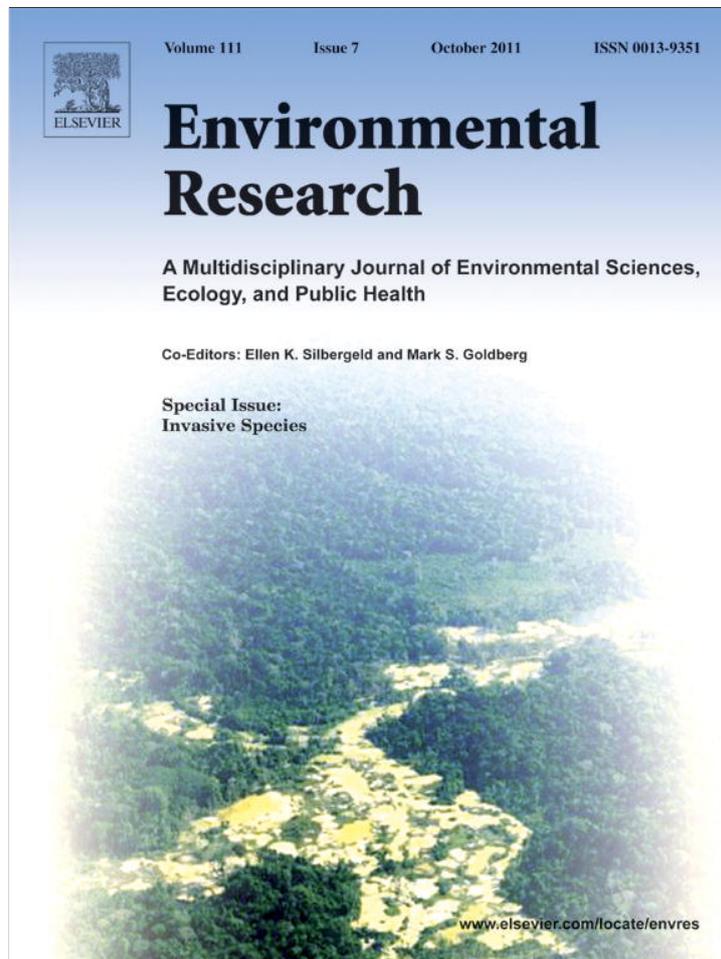


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A broad framework to organize and compare ecological invasion impacts

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ABSTRACT

Invasive species have transformed local, regional and global biotas; however, few generalities about the mechanisms driving impacts of invaders have emerged. To explain variation in impacts among studies, we propose a broad framework that separates drivers of impacts into universal and unique attributes of the invasive species and the invaded habitat. Universal attributes are relevant to all invasions whereas unique attributes are distinct to a specific invasion. For example, impacts associated with the abundance of any invader or the properties of a specific invader (e.g., a rare toxin) represent a universal and unique impact attribute. Through meta-analyses of aquatic field experiments, we demonstrate the utility of our framework, documenting that both the abundance and the taxonomic identity of the invader significantly influence invasion outcomes for marine and freshwater plant and animal invaders. Our review also highlights that many more experiments are needed to test for universal attributes, such as priority effects, age and size, and how the attributes of the invaded habitat further modify invasion impacts. We hope that our framework will stimulate experimental invasion ecology and begin to reconcile the idiosyncrasies that currently impede the development of a unified framework for invasion impacts.

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1. Introduction

Ecological impacts of invasive species on ecosystem structure and function have been documented around the world (Parker et al., 1999; Byers et al., 2002; Grosholz, 2002; Levine et al., 2003; Olden et al., 2004; Strayer et al., 2006). Upon arrival to a new region, some non-native species can quickly integrate and become part of the recipient food web (Agosta and Klemens, 2008) and, like any other organism, participate in biotic interactions such as predation, competition and habitat engineering. The impact of an invasive species can be defined according to a “measurable change to the properties of an ecosystem” (Ricciardi, 2003), thus implying that *the invader is the causal agent of ecological change*. In the present paper, we focus on the impacts of invasive species on the resident biota, and do not consider impacts on economic or cultural values, or on abiotic ecosystem properties. We use ‘impact on’ as a synonym of ‘effect on’, ‘changes to’ and ‘consequence of’, without implying any anthropocentric negative connotation (Strayer et al., 2006).

To date, few generalizations have emerged from studies on ecological impacts of species invasions. For example, Parker and colleagues, in the inaugural publication of *Biological Invasions* (1999), provided a comprehensive review of the current understanding of impacts but concluded that “our lamentable paucity of data on impacts leaves us largely ignorant about the ecological changes they have brought about” (p. 15). More recently, Pyšek and Hulme (2009) have stated that “invasion biology as a separate discipline will continue to be questioned until we have a better framework for understanding the impacts of invasive species”. We concur with these viewpoints and assert that the challenge for research is not to separate non-native species into artificial groups of organisms that have or do not have ecological effects, but to address the community and environmental context within which the effects of non-native species are manifest. Indeed, one of the few generalizations that we can make from past studies is that invasion impact depends on the specific spatio-temporal context in which the invasion event is embedded (Ricciardi, 2003; Ricciardi and Atkinson, 2004; Padilla, 2010).

Several frameworks for organizing invasion impacts have already been proposed (Table 1). These frameworks argue that a few essential ‘impact factors’ overwhelmingly determine the directions and magnitudes of the observed ecological impacts. These factors/drivers should therefore be quantified to enable comparisons among studies, invaders and invaded habitats. Key impact factors include

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Table 1
Examples of invasion impact frameworks. These frameworks aim to organize impact studies around a few fundamental test factors. Frameworks are useful to organize impact studies, identify research gaps and rank the importance of fundamental impact factors and impact attributes.

