

# Global meta-analysis of native and nonindigenous trophic traits in aquatic ecosystems

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## Abstract

Ecologists have recently devoted their attention to the study of species traits and their role in the establishment and spread of nonindigenous species (NIS). However, research efforts have mostly focused on studies of terrestrial taxa, with lesser attention being dedicated to aquatic species. Aquatic habitats comprise of interconnected waterways, as well as exclusive introduction vectors that allow unparalleled artificial transport of species and their propagules. Consequently, species traits that commonly facilitate biological invasions in terrestrial systems may not be as represented in aquatic environments. We provide a global meta-analysis of studies conducted in both marine and freshwater habitats. We selected studies that conducted experiments with native and NIS under common environmental conditions to allow detailed comparisons among species traits. In addition, we explored whether different factors such as species relatedness, functional feeding groups, latitude, climate, and experimental conditions could be linked to predictive traits. Our results show that species with traits that enhance consumption and growth have a substantially increased probability of establishing and spreading when entering novel ecosystems. Moreover, traits associated with predatory avoidance were more prevalent in NIS and therefore favour invasive species in aquatic habitats. When we analysed NIS interacting with taxonomically distinctive native taxa, we found that consumption and growth were particularly important traits. This suggests that particular attention should be paid to newly introduced species for which there are no close relatives in the local biota. Finally, we found a bias towards studies conducted in temperate regions, and thus, more studies in other climatic regions are needed. We conclude that studies aiming at predicting future range shifts should consider trophic traits of aquatic NIS as these traits are indicative of multiple interacting mechanisms involved in promoting species invasions.

**Keywords:** biological invasions, comparative studies, effect size, freshwater, invasive species, marine, range expansion, range shift

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## Introduction

One of the most striking characteristics of the Anthropocene is the global transport of nonindigenous species (NIS), which leads to unplanned natural experiments across vast spatial scales (Sax *et al.*, 2007). Hence, understanding the drivers of biological invasions is a fundamental topic in ecology, and of considerable applied relevance. Ecologists have often attempted to identify a suite of traits associated with NIS that establish and spread in novel habitats (van Kleunen *et al.*, 2015). Comparative analyses of native vs. NIS traits have largely been focused on terrestrial ecosystems (Blackburn *et al.*, 2009; Leffler *et al.*, 2014), with less research conducted on aquatic species. This is despite

the growing recognition that aquatic ecosystems are among the most heavily invaded ecosystems globally (e.g. Cohen & Carlton, 1998).

Studies have identified functional traits that influence physiological tolerance (Blossey & Notzold, 1995), life-history strategies (Sol *et al.*, 2012) and biotic interactions (Dick *et al.*, 2002; Twardochleb *et al.*, 2013) as key factors determining the colonization and establishment of NIS at different stages of the invasion process. For example, antipredator traits, such as predator avoidance behaviour, can facilitate introduced prey species allowing them to deter or avoid native predators (Holomuzki & Biggs, 2012). Conversely, native prey may be naïve to new predators (Cox & Lima, 2006). This is because native and NIS lack a common evolutionary history and thus antipredator responses may be absent, producing unprecedented levels of predation upon native species (Sih *et al.*, 2010). Other studies suggest that phylogenetic relatedness may influence the interaction between native and NIS (Ricciardi & Atkinson,

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2004) and thus be key to understanding invasiveness (Strauss *et al.*, 2006). Consequently, biotic interactions and phylogenetic relationships among native and NIS can influence the way communities are structured with NIS traits being key determinants of community assembly.

Meta-analyses have identified body size, shoot allocation, high fecundity, growth rate, and leaf area as key traits to explain plant invasions (van Kleunen *et al.*, 2010b). A recent meta-analysis of plant traits by Leffler *et al.* (2014) reported important differences between native and NIS, particularly when traits associated with fitness were considered. In line with this, a meta-analysis comparing native and nonindigenous birds identified growth as a significant trait promoting successful invaders (Blackburn *et al.*, 2009). Further traits associated with NIS include wider physiological tolerance (Marchetti *et al.*, 2004) or generalist ecological strategies (Kolar & Lodge, 2002). Some studies have found contradictory results in key traits such as phenotypic plasticity (Daehler, 2003) and growth (Pyšek & Richardson, 2007). Differences in approach and type of studies included may explain the discrepancies reported. However, traits that promote broader physiological tolerance and ecological roles are consistently reported in species invasions.

