Chisholm & Moulin, 2003), which affect the utilization of this habitat by fish and benthic invertebrates (Jayawardana *et al.*, 2006; Carniatto *et al.*, 2013). Likewise, the massive amounts of slime generated after algal blooms accumulates and decomposes in the deepest parts of lakes, interfering with resource use by invertebrates (Angeler & Johnson, 2013). While introduced plants may in some cases provide food and habitat for other animals (Schultz & Dibble, 2012), both benthic invertebrates and fish displayed a decrease in abundance in invaded habitats. An increased growth rate and the production of allelopathic chemicals have been found to underlie such negative impacts of invasive macrophytes on aquatic fauna (Schultz & Dibble, 2012). Our analyses also suggested a very large increase in organic matter content in habitats invaded by primary producers and a concomitant increase in phytoplankton. Under harsh environmental conditions (e.g. strong water current, low nutrient concentration,

Table 2 Mean and SD of effect sizes observed in three different habitats. The trophic position of the invader is indicated in the first column. Response variables are the abundance of five aquatic functional groups and four physicochemical variables. Empty cells indicate not enough data to calculate statistics ($N < 3$). Significant differences among the three habitats (ANOVA, $P \leq 0.05$) are indicated with*

Trophic position (invader)	Response variable (invaded ecosystem)	Lake	River	Estuary	
Primary producer	Macrophytes	1.65 ± 2.13		6.59 ± 7.14	*
	Phytoplankton	0.26 ± 0.66		1.18 ± 0.99	
	Benthic invertebrates	−0.60 ± 1.70	−0.51 ± 2.22	−0.33 ± 1.75	
	Fish			−2.44 ± 1.02	
	Nitrogen nutrients	−0.27 ± 0.03	−2.12 ± 1.92	−0.16 ± 0.42	
	Phosphorus nutrients	−0.06 ± 0.71	−1.38 ± 1.11	0.09 ± 0.06	*
	Organic matter	1.55 ± 1.80		0.52 ± 1.06	
	Turbidity	0.41 ± 0.36			
Filter collector	Macrophytes	1.76 ± 3.41			
	Phytoplankton	−1.12 ± 1.05		−1.11 ± 0.86	
	Zooplankton	−5.40 ± 5.70	−3.57 ± 5.46		
	Benthic invertebrates	2.19 ± 2.65		2.01 ± 1.66	
	Fish	0.20 ± 1.81			
	Nitrogen nutrients	−0.23 ± 1.34	4.05 ± 5.66	0.18 ± 0.43	*
	Phosphorus nutrients	−2.66 ± 2.36	−0.33 ± 1.06	−0.10 ± 0.01	
	Organic matter	1.57 ± 0.80		3.82 ± 11.14	*
	Turbidity	−0.24 ± 0.28		−0.74 ± 0.69	
Omnivore	Macrophytes	−1.47 ± 1.90			
	Phytoplankton	1.11 ± 2.04	−1.15 ± 1.96		*
	Zooplankton	0.02 ± 1.58			
	Benthic invertebrates	−1.36 ± 0.99	−0.45 ± 1.16		
	Fish		0.06 ± 2.05	−6.27 ± 3.44	*
	Nitrogen nutrients	1.25 ± 2.45			
	Phosphorus nutrients	1.04 ± 1.76			
	Organic matter	−0.29 ± 1.06	−2.07 ± 3.94		
	Turbidity	1.73 ± 1.43			
Predator	Macrophytes	−2.24 ± 2.28			
	Phytoplankton	0.66 ± 1.22	1.36 ± 2.58		
	Zooplankton	−1.08 ± 2.39	0.49 ± 0.49		*
	Benthic invertebrates	−2.08 ± 1.83	−0.83 ± 1.89		
	Fish	0.20 ± 2.64	−2.22 ± 1.79		*
	Nitrogen nutrients	1.18 ± 0.86	0.78 ± 0.96		
	Phosphorus nutrients	0.15 ± 1.88	−5.58 ± 7.75		*
	Turbidity	0.11 ± 0.12	0.51 ± 0.64		

unsuitable substrate), the introduction of invasive macrophytes that can change habitat conditions and increase detrital loading often leads to an increase in chlorophyll-*a* (Bishop & Kelaher, 2013), as well as the abundance of other macrophytes. This would explain the increase in phytoplankton and macrophytes abundances observed in invaded habitats. However, we must take results for macrophyte abundance with caution, because the eight studies reporting the impacts of invasive macrophytes upon aquatic plants considered in our meta-analysis compare invaded vs. uninvaded sites and do not discriminate between native and invasive plant productivity (as in Angeloni *et al.*, 2006; Scharfy *et al.*, 2009), which would result in inflated abundance scores. On the other hand, our analysis showed a lower diversity of aquatic macrophytes, which can be attributed to a combination of competition and habitat alteration (e.g. Angeloni *et al.*, 2006).