Reference	Total impact (I) ^a	Impact factors emphasized
Parker et al. (1999)	$I = A \times R \times E$	Simple impact model that emphasize the importance of A and R of the invader (“the more there is—the higher the impact”). Does not explicitly address mechanisms of—or how to measure and standardize—per capita effects.
Thiele et al. (2010)	$I = \sum(A_j \times R_j \times E_j)$	Essentially as Parker et al. (1999). Emphasize that impacts should be integrated along sub-habitats/sub-ranges to incorporate non-linear differences in per capita effects across its range [Parker et al. also discussed this].
Lockwood et al. (2007)	$I = A \times R \times (E \times Ft \times Fe \times Fs)$	Emphasize that per capita effects vary along invasion stages. The aim to quantify conversion factors that translate units of success per stage into relevant impact.
Ricciardi (2003)	$I = A \times C \times EF$	Emphasize that impact is high if the invader is functionally different from the resident biota and in proportion to invader abundance. Functional distinctiveness can be difficult to define but taxonomy may be used as proxy. Note that for certain ecological interactions, such as competition or hybridization, impacts may be highest when functional or taxonomic distinctiveness is small.
Ricciardi et al. (2011)	$I = A \times C \times EF$; modified by propagule pressure	As Ricciardi (2003) but highlight that the initial invasion propagule pressure modify A , C and EF .
Strayer et al. (2006)	I depends on invader, resident biota, abiotic environment and species interactions, and is modified by time	Does not assume any particular functional relationships within and between impact factors. Emphasizes that impact factors change over short and long time-scales.
Thomsen et al.	I depends on unique and universal interacting attributes of the invader, resident biota, resource levels and abiotic conditions	Impact attributes differ in generality from unique (relevant to a single invasion) to universal (relevant for all invasions). A and R are examples of universal attributes of the invader. EF represents an interaction between the invader and resident biota, e.g., if the invader is functionally similar to resident biota “ I ” may be large via competition and hybridization, but small via engineering and habitat-modification. $Ft \times Fe \times Fs$ and PP are important when they affect invader attributes. Time (and space) is not considered a separate impact factor; instead, the attributes of the impact factors and their interactions, vary in time (and space).

^a Abbreviations: I =overall impact, A =abundance; r =range; e =per capita effect; j =impacted sub-habitat; C =composition of recipient community; EF =ecological function of invader; Ft , Fe , Fs =the invaders success at the transport, establishment and spread invasion stages.

the invader’s distributional range (R) and abundance (A) in the invaded region, the invader’s per capita or biomass effect (E) and the community composition of the resident biota (C) (Parker et al., 1999; Ricciardi, 2003; Strayer et al., 2006; Lockwood et al., 2007; Thiele et al., 2010; Ricciardi et al., 2011). In theory, R and A are well-defined and relatively straightforward to quantify, whereas it is less clear how E and C should be defined, standardized and quantified. Also, an explicit emphasis on R , A , E and C may lead researchers to overlook other factors that also influence invasion impact, such as priority effects, or the size, longevity, sex and age of invaders. In addition, factors associated with key resident species like their age, size and abundance could also be important (Hanson et al., 1990; Walton et al., 2002; Eisenhauer and Scheu, 2008). To date, few studies have assessed if the impact factors listed in Table 1 are ecologically relevant across different invasive taxa, habitats and ecosystems (Ricciardi and Atkinson, 2004; Ricciardi and Cohen, 2007; Ricciardi and Kipp, 2008), and no quantitative synthesis has compared the magnitude of impact between multiple impact factors. Instead, the existing frameworks have mainly been applied to interpret invasions of individual species (Ricciardi, 2003; Thiele et al., 2010; Thomsen et al., 2010b).

Although the quantification of R , A , E and C is important, a broad framework should additionally (i) strive to organize all impact studies under a common framework, (ii) challenge researchers to identify specific attributes associated with different impact factors and not confuse causative agents, (iii) facilitate a way to quantify and compare the magnitude and direction of the impact factors and impact attributes from different studies to allow impact ranking and aid management prioritizations, and (iv) stimulate the development of scientific testing of new impact attributes to refine more advanced impact models over time. Our objective here is to propose a general framework that embraces the context-specificity of invasion impacts, and which targets the points listed above. It is our hope that the provision of this framework emphasizing a comparative and systematic, rather

than an anecdotal and piecemeal, approach to the study of invasive species impacts will help to stimulate and prioritize research needs and advance our quantitative understanding of ecological impacts of invasive species.

In the following sections we first describe a general impact framework, borrowing from and expanding on previous frameworks (Table 1). We then provide a simple case study to demonstrate how the framework can be used to identify causative agents of impact, extract data from disparate impact studies, quantify common impact metrics, test if these differ from zero and discuss their ecological implications. Finally, we examine different general aspects of the framework, including how the framework can be improved, what impact factors should be further studied, and what type of impact data should be reported to facilitate rapid progress in invasion ecology.

2. The invasion impact framework

We differentiate between *impact-studies* that focus on the ecological consequences of the invasive species (=independent variable) on the physical and biological features of the receiving environment (=dependent variable) and *success-studies* that quantify any feature (=independent variable) that can promote the establishment and spread of invasive species (=dependent variable). These two study types are often thought of as separated in time, in part because the invasion process is considered as a step-wise progression of events starting with ‘uptake’, ‘transport’, ‘release’, ‘initial survival’, ‘establishment’ and ‘spread’, which is only then potentially followed by ‘impact’ (Sakai et al., 2001; Catford et al., 2009). Somewhat less recognized is that success and impact are intricately linked, in particular via the positive role of A and R on both success and impact (Parker et al., 1999; Catford et al., 2009). Invasion impact should therefore be viewed as a dynamic process (Strayer et al., 2006). This implies that all non-native species have

some ecological impact and that impacts can occur immediately upon arrival to the new region (but see Schlaepfer et al., 2011), despite the difficulties in isolating minor effects from the noise and variability that characterise ecological phenomena.