Most literature that deals with meta-analysis of species traits is centred around terrestrial systems (Estrada *et al.*, 2016), and therefore, their conclusions may not apply across all ecosystem types. In particular, intrinsic differences between terrestrial and aquatic systems suggest that the strength and mechanisms behind species traits and interactions may differ (Chase, 2000). For example, native primary producers (hereafter, producers) differ between terrestrial and aquatic systems in traits such as growth rate, nutritional quality, and size (Cebrian & Lartigue, 2004). As a result, native producers may be more strongly affected by consumption in aquatic than in terrestrial systems. If this variation in traits also applies to invasive producers, then aspects such as biotic resistance from native consumers may be stronger in aquatic communities. Furthermore, as species diversity may enhance biotic resistance (Stachowicz *et al.*, 1999) and provide significant selective forces on aquatic NIS (Kimbrow *et al.*, 2013), phylogenetic relatedness may be more important than in terrestrial ecosystems.

Aquatic habitats form an intricate system of increasingly interconnected waterways across the globe. This connectivity aided by human activities can exponentially enhance the transport of aquatic organisms and their propagules. Furthermore, introduction vectors are different between aquatic and terrestrial ecosystems. For example, ballast waters of large vessels allow for a

much more indiscriminate and massive transport of propagules than most terrestrial vectors (Carlton & Geller, 1993). Therefore, traits that facilitate NIS in terrestrial systems may not be as represented in aquatic invasions.

Here, we compare native and NIS traits under common experimental settings to provide the first global meta-analysis of traits in aquatic ecosystems. The specific objectives of our study were (i) to assess what traits are important in determining the colonization and establishment of aquatic NIS and (ii) to determine what additional factors (i.e. geographic location, experimental duration, and phylogenetic relatedness) improve our understanding of aquatic species invasions.

## Materials and methods

### Data selection

A literature search was carried out to gather quantitative information from experimental and observational studies on the comparison between native and NIS traits under common environmental conditions. The search was conducted on the 24th May 2016 in the Web of Science (<https://webofknowledge.com>), using the keyword combinations: (invas\* or non-nat\* or non-nat\* or alien\* or exotic or nonindig\* or non-indig) and (nat\* or indig\*) and (freshwater or marine or aquatic) and (trait\* or performance or experiment\* or observation\* or effect or consumption or predation or behaviour or competition), with no restrictions on publication year. Additional papers were extracted from citations within the papers found in the search. Studies were only included if they fulfilled all the following objective criteria: (i) studies were carried out in marine or freshwater environments; (ii) they measured the performance or interaction of pairwise trait differences of native and NIS; (iii) they evaluated quantifiable traits; and (iv) they compared species that were nonindigenous to the location of the research.

As many studies conducted different measurements through time, we selected the most relevant time for calculating effect sizes. For example, when a response variable was measured at different times (e.g. sampling at different dates or repeated-measure experimental designs), the final measurement was used (Maggi *et al.*, 2015). In some cases such as that of algal growth, the measure was taken at a point of maximal irradiance, as this produced results for all species. When a study examined different treatments (e.g. location or predator species), these data were considered separately (Leffler *et al.*, 2014). Where examination of traits was crossed with additional factors (e.g. density or environmental factors), those treatments which most closely matched ambient conditions were used (Levine *et al.*, 2004). In multispecies studies that included more than one native or NIS, the pairing depended on the information available for the study. If the study explicitly assigned species to pairs, this pairing was used; if the study did not, all potential pairs of native and NIS within that

study were compared. In competition experiments with multiple density treatments, we used the interspecific (native and NIS) treatment density that matched the density of the intraspecific (NIS only) control (Alofs & Jackson, 2014).

Information collected consisted of trophic traits promoting species ability to exclude or outcompete other species (see Table 1), as well as characteristics of the study. For example, different types of traits may be important under different climatic conditions (van Kleunen *et al.*, 2010b). Aspects such as laboratory or field conditions or habitat type were included as studies have suggested differences may be due to these variables (Daehler, 2003). Trophic trait differences may depend on taxonomic relatedness between species (Strauss *et al.*, 2006); therefore, we considered whether the studied species were confamilial or not. Additionally, some native species may be a NIS elsewhere, which would imply that some studies compared NIS to other NIS on a global scale (van Kleunen *et al.*, 2010b). Hence, the trait comparisons analysed here included whether the native is known or not known to be a NIS elsewhere. Therefore, potential explanatory variables included geographic location, habitat, experiment duration (days), type of study (e.g. field or laboratory), climate, confamilial matching, functional group, and phylum of the NIS. The dispersion measure reported (SD, standard deviation; SE, standard error; or CI, confidence interval) was recorded along with the sample size for each response variable and treatment. All SE and CI obtained were converted into SD for analyses. Studies were not included when the estimates of variation in the effect sizes, necessary for weighted analyses, were not available. Means and dispersion statistics were obtained from published figures using the DATATHIEF III software (Thumers, 2006) or extracted from tables.