Filter collectors exerted a particularly negative impact on planktonic communities, and a positive influence on benthic invertebrates and macrophytes (Fig. 5b), changes that have been extensively documented in the literature (for a review see Higgins & Zanden, 2010). The mechanisms responsible for these changes include a combination of direct filtering and the indirect alteration of habitat conditions. Organisms such as the zebra mussel, the golden mussel (*Limnoperla fortunei*) and the Australian tube worm (*Ficopomatus*

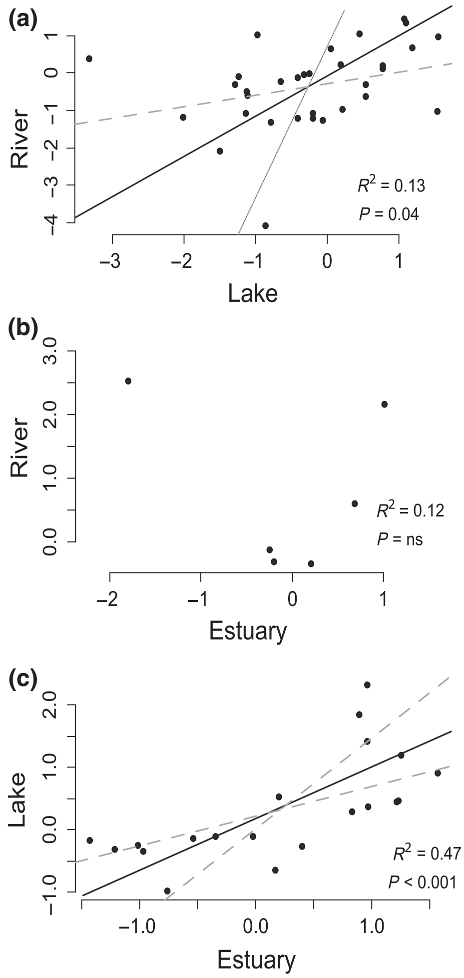

Fig. 4 Correlation between the impacts of invasive species in three different types of habitats. Regression lines (black), 95% confidence intervals (grey dashed lines) and statistics have been obtained through type II regression models. A significant positive slope indicates that impacts are consistent between habitats. Consult full statistics in Table S4.

enigmaticus) directly filter large quantities of particles from the water column and reduce the concentration of phosphorus compounds, usually considered a limiting nutrient for phytoplankton production in freshwater ecosystems (Higgins & Zanden, 2010). Both factors explain the large decline in phytoplankton abundance registered in our analyses. Filter feeders also collect small zooplankton (e.g. nauplii) and deplete food resources for larger zooplankton (e.g. Bowen & Johannsson, 2011). Increased water clarity allows for aquatic macrophytes to grow, with studies registering up to threefold increases in macrophytes biomass (Karatayev, 1992; Karatayev & Burlakova, 1995). Additionally, filter feeders are commonly considered ecosystem engineers because of the complex substrate structure they create, which explains the strong increase observed in the abundance of benthic invertebrates in invaded habitats (e.g. Higgins & Zanden, 2010; Bazterrica *et al.*, 2012).

Several studies have reported massive reductions in the coverage of submerged macrophytes within a few years of invasion by omnivores such as crayfish (e.g. Feminella & Resh, 1989; Rodríguez *et al.*, 2003). In fact, the largest decrease in macrophytes abundance and diversity was associated to invasive omnivores. This could be due to significant alteration of nutrient dynamics through excretion and bioturbation (Angeler, 2001; Matsuzaki *et al.*, 2007). Accordingly, turbidity and nutrient concentration considerably increased in the presence of omnivore invaders. In addition, we observed a large decrease in benthic invertebrates which could be related to direct consumption, but also to habitat disturbance (e.g. resuspension of sediments) and nonconsumptive destruction of macrophytes (e.g. the uprooting of plants while foraging invertebrates) (Matsuzaki *et al.*, 2009; Lodge *et al.*, 2012).