The ecological impact of invasive species depends on attributes related to the invader and the invaded habitat (Fig. 1). This is a simple and effective framework that classically has been used to explain invasion success (Drake et al., 1989; Mack, 1996; Heger and Trepl, 2003; Catford et al., 2009). The attributes of the invader include both genotypic and phenotypic traits, such as abundance, longevity or sex (Hanson et al., 1990; Walton et al., 2002), the filtering capacity of invasive molluscs' (Talman and Keough, 2001; Ricciardi, 2003) or toxins of certain invasive fish (Whitfield et al., 2002). We suggest conceptually partitioning the invaded habitat into 'the resident organisms', 'the resource levels' and 'the abiotic conditions' (Fig. 1). Many attributes of the resident organisms, such as their abundance, size-structure and assemblage structure are likely to influence invasion impacts. The resource factor refers to the characteristics of the invaded habitat that are utilized, such as nutrients or space, and thereby potentially modified by the invasive or resident organisms. Changes to the availability of resources alter the performance of the invader and/or resident biota, and can ultimately influence the observed invasion impact. The abiotic

conditions, such as temperature, salinity or pH, also affect the performance of the invader and resident biota but are not depleted (Chase and Leibold, 2003; Begon et al., 2006). The distinction between how the resource levels and the abiotic conditions of the habitat influence invasion impact is important from both a conceptual and modelling perspective (Chase and Leibold, 2003). For example, if nutrient levels of the invaded habitat are high, an opportunistic nutrient-dependent invader may initially have a high ecological impact, but, when its resource-base is depleted, may cause less impact over time. In this case, the impact depends on depletion rates. By contrast, if the temperature range of a habitat is stressful to the invader, we can more safely predict that this invader will have a constant low impact.

In our framework, the invasive organism is the primary impact factor; without the invader there would be no impact. The three habitat-associated impact factors are secondary factors that further modify the direction and magnitude of impacts (Fig. 1). The four impact factors attempt to be all encompassing of the key ecological interactions and processes (Begon et al., 2006) and have therefore recently also been suggested as a framework to organize invasion success studies (Catford et al., 2009). Note that these factors are not entirely mutually exclusive. For example, ontogenetic niche shifts may result in an invasive predator being a competitor as a juvenile, but a predator that utilizes the resident organism as a food resource when reaching the adult life-stage. In this case, a particular resident organism can both represent the resident biota and a resource.

Next, we emphasize that attributes associated with the invader, the resident biota, the available resources, and the abiotic conditions have different levels of generality. For example, the abundance and range of the invader can be quantified in all impact studies, whereas it is only relevant in a limited number of cases if an invader's defence toxins modify the invasion impact. It is important to correctly identify impact attributes and their associated level of generality to ensure robust inferences. For example, manipulative experiments often compare a single removal treatment to untouched control plots (Thomsen et al., 2009). The generalities that can be inferred from this binary presence-absence experimental design are limited because no explicit impact attribute is addressed and a specific level of generality therefore cannot be identified. In this experiment, observed impact can equally be attributed to the abundance, size, age or fitness of the invader. By contrast, if the design had included both a 50% and 100% removal treatment, inferences could have centred on how the abundance of the invader, as a general rule, influenced impact. Thus impact attributes, for each of the four impact factors, fall along a continuum of generality ranging from being of 'universal' to 'unique' relevance (Fig. 1).

Universal attributes refer to impact attributes that, at least in theory, can be extracted, standardized and compared between all studies, invaders, and invaded habitats. Potentially important universal attributes include the abundance, range, size, age, longevity, resource acquisition mode and vitality/vigour of the invader (Carlsson et al., 2004; Ross et al., 2007; Griffen and Byers, 2009). These attributes can be measured for any invasion and may influence the outcome of an invasion irrespective of other impact attributes, such as more specific genetic characteristics of the invaders or residents species. At the other end of the spectrum, unique impact attributes refer to attributes that are relevant to measure for only a single invasion, and where findings therefore cannot be extrapolated across studies. Truly unique attributes may be rare, but some impact attributes are only relevant to a few invasions, for example; impacts related to rare defence toxins. It is relatively common to compare the impacts of two invasive species on the same native species (Nystroem et al., 2001; Levin et al., 2002; Lohrer and Whitlatch, 2002b). However, general impact inferences are difficult to derive from two-species comparisons

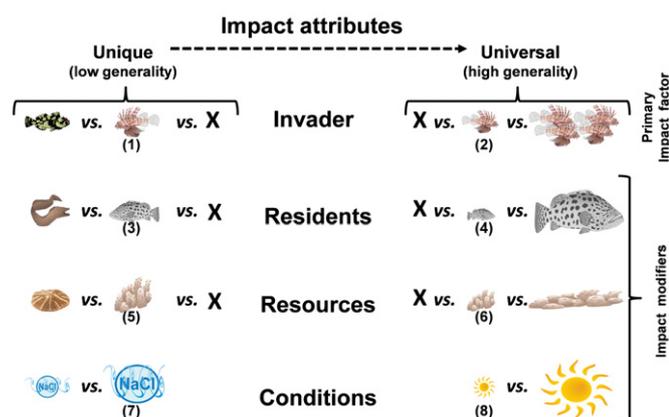


Fig. 1. The proposed framework to organize studies quantifying ecological impacts from invasive species. Numbers in brackets represent 8 hypothetical experiments with invasive species. Impact attributes can range from unique (1, 3, 5 and 7) to universal (2, 4, 6 and 8) attributes of the invader (1 and 2), and of the resident biota (3 and 4), resource levels (5 and 6), and abiotic conditions (7 and 8) of the invaded habitat. Resources are utilized by the invader and/or the resident biota and can be depleted whereas conditions are not utilized. A unique attribute is only relevant to measure in a single specific invasion event whereas universal attributes can be quantified in all invasions. Three (or more) treatments in an experiment can detect an invader impact attribute (1, 2; treatments separated by 'vs.' and 'X' corresponds to absence of the invader). A minimum of three additional treatments are needed, orthogonal to the primary impact factor (1 and 2), to quantify how a specific attribute of the resident biota (3 and 4) or resources (5 and 6) modifies invasion impact (the 'X' correspond here to absence of this attribute). Only two orthogonal treatments are needed to quantify how abiotic conditions (7 and 8) modify invasion impact because the 'absence of a condition' does not exist. Hypothetical examples explained: Impact on focal organisms may depend on the rare venom of an invasive lionfish that another invasive fish lack, i.e. a near-unique attribute (1) and/or on the abundance of the lionfish, i.e. a universal attribute (2). The impact of the lionfish can be modified by the resident biota, e.g., if a resident predatory fish have unique anti-venom that the other resident species lack (3), or by the size-structure (4) that allows the predator to engulf the lionfish. Impact may also be modified by resource levels; a unique combination of interstitial spacing and coral polyp toxicity (which the other reef-former lack), (5) may provide a safe nursery ground for juvenile lionfish to reach sizes that cause large impact. Alternatively, the spatial extent of the habitat (6) may determine recruitment success of the lionfish and ultimately its impact. Finally, impacts are also modified by abiotic conditions: a unique combination of salinity and hydrodynamics (7) or the level of a universal condition like temperature (8) may be required for the lionfish to impact focal organisms. Images and symbols used in the figure courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