Trophic traits were grouped into consumption (e.g. predatory consumption, species feeding capacity, or filtering rate), growth (e.g. growth rate), predator escape (e.g. enemy release, whether native or NIS are a preferred choice of prey by native predators or herbivores), predatory avoidance (e.g. behaviour when given predator cues), and competition (interspecific treatments). Competition was split as the nature of competitive ability was measured in various ways; this included

exploitative competition (i.e. competition for food) and interference competition (e.g. competition for space; see Table 1).

### Data analysis

For comparisons between species, Hedges'  $d$  was calculated as a measure of effect size (Rosenberg *et al.*, 2013). Each data point consisted of one effect size, the difference between the mean trophic trait or performance measure of the NIS ( $X_{\text{NIS}}$ ) and the native ( $X_{\text{NATIVE}}$ ), normalized by the pooled SD and a sample-size weighting factor and was calculated as follows:

$$d = \frac{X_{\text{NIS}} - X_{\text{NATIVE}}}{S} J,$$

where  $S$  is the pooled standard deviation and calculated as

$$S = \sqrt{\frac{(N_{\text{NIS}} - 1)S_{\text{NIS}}^2 + (N_{\text{NATIVE}} - 1)S_{\text{NATIVE}}^2}{N_{\text{NIS}} + N_{\text{NATIVE}}}}.$$

Here,  $S_{\text{NIS}}$  and  $S_{\text{NATIVE}}$  are the standard deviations of the native and NIS groups, respectively.

$J$  is a weighting factor based on the number of replicates ( $N$ ) in each case, for the two groups, and is calculated as follows:

$$J = 1 - \frac{3}{4(N_{\text{NATIVE}} + N_{\text{NIS}} - 2) - 1}$$

The variance of Hedges'  $d$  ( $V_d$ ) was computed as follows:

$$V_d = \frac{N_{\text{NATIVE}} + N_{\text{NIS}}}{N_{\text{NATIVE}}N_{\text{NIS}}} + \frac{d^2}{2(N_{\text{NATIVE}} + N_{\text{NIS}})}.$$

Zero  $d$  values signify no difference in the variable measured, and positive values indicate better performances by the NIS. The sign was changed for the effect sizes of those variables in which a low value indicated the same as a high value for related variables (see Table 1). When a CI does not include zero, it indicates a statistically significant effect size.

The meta-analysis was performed using function 'rma' (meta-analysis via the linear [mixed-effects] models, with the restricted maximum-likelihood), within package 'metafor' (Viechtbauer, 2010) in the R statistical software

**Table 1** Classification of trait types in the meta-analysis. Effect sizes were computed using the difference between the nonindigenous minus the native averages: a negative sign '(−)' indicates that the sign of the effect size was changed because of the opposite meaning of some variables (e.g. increased mortality in presence of predator is equivalent to decreased survival)

Trait type	Response variables
Consumption	Feeding rate, percentage/mass consumption, growth rate as a measure of consumption, percentage mortality or prey consumed, filter feeding capacity
Exploitative competition	Food ingestion, prey captured, change in mass, survival, time spent feeding, stem length, growth efficiency while competing, biomass, mortality (−)
Growth	Biomass, specific growth rate, growth efficiency, growth after herbivory, elongation rate
Interference competition	Settlement rate of recruits, individuals found in refuge, survival rate %, mortality (−), growth during competition, metamorphosis %, biomass
Predator avoidance	Subsurface use when predator present, time spent in refuge, individuals found in refuge, measure of drifting behaviour (−)
Predator escape	Change in area/growth when herbivores present, mass/%/individuals consumed by predator or herbivore (−), feeding rate of predator/herbivore (−), mortality under predation (−)

(R Development Core Team, 2014). This method is an approximately unbiased and efficient estimator to test whether mean effect sizes of each variable type differ significantly from zero (Viechtbauer, 2010).