Acting through selective predation, the introduction of invasive predators such as the rainbow trout (*Oncorhynchus mykiss*) and the spiny water flea (*Bythotrephes longimanus*), was related to a considerable decrease in the abundance of fish, benthic invertebrates and zooplankton, which in turn increased the abundance of phytoplankton. This observation is congruent with an ample body of literature reporting on the cascading impacts of fish in aquatic habitats (e.g. Power, 1990; Brett & Goldman, 1996), which are partly explained by the inability of native prey to respond to predators that they do not naturally coexist with (e.g. Simon & Townsend, 2003; Stoks *et al.*, 2003; Kadye & Booth, 2012). The large increases in nitrogen compounds in invaded habitats have been related to excretion and bioturbation and are thus proportional to the invader's biomass (Driver *et al.*, 2005). For instance, fish suspend sediments and associated nutrients in the water column by directly feeding on or uprooting macrophytes while foraging for benthic invertebrates (Miller & Crowl, 2006; Matsuzaki *et al.*, 2009; Fischer *et al.*, 2013).

Context dependency of impacts

Multiple studies have highlighted that the impacts of invasive species are context-dependent, differing between species and habitats (Ricciardi & Atkinson, 2004; Ricciardi *et al.*, 2013). To give some examples, the impact of filter-feeding dreissenids is greater on fine sediments than rocky habitats, because the mussel patches are quickly colonized by highly mobile fauna unable to occupy otherwise fine sediments (Ward & Ricciardi, 2007). Fish abundance increases in littoral habitats colonized by the zebra mussel because of the