because 'species-identity' reflects a highly complex aggregate of genetic and phenotypic attributes. Two-species comparisons are therefore positioned near the unique end of the generality spectrum. Many additional impact attributes can be identified along the generality continuum; in a few cases invaders may cause dramatic effects due to rare plant-toxins (Callaway and Ridenour, 2004), rare morphologies of sessile organisms (Heiman and Micheli, 2010), or rare and novel behaviours of mobile predators (Sih et al., 2010); in more cases invasions can be related to general filtering or substratum-forming capacities of relatively common invasive molluscs (Ricciardi et al., 1997; Crooks and Khim, 1999); and in yet many more cases impacts may be related to seed size of common invasive angiosperms (Eisenhauer and Scheu, 2008), or the sex of the invader (Hanson et al., 1990; Walton et al., 2002).

We also note that even though some attributes are relevant to measure only in a few invasions, the same attributes can also be compared quantitatively in a more general context. For example, a study documenting invasion impacts associated with a unique plant toxin can still be compared to other studies on a coarser scale; do invaders with (any kind of) toxins have higher impact than invaders without toxins?

Above examples have focused on how invader attributes support different levels of generality. The same arguments are valid for the three habitat-associated impact factors (Fig. 1). Resident organisms may be impacted because of their universal attributes such as their abundances or sizes (Walton et al., 2002) or because of their relatively unique attributes such as a specific evolutionarily naivety having evolved in an enemy-poor biogeographical region (Cox and Lima, 2006; Verhoeven et al., 2009; Sih et al., 2010). Analogous examples can also be identified for resources and abiotic conditions. For example, it is possible to standardize and quantify how universal attributes, such as the concentration, frequency or duration of any resource, will influence impacts. By contrast, it is more difficult to compare how two different resources, such as water and nitrogen for plant growth, will modify invasion impact. Again, from a practical viewpoint it is important that experiments compare a minimum of two treatment levels of habitat-associated impact factors to a control in order to be able to infer generalities about impacts and avoid confusing causative agents of impact.

In summary, invasion impact depends on attributes of the invader, the resident biota, the available resources, and the abiotic conditions where the invader is the primary test factor of interest and the three latter factors represent impact modifiers. These impact attributes vary in importance, from universal attributes, such as abundance and size that may be relevant to all impact studies, to more unique attributes, such as rare toxins or other peculiarities of species-identity that are relevant to fewer invasions. To progress from idiosyncratic and context-dependent interpretations of impacts, research should identify impact generalities along the unique-universal continuum, design experiments that explicitly target individual attributes, and ultimately quantify the relative importance, interactions and feedbacks between the different attributes. In the next section, we provide a simple case study to show how the framework can facilitate the identification of two unconfounded impact attributes. We then proceed to extract data from disparate studies to quantify standardized impact metrics.

3. Case study: Ecological impacts of invader abundance and invader identity

3.1. Introduction

Meta-analysis provides a quantitative method to standardize different studies to test for general patterns (Gurevitch and

Hedges, 1999; Rosenberg et al., 2000; Borenstein et al., 2009). We explored if our framework, combined with meta-analysis, could be used to organize invasion studies and test if individual impact attributes were statistically significant and different from each other. To do this, we searched for invasion impact literature that fulfilled six key requirements.

(1) We focused on impact studies in the aquatic sciences because this is our area of expertise, enabling us to conduct a near-exhaustive review, and minimize meta-analytical problems associated with selective and biased data-inclusion (Englund et al., 1999). (2) We only included manipulative experiments where the presence of the invader was under investigator control. In these studies, invaded treatment plots are compared to non-invaded control plots, facilitating causal inferences (Parker and Hay, 2005; Thomsen et al., 2009). We avoided mensurative experiments because these cannot, logically and unambiguously, distinguish invasion impacts from invasion success. (3) We focused on field/outdoor experiments to ensure high realism, where organisms share natural background fluctuations in environmental conditions such as temperature, light, salinity, tidal levels and climate. (4) To ensure high data quality, we only included studies published in peer-reviewed journals based on true replicated treatments and controls (Hurlbert, 1984). (5) We were only interested in ecological responses reported on individual and population levels because these can be interpreted as beneficial or adverse for the impacted resident organisms, in contrast to some behavioural responses or community-aggregated metrics. These responses included the organisms' size (length, area and biomass), fitness (growth, survival, mortality and reproduction) or abundance (counts, coverage and biomass). (6) Most importantly, we only included those studies where specific impact attributes could be identified in isolation. From an experimental design point of view, this implied that at least two treatment levels of an impact attribute were compared to uninvaded control plots. We therefore excluded all binary presence-absence test designs where a single level of invaded treatment plot was compared to the non-invaded control plot.