Additional tests were performed to consider different mean effect sizes among the explanatory variables. Heterogeneity ( $Q_T$ ) was tested with Cochran's  $Q$ -test (Cochran, 1954). The percentage of variation across studies due to heterogeneity ( $I^2$  statistic) was also obtained to summarize heterogeneity importance and classified as low, moderate, high, and very high heterogeneity ( $I^2$  values <25%, 25–50%, and 50–75%, >75%, respectively) among study groups (Higgins *et al.*, 2003). Significant  $Q_T$  indicates that the variance of effect sizes among studies is greater than expected by sampling error and implies that there may be some underlying structure to the data. In those cases, a mixed-effects model (i.e. meta-regression) with categorical moderator variables was applied to test whether effect sizes differed between groups (e.g. climate, habitat, functional feeding group, or phylum), and with continuous predictors to test whether variance in effect sizes covaried with them (e.g. experimental duration and absolute latitude). If the model proved to be significant, the slope of the model was further assessed for its significance. The model sum of squares ( $Q_M$ ) explained the amount of heterogeneity, and if a structural model describes a large portion of the total heterogeneity,  $Q_M$  will be significant (Rosenberg, 2013). The residual sum of squares ( $Q_E$ ) explained the amount of heterogeneity which is left unexplained after the model is taken into account. Therefore, a significant  $Q_E$  indicates that there is additional variance to be explained in the effect sizes (Rosenberg, 2013).

To address the file drawer problem (Rosenthal, 1979), which can introduce publication bias to meta-analysis, a regression test was applied to check for funnel plot asymmetry (Egger *et al.*, 1997). The fail-safe number, that is the number of null results (nonsignificant, unpublished, or missing studies) that would have to be added to make the overall test of an effect statistically nonsignificant, was calculated as a measure of strength of the result, following Rosenthal (1979). Finally, the trim and fill method (Duval & Tweedie, 2000) was used to estimate the number of missing studies on one side of the funnel plot for the overall data set. All computations were performed with the above-mentioned 'metafor' package in R.

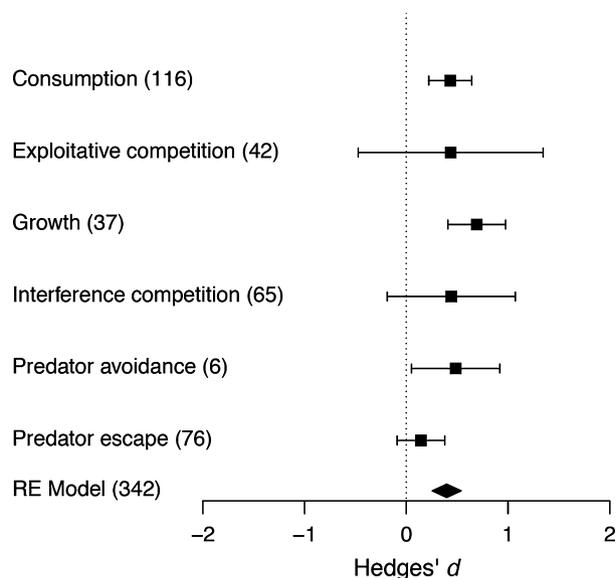
## Results

A total of 342 data points were obtained from 74 peer-review papers published between 1991 and 2015 (Table S1). There was no global spread of research papers, and most studies were from North America and Europe (Fig. S1). Some studies were found in South Africa and Australia, but there was a considerable lack of studies from the tropics (see Appendix S1 for further information of geographic distribution of studies). A total of 54 NIS were identified with the most commonly studied species being *Sargassum muticum* (8), *Mytilus*

*galloprovincialis*, (7) and *Dikerogammarus villosus* (5); however, most species were addressed by a single study (Table S2).

The funnel plot showed significant asymmetry ( $P = 0.0011$ ) for the overall data set. The funnel plot was similar in pattern to a previous ecological meta-analysis by Maggi *et al.* (2015) suggesting that there are large variations across studies. Furthermore, the fail-safe number was 26 598, which is larger than  $5k + 10 = 1720$ , where  $k$  is the number of case studies in the data set. Therefore, the observed results can be seen as reliable estimates of the true effect. However, the trim and fill method indicated that there were 48 missing studies to the left of the funnel plot for the overall data set.