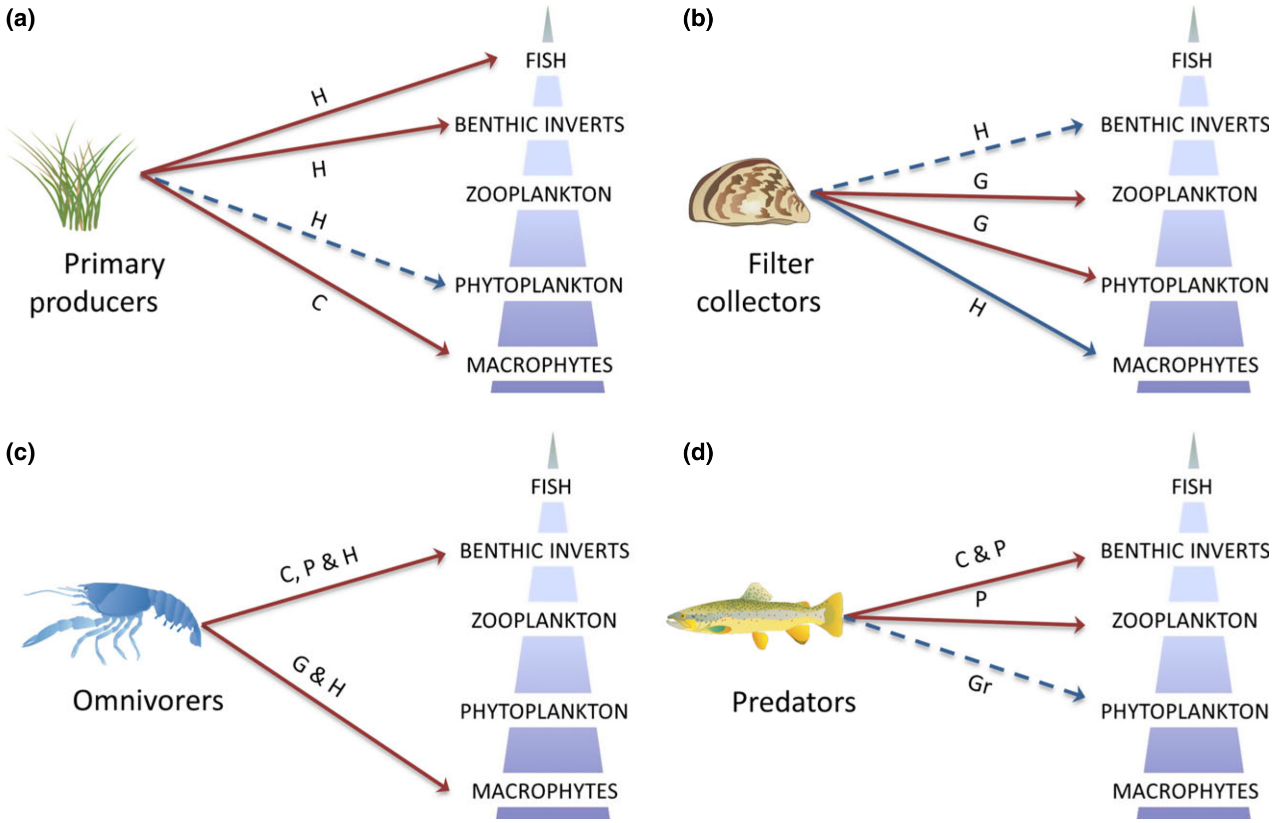

Fig. 5 Empirical framework summarizing links identified in this study. Arrows reflect the negative (continuous) or positive (dashed) impacts of invasive species on the abundance of five different functional components of resident communities. Impacts are the result of a combination of direct ecological (C, competition, P, predation, G, grazing, Gr, grazer release) and indirect physicochemical impacts of invasive species (H, habitat alteration). A simplified version of this framework can be found in Thomsen *et al.* (2014). Images extracted from the Integration and Application Network (http://ian.umces.edu).

associated increase in food resources, but decreases in open waters (Strayer *et al.*, 2004). Because dead organic matter accumulates in the deepest part of lakes, this habitat suffers the consequences of algal blooms more intensively than the littoral or pelagic parts of the lake (Angeler & Johnson, 2013). Plant invasions have a particularly significant impact when colonizing otherwise unvegetated tidal flats, where they can significantly change the hydrological conditions and thus habitat availability for fish benthic fauna (Stenzel *et al.*, 2002).

Indeed, our meta-analysis evidenced a very high level of between-study variation, which ranged between 23% and 94% (Tables 1, S5 and S6). Nevertheless, the size of effects was correlated between habitats, experimental approaches and types of control at a modest, yet significant, rate of 12–53% (Table S4). This means, for instance, that invasive species with a particular negative impact in lakes, are likely to exert similar effects in rivers and vice versa.

While the variation associated with observational studies was greater than that of experimental or manipulative studies, our analyses indicate that impacts are also consistent across experimental approaches. This is in agreement with the suggestion of Hillebrand & Gurevitch (2014) that, despite the greater between-study variation associated with field rather than laboratory studies, this difference is unlikely to affect conclusions from research synthesis. One significant conclusion from our context dependency analysis is that experimental studies using single (native) species as a control constitutes an oversimplification of natural conditions that underestimates the capacity of invasive species to trigger wide multi-level changes.

Conclusions

Over the last century, the potential for aquatic invaders to expand their range of distribution has been enhanced by the construction of new canals and increasing trade (Panov *et al.*, 2009). At present, the understanding of the dispersal and establishment of invasive species is far more advanced than that of their impact, scattered across multiple local studies (Simberloff *et al*., 2013). This has led to the general impression that the impacts of invasive species in aquatic ecosystems are context-dependent (Thomsen *et al*., 2011). This study demonstrates that generalities in the impacts in multiple trophic levels do exist and are likely related to the trophic position of the invader and its ability to modify habitats (Thomsen *et al*., 2014; Maggi *et al*., 2015). In some cases, impacts propagate up and down the food web, as in the case of filter collectors and predators. In others, however, changes dissipate within one functional level, suggesting compensatory effects to the introduction of invasive species, such as the presence of refuges, the ability to shift food sources (in the case of omnivores) and mechanisms to avoid predation (Pace *et al*., 1999). Nevertheless, the tests of residual heterogeneity suggest the existence of additional structural moderators affecting the outcomes of invasion. Further research is therefore needed to unravel the multiple determinants of the impacts of biological invasions, which may include characteristics of the invader (such as abundance and life history), and of the invaded ecosystem (such as the system's evolutionary experience with similar species and the presence of other invaders) (Ricciardi & Atkinson, 2004).

Overall, this study demonstrates that invasive species trigger strong and relatively consistent ecological impacts on aquatic ecosystems. The resulting global synthesis proposes a general framework for predicting the consequences of invasion that can be used by invasion ecologists as a reference for hypotheses testing. This framework is also relevant for environmental practitioners, because distinguishing invaders with minor effects from those with large multilevel effects is critical for guiding management and prevention efforts (McCarthy *et al*., 2006; Ricciardi *et al*., 2013).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Top 10 invasive species covered in this study.
Figure S2. Characteristics of the database.
Figure S3. Test for pseudoreplication.
Figure S4. Impacts of invasive species on the richness of resident aquatic communities.
Table S1. Aquatic invasive species reviewed in this study.
Table S2. List of references reviewed in this study.
Table S3. Database used to perform meta-regression analyses.
Table S4. Results from publication bias analyses.
Table S5. Results from meta-analysis testing impacts on the abundance of aquatic communities in the invaded ecosystem.
Table S6. Results from meta-analysis testing impacts on the physicochemical conditions of the invaded ecosystem.
Table S7. Results from context dependency analysis.