3.2. Methods

We examined the abstracts of > 900 peer-reviewed papers that appeared to address invasion impact in marine and freshwater ecosystems. Of these > 900 papers, 167 manipulated the presence of the invader in field/outdoor experimental settings, thereby fulfilling data requirements 1–5. However, the majority (56%) of the 167 studies applied binary presence-absence manipulations and could therefore not be used to identify individual impact attributes. A few studies that tested for specific impact attributes with a minimum of 2 manipulations and a control were not amendable for meta-analysis because we required at least five independent studies on a specific attribute to calculate standardized cumulative effect sizes with associated confidence limits (Borenstein et al., 2009). These attributes included the sex of the invader (Hanson et al., 1990; Walton et al., 2002), priority effects between invader and resident biota (Carlsson and Bronmark, 2006), size of the invader or resident biota (Kupferberg, 1997; Walton et al., 2002) or species-identity of the resident biota (Carlsson and Lacoursiere, 2005; Nilsson et al., 2008). Still, a sufficient number of studies tested specifically for effects of invader abundance or invader species identity ($n=39$ and 15 research papers, respectively, Supplementary material Table 2). In these studies, multiple levels of the invader abundance or several different invasive species were compared in a single experimental setting to the uninvaded control plots. Note that the abundance tests represent one of the most important universal attributes that can be reported for all invasion impact studies (Table 1). In this test we have a clear and simple *a priori* hypothesis;

impacts increase with increasing invader abundance. By contrast, comparisons of ecological impacts between two different invasive species represent a test of a unique attribute because differential impact between the invaders may be linked to an almost infinite number of genetic and phenotypic trait differences (Agrawal and Kotanen, 2003). Note also that in this test we cannot identify a clear directional expectation of impact.

We used Hedges effect size d , corrected for small sample sizes, to standardize effects between treatment plots where the invader is present and control plots without invaders for each of the 39 abundance and 15 identity studies. Hedges d is widely used in ecology, and it requires, and therefore encourages, researchers to replicate treatments and report measures of dispersal. Hedges d is statistically related to ANOVA methods and allows the use of zero-value responses (e.g., Gurevitch et al., 2000; Morales and Traveset, 2009; van Kleunen et al., 2010), which would otherwise have forced us to exclude another ~10% of the extracted effect sizes.

An all-inclusive unbiased data selection criterion (Englund et al., 1999) was used to extract effect sizes for each study. We calculated non-independent d -values for all reported impacted resident organisms (Ross et al., 2007), test-combinations (e.g., different depth levels, Thomsen, 2010), or for multiple quantified response variables of the same resident organisms, such as coverage and biomass (Airoldi, 2000). To avoid problems associated with temporal autocorrelation, we only included the last data points from repeated measure experiments (Parker et al., 2006). A reversal marker (-1) was used when needed (e.g., on mortality responses) to ensure d always was negative if the invader caused a reduction in ecological performance.

Following the calculations of Hedges d between controls and invaded treatments, we calculated the absolute value of Δd for paired responses (see Supplementary material Table 2 for calculation example). We calculated $\Delta d_{abundance}$ as $|d_{high} - d_{low}|$, where d_{high} and d_{low} correspond to the impact of the invader at high and low abundance levels, respectively. This formula ensures that $\Delta d_{abundance}$ is positive and does not cancel each other, if the *a priori* abundance hypothesis is supported, irrespective if the individual study aimed to test for negative (Byers, 2000) or positive (Thomsen, 2010) abundance-dependencies. We did not have a similar directional hypothesis for the identity test and we therefore calculated $\Delta d_{identity}$ simply by subtracting the effect size of the invasive species with the lowest d -value from the species with the highest d -value. This method always resulted in a positive $\Delta d_{identity}$ and represented a broad test of whether different invasive species have different impacts on the resident biota. The multiple non-independent Δd values from within a study were averaged to produce a single independent Δd value per study, using equal weight for each reported type of impact. Finally, we conducted unweighted cumulative meta-analyses on the 39 independent $\Delta d_{abundance}$ and 15 independent $\Delta d_{identity}$ values in Metawin 2.0 (Rosenberg et al., 2000). We used random-effect models to test if the cumulative effect sizes were significantly different from zero. Meta-analytical random-effect models assume that summary statistics have both sampling error and a true random component of variation in effect sizes between studies. We also tested if Δd differed between marine vs. freshwater invaders, plants versus animal invaders, between animal invaders with different feeding modes (separated into filter feeders, predators or grazers), or between invaders classified into different taxonomic groups (see Supplementary material Table 2 for taxonomic groupings).

3.3. Results

From the 39 abundance and 15 identity research papers, we tallied a total of 27 and 24 different invasive species, respectively (Supplementary material Table 2). These species covered a wide

range and type of invaders, including red, green, and brown algae, angiosperms, bivalves, crustaceans, polychaetes, fish and amphibians (Supplementary material Table 2) and invaded ecosystems such as estuaries, open coast, lakes, ponds, rivers, streams and rocky subtidal and intertidal coasts. We therefore consider our meta-analysis to have broad implications for diverse taxonomies, abundances and environments in aquatic ecosystems.

The meta-analyses showed that Δd were significantly different from zero in both the abundance and identity tests because the 95% CL did not overlap zero ($\Delta d_{abundance} = 3.14 \pm 2.00$; $\Delta d_{identity} = 4.96 \pm 4.23$). The effect size of identity was larger than for abundance (4.96 vs. 3.14), although the overlapping confidence limits demonstrate that $\Delta d_{abundance}$ and $\Delta d_{identity}$ were not significantly different from each other. Heterogeneity tests showed that cumulative effect sizes were consistent across studies ($Q_{total} = 38,000$ and $14,000$; $p = 0.469$ and 0.449 for the abundance and identity tests, respectively). More specifically, Δd did not vary significantly between marine or freshwater invaders ($p_{abundance} = 0.142$; $p_{species} = 0.377$), between plant or animal invaders ($p_{abundance} = 0.251$), between feeding modes of the invaders ($p_{abundance} = 0.738$, $p_{identity} = 0.338$) or between the invaders taxonomy ($p_{abundance} = 0.375$, $p_{identity}$ could not be calculated because of too few groupings) (Table 2). Several of the test-comparisons included relatively few studies (Table 2) and therefore had low statistical power.

3.4. Conclusions and discussion

We conclude that the abundance and species identity, representing a universal and a unique invader attribute, respectively, fundamentally influence the final outcome of invasion events in aquatic ecosystems. It is therefore of paramount importance that these attributes are clearly reported in all impact studies. We believe this is the first meta-analytical demonstration that manipulations of invader abundance affect the outcome of invasions across taxa, habitats and ecosystems. We did not here take into account absolute or relative differences in invader densities, but test-densities typically represented zero, ambient and 0.5 or $2 \times$ the ambient level, with no systematic differences between taxa or habitats. When more manipulative experiments become available that apply many abundance levels (e.g., Kotta et al., 2006), it will be important to also quantify and compare slopes calculated from impact vs. invader abundance curves for different invasive species and habitats, instead of the Δd values shown in the present paper. Such impact slopes represent strong per capita impact data and will provide more comparable means to rank invasion impact between disparate

Table 2

Categorical random-effect meta-analysis testing if $\Delta d_{abundance}$ or $\Delta d_{identity}$ differed between marine and freshwater invaders, animal or plant invaders, invaders with different feeding strategies (carnivores, herbivores, filter feeders and plants) or between broad taxonomic groupings of invaders (see Supplementary material Table 2). It was not possible to include identity tests for animal vs. plants or between taxa because of too few treatment-comparisons.

Attribute	Test	Model	df	Q	p (χ^2)
Abundance	Marine vs. freshwater	Between	1	2.148	0.142
		Within	37	37.000	0.469
	Animal vs. plants	Between	1	1.131	0.251
		Within	37	37.000	0.469
	Feeding	Between	3	1.261	0.738
		Within	35	35.000	0.468
Taxa	Between	5	5.344	0.375	
	Within	29	29.000	0.465	
Identity	Marine vs. freshwater	Between	1	0.778	0.377
		Within	13	13.000	0.447
	Feeding	Between	1	0.914	0.338
		Within	10	10.000	0.440

studies. The same experiments should also be used to compare curve-shapes of abundance-dependencies and under what conditions impact-thresholds become important (Thiele et al., 2010; Elgersma and Ehrenfeld, 2011). Additional data may also facilitate the refinement of the analysis to test if invasion impact varies predictably with abundances for different taxa, form-groups, habitats, etc. However, based on our simple analysis on a limited dataset we did not see any indication of this, suggesting that abundance is a very general impact attribute that has the same type of effects in different systems. In summary, we have here provided strong causal evidence of the essential importance of incorporating abundance in invasion impact frameworks (Table 1, Parker et al., 1999; Ricciardi, 2003; Strayer et al., 2006; Thiele et al., 2010).

Based on a smaller number of studies, we also found significant effects associated with the identity of the invader. Again, this may be the first synthetic demonstration, across species, habitat and ecosystems and based on experimental evidence, that not only the quantity (abundance and universal attribute) but also the quality (identity and unique attribute) of the invader influences the effect size of invasion impact. However, in contrast to the abundance analysis where the direction of impact is straightforward to predict and analyse, our determination that species-identity also affects invasion outcome is clearly of less predictive value. Still, with more studies, it may be possible to derive detailed generalities; for example, there was a tendency for larger Δd values between omnivorous crabs as compared to filter feeders, where the latter also had smaller overall effect sizes (Lohrer and Whitlatch, 2002a; Ross et al., 2007; Byrnes and Stachowicz, 2009). We see an important niche for studies that compare impact between invaders that are functionally and/or taxonomically similar. In these studies taxonomic or functional affinity can be used as trait surrogates (Agrawal and Kotanen, 2003; Agrawal et al., 2005). For the studies included in our analyses, most compared functionally similar invaders, such as omnivorous crabs (Lohrer and Whitlatch, 2002a; Lohrer and Whitlatch, 2002b; Griffen and Byers, 2009), predatory fishes (Young et al., 2009), or sessile filter feeders (Ross et al., 2007; Byrnes and Stachowicz, 2009). The significant cumulative effect sizes in these tests, where functional equivalency theoretically suggest small Δd values, highlight that genetically and phenotypic traits within functional groups are of essential importance to understanding invasion impacts. We therefore advocate that more studies manipulate abundance levels of multiple functionally similar species in orthogonal designs. Currently, we are only aware of a few studies that have done this (Kupferberg, 1997; Griffen and Byers, 2009), precluding formal meta-analysis of interaction terms.

4. General discussion

4.1. Research gaps in the study of invasion impacts

Over 25 years ago, the advisory committee for the Scientific Committee on Problems of the Environment articulated research questions to encourage a focus on biological invasions (Drake et al., 1989); “What factors determine if a species will be an invader?”, “What makes a habitat vulnerable to invasions?” and “How can invasions be managed?” These questions stimulated studies to explain invasion success (Drake et al., 1989; Davis, 2006, 2009) but not impact. The imbalance between a large number of studies on invasion success compared to a more limited research focus on invasion impacts is also reflected in text books that describe advanced ecological theories in chapters on invasion success, but typically focus on less theory-laden case-studies of impact (Hengeveld, 1989; Williamson, 1996; Myers and Bazely, 2003; Davis, 2009, but see Lockwood et al. (2007) for detailed impact synthesis). Thus, a perception dominates that invasion impacts

have limited generality, and there are few frameworks to synthesize studies and test meaningful hypotheses (Parker et al., 1999; Pyšek and Hulme, 2009). The perspective taken in our paper is that impact studies should be addressed with general ecological concepts and theories. A great opportunity exists to revisit decades of case-based impact research to extract generalities about what determines the strength and magnitude of invasion impact. To promote such a research agenda, we outlined a simple framework to organize disparate impact studies. Specifically, we suggest that impact factors can be sorted by attributes, ranging from universal to unique, associated with the invasive organisms, the resident biota, the available resource levels and the abiotic conditions (Fig. 1). Here, unique attributes are distinct to a specific invasion whereas universal attributes are relevant to all invasions. For example, impacts associated with the abundance of any invader or the properties of a specific invader (e.g., a rare toxin), represent a universal and unique impact attribute.

A similar distinction between unique and universal attributes may also be pivotal to understanding invasion success. For example, many studies have shown that the success of an invader can depend, among other attributes, on both the invader's traits and propagule pressure, i.e., the number of individuals that are introduced (Lockwood et al., 2005; Colautti et al., 2006; Lockwood et al., 2009). In this framework, the invader's traits reflect the sum of the unique genetically based attributes that facilitate the invader's success, whereas the propagule pressure reflects a universal attribute that is important to all invasions. Thus, by thinking in terms of attributes of basic impact factors it may be possible to advance from case-studies that focus on the spatio-temporal and taxonomic context, to identifying simple mechanisms that determine the degree of impacts and quantify these using common currencies (see the meta-analytical case study as an example).

4.2. Our framework in relation to other impact frameworks

Several impact frameworks have been proposed to identify key impact factors (Table 1), and our framework builds on this previous research. Identified impact factors include the invader's abundance (A), entire or habitat-specific range (R , R_i), ecological function (EF), effect per unit biomass/individuals (E), and the compositions of the invaded community (C) (Parker et al., 1999; Ricciardi, 2003; Strayer et al., 2006; Lockwood et al., 2007; Thiele et al., 2010; Ricciardi et al., 2011). In our framework, A , R , and EF are not individual impact factors but represent attributes that could be relevant to quantify for both the invader and resident biota. Here, A , R and EF of the invader or the resident biota modify the impact on native ecosystems, as does the invader's sex, vigour, size, longevity, age, toxins, behaviours, etc. Also, EF can, in our framework, be characterized by different attributes ranging from universal, such as an invader's way of acquiring resources, to less general attributes, such as functionalities related to defence mechanisms. We did not include E as an independent causal impact factor. Instead, E is the impact observed at the local scale that depends on all the possible combinations of unique and universal attributes of the invader, resident biota, resources and conditions (Fig. 1). Specific E -values can be calculated and standardized, for example based on manipulative impact experiments (see our case study) using metrics such as Hedges d , or the log-response ratio (Rosenberg et al., 2000), Paines' index, The Dynamic index, or Community Importance (Berlow et al., 1999). Finally, C is in our framework represented as one of many attributes related to the resident biota. Thus, the resident biota can modify impact via community measures (i.e., diversity, richness and species composition), and population measures, including the abundances, size frequency and vigour or toxicity

of key resident species. Most of the frameworks listed in Table 1 do not include metrics quantifying how abiotic conditions or available resources modify impacts. This contrasts with invasion success studies where many theories emphasize how fluctuations in resources or disturbances influence the likelihood of an invader to become established and spread (Sher and Hyatt, 1999; Davis et al., 2000; Catford et al., 2009). The lack of explicit attention to abiotic conditions and resource levels in some impact frameworks (Parker et al., 1999; Ricciardi, 2003; Thiele et al., 2010) mirror an experimental research gap on how universal attributes of the invaded habitat modify invasion impact (but see Kupferberg, 1997; Walton et al., 2002; Carlsson and Lacoursiere, 2005; Nilsson et al., 2008).

A broader impact approach was taken by Strayer et al. (2006) who argued that temporal dynamics are central to understand impact; impact changes constantly due to temporal changes to the invader, the invaded community, the interactions between the invader and the community, and the abiotic environment. In our framework, we further separate the abiotic environment into abiotic conditions that are not utilized and the resources that are utilized and potentially depleted by biota. We do not consider time as a separate impact factor. Instead, we interpret time as we interpret space, to be the domain in which the impact factors and attributes operate. Space and time are not causative agents in themselves, but the multi-dimensional world in which causative processes and mechanisms operate (Hawkins and Diniz, 2004; Catford et al., 2009). Obviously, tests of invasion impact needs to be addressed at appropriate spatial and temporal scales (Englund and Cooper, 2003), and more attention should, for example, be given to rapid adaptations of resident biota (Kiesecker and Blaustein, 1997). In short, to understand impact and facilitate future synthesis, it is paramount to report all main spatio-temporal facts such as when and where the invader was observed first time, and the extent, grain, time-course and sample/manipulation frequency associated with impact experiments.

4.3. Revisiting the objectives

We argued that a broad impact framework should be all-encompassing, challenge researchers to identify causative agents of impact, facilitate a way to quantify, compare and predict impacts between studies, and be open to allow for future refinement of the framework and to incorporate more advanced impact modelling.

We believe our framework is all-encompassing because all impact studies can be organized and classified around the four fundamental ecological impact factors (Chase and Leibold, 2003; Begon et al., 2006; Catford et al., 2009). Our framework should challenge researchers to search for and identify more causative agents, via our emphasis on any attribute that may influence an impact factor—and thereby also the observed invasion impact. To do this in practice, we recommended applying treatment gradients, and whenever possible avoiding binary presence–absence tests because these incorporate an unknown mixture of causative attributes. The identification of specific impact attributes also encourages researchers to be cautious before extrapolating results beyond what is tested. The identification of impact attributes also allows us to propose simple predictions that only require limited ecological theory and which should be tested before more advanced theories are targeted. For example, effect sizes should increase monotonically with attributes such as body size, vigour, longevity, etc. (all else being equal). However, it may be more difficult to predict how the same attributes associated with the resident biota may modify impact. For example, high abundance of a resident prey species may simultaneously cause high predation rates and facilitate its persistence.

We have here demonstrated how meta-analytical methods can be used in praxis to quantify the magnitude and direction of specific impact attributes, standardized from different studies with different invaders in different invaded habitats (see ‘case study’ for details). We see a great prospect for such analysis to compare invasion impact in a quantitative and standardized setting, as also evidenced in recent synthesis papers on invasion predation (Salo et al., 2007), grazing (Parker et al., 2006) and competition (Mason et al., 2009; Morales and Traveset, 2009) effects. Finally, because we do not limit our framework to a few named impact factors with defined mathematical formulas (Table 1), our approach is open to encourage researchers to search for more impact attributes as well as test attributes that have only been briefly addressed. For example, more research is needed to test if the feeding mode or size of invaders and resident biota, and the available resources and abiotic conditions, affect the direction and magnitude of impact.

Our proposed framework provides a small step in a broader appreciation of the ecological impacts of invasive species. It could be improved by further strengthening the linkages between specific invasion success theories (reviewed in Catford et al., 2009) and broad invasion success frameworks (reviewed in Gurevitch et al., 2011). This could result in a more sophisticated hierarchical framework that also can incorporate specific underlying mechanisms, such as enemy release, to understand impact. Also, we consider it important to refine methods to detect and incorporate scale-dependent interactions and feedbacks within and between multiple impact factors and attributes. We were unable to conduct factorial meta-analysis on universal impact attributes because only a handful of studies have tested for interactions. However, several impact attributes target interactions between invaders and resident biota; for example, if the frequency and extent of encounters between invaders and resident biota, or their priority effects, modify invasion outcome (Hofstra et al., 1999; Knight et al., 2009). Similarly, functional attributes of invaders are mainly relevant to study in a context of a specific group of resident biota. Just because an invader establishes itself in a habitat does not imply that it interacts with or impacts all co-occurring resident organisms. Previous impact frameworks have emphasized how the functional distinctiveness between the invader and the resident biota influences invasion impact (Ricciardi, 2003; Ricciardi and Atkinson, 2004). We note that this interaction is not a unidirectional function of distinctiveness. For example, invasion effects within trophic levels, such as competition and hybridization, are likely to be high if an invader is functionally *similar* to the resident biota (Mallet, 2005; Ainouche et al., 2009; Byers, 2009). By contrast, invasion effects between trophic levels, as well as effects of ecosystem engineers and habitat-formers, are likely to be high if the invader is functionally *different* from the resident biota (Ricciardi and Atkinson, 2004; Crooks, 2009; Thomsen et al., 2010a). We argue, however, that the interaction between invaders and resident biota should not, *per se*, be more important than other two-, three- or higher factorial interactions that may occur between impact drivers and their attributes.

4.4. Data reporting limits the ability to make generalizations about invader impacts

During our literature survey, we often encountered studies that reported pooled data results or omitted non-significant test-factors and treatments (i.e., the ‘file drawer effect’, Rosenthal, 1979). These are valid choices from the perspective of the individual study; yet it limits our ability to extract generalities across multiple studies. Many studies also pooled data into coarser taxonomic units or between non-significant treatments.

Given the high variability in ecological measurements, this results in the exclusion of many small and non-significant effects from quantitative reviews, thereby resulting in over-estimation of cumulative effect sizes (Gurevitch and Hedges, 1999). Thus, we urge researchers to report all test-factors, treatments and quantified responses, either in the paper or in Supplementary materials, even if statistically non-significant (Morrison, 2002; Pysek and Hejda, 2006; Ross et al., 2007). This added information will not only improve synthetic analysis and facilitate extraction of generalities, but will also increase transparency in the interpretation process. This way, critical readers can more easily evaluate both what is statistically significant and what is ecologically important. Perhaps more problematic was that many studies did not report the abundance of the invasive species but simply compared removal plots to untouched control plots (see also Thomsen et al., 2009). We here demonstrated that the abundance of the invader determines the magnitude of impact across species and habitats. It is therefore vital that all impact studies include information about abundances to allow comparisons across studies. In addition, many studies did not report the time when the invasive species was introduced as also noted by Strayer et al. (2006), or the origin of the resident biota (but see Morrison, 2002; Cushman and Gaffney, 2010). This information is highly relevant in invasion biology, as invaders and native organisms adapt and evolve in response to their novel interactions over time (Strayer et al., 2006; Agosta and Klemens, 2008) (see also Supplementary material Table 3 for more detailed list of data to report in impact studies).

4.5. Experimental design limits the ability to make generalizations about invader impacts

Based on our review, we identified several key research gaps in aquatic field experiments that should be addressed to increase our ability to understand and predict invasion impact. First, most experiments compared a single treatment to a control in a binary presence-absence design. This design makes it difficult to extract generalities about the role of universal and unique attributes in determining invader impacts. We did find 39 experiments that applied multiple abundance treatments; however, limited data still made it inappropriate to quantify detailed relationships between invader abundance and degree of impact. Hence, future experiments should aim to compare many invader abundances using continuous impact-models (regression techniques, Byers, 2000; Kotta et al., 2006) or by combining categorical and continuous impact-models (Cottingham et al., 2005). Such experiments will allow for extraction of curve-fitting parameters (e.g., shapes, slopes, thresholds and interceptions) and the modelling of abundance-dependent impacts (rather than simply identifying that it exists). With the rapidly increasing number of case-studies from different locations, habitats, ecosystems and invasive taxa, such models can eventually be used to test if curve-parameters differ systematically between invaders or other test-groups.

We also encourage more research focusing on how habitat-associated impact factors interact with and modify invader impacts. A few studies have manipulated resource levels or abiotic conditions orthogonally to manipulate the invader. Existing examples include manipulations of nutrient levels (Ceccherelli and Cinelli, 1999), sediment levels (Piazzi et al., 2005), light levels (Knight et al., 2009), stream discharge (McIntosh et al., 2004) and substratum stability (Nystroem and McIntosh, 2003). However, we did not find any aquatic experiment that manipulated > 2 habitat treatments independent of manipulating the invader, and could therefore not conduct formal meta-analysis. Thus, currently, we simply do not have a strong mechanistic understanding on how unique or

universal attributes of the resident biota, the resource levels, or abiotic conditions interact with and modify invasion impact.

5. Conclusions

Scientific studies that quantify the impact of invasive species across habitats and ecosystems remain rare, but are growing in number. The lack of investigation has led to the perception that invasion impacts are idiosyncratic, depending on the invader and recipient community in question and the environmental context. The end result is that few generalities regarding the impact of aquatic invasive species have emerged. Here, we proposed a general framework to facilitate the comparison of invasion studies across taxa, spatio-temporal domains, habitats and ecosystems. This framework separates attributes of the invasive species, the resident biota, the resources levels and the abiotic conditions of the invaded habitat, along a continuum from the universal (general to all invasions) to the unique (specific to a single invasion). We then showed that both universal (abundance) and unique (species-identity) attributes of the invasive species significantly influenced invasion outcomes. However, we also noted that many more studies are needed to understand how impact depends on (a) abundances, (b) species-traits, (c) additional invader impact attributes (e.g., size, longevity, toxins), (d) interactions between the invader and habitat-associated impact factors and (e) interaction with other anthropogenic stressors. In conclusion, we hope our framework will stimulate invasion ecologists to structure their empirical work to maximize the insights into which universal and unique attributes cause the largest impacts, to improve the identification of particularly threatening invaders and vulnerable habitats and, ultimately, management responses to invasions.

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Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.envres.2011.05.024](https://doi.org/10.1016/j.envres.2011.05.024).

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