Averaged over all species comparisons, the absolute value for the difference between native and NIS was significantly larger than zero (Fig. 1, Table 2), and the mean effect sizes of the trophic trait variables differed significantly among the six groups ( $Q_M = 36.36$ ,  $df = 6$ ,  $P < 0.0001$ ; Table 3). Consumption was the most commonly studied (Table S3), whereas the predator avoidance trait was the least. NIS had significantly higher trophic trait values for consumption, growth, and predator avoidance. The functional feeding groups driving consumption were omnivores and predators with 70 and 36 observations, respectively. Regarding growth, the functional feeding group



**Fig. 1** Mean effect sizes ( $d$ ) of the six trait categories (detailed values in Table 1). RE Model indicates absolute value of trait differences. Sample sizes shown in parentheses. Positive mean effects sizes indicate a better performance by nonindigenous species. Significance occurs when 95% CI bars do not include zero.

**Table 2** Mean effect sizes ( $d$ ), 95% confidence intervals (CI; significant results are in bold), heterogeneity across all studies ( $Q$ ) from the random-effects model, sample size ( $k$  = number of case studies), and residual heterogeneity ( $I^2$ : percentage of total variance across studies due to heterogeneity) for each trait variable across all data

Trait variable type	$d$	CI		$Q$	df	$P$	$k$	$I^2$ (%)
		$L$	$U$					
Consumption	<b>0.4319</b>	<b>0.2209</b>	<b>0.6430</b>	886.2	115	<0.0001	116	88.6
Exploitative competition	0.4361	-0.4727	1.3449	350.8	41	<0.0001	42	95.74
Growth	<b>0.6925</b>	<b>0.4092</b>	<b>0.9758</b>	127.9	36	<0.0001	37	70.48
Interference competition	0.4425	-0.1870	1.0721	484.9	64	<0.0001	65	95.83
Predator avoidance	<b>0.4852</b>	<b>0.0512</b>	<b>0.9191</b>	10.2	5	0.0692	6	54.97
Predator escape	0.1439	-0.0904	0.3783	337.8	75	<0.0001	76	80.62
Full Model	<b>0.3794</b>	<b>0.5267</b>	<b>0.2321</b>	2278.7	337	<0.0001	338	88.65

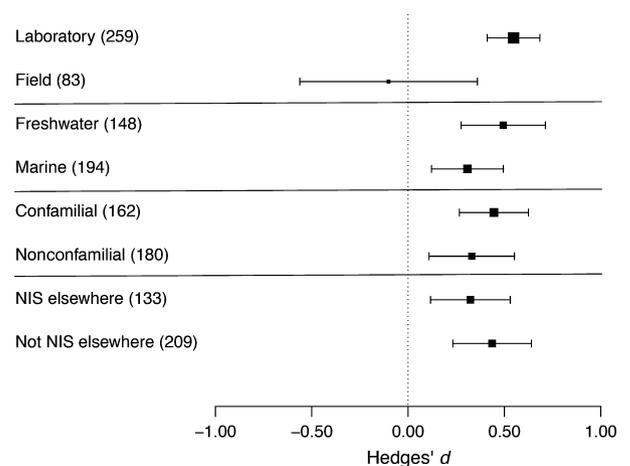
**Table 3** Meta-regression of mean effect sizes for the overall data set and the various trait categories. Dur: experimental duration (days), Lat: absolute latitude (degrees). Sample size ( $k$  = number of case studies), heterogeneity explained by the model and its significance ( $P$ ), and residual heterogeneity ( $I^2$ ; percentage of total variance across studies due to heterogeneity)

Model		$Q_M$	$k$	$P$	$I^2$ (%)
Overall	-0.7806 + 0.0299 Lat - 0.0054 Dur	32.17	342	<0.0001	87.96
Growth	1.0398 - 0.0215 Dur	6.63	37	0.01	64.46
Interference competition	-6.3476 + 0.1916 Lat - 0.0051 Dur	39.76	65	<0.0001	93.82
Predator escape	0.2117 - 0.0065 Dur	8.89	76	0.0029	78.83

producers and herbivores were the most important, with 22 and 14 observations, respectively, and the positive effect size was largely driven by producers (Fig. S2). Although the mean effect size for exploitative competition, interference competition, and predator escape was not significantly different from zero, the heterogeneity for each was significant ( $P < 0.001$ ) and high (Table 2). Predator avoidance effect size was significantly higher than zero but was only marginally heterogeneous ( $P = 0.069$ ).

Across all comparisons, residual ( $Q_E$ ) and moderator heterogeneity ( $Q_M$ ) were significant and high (Table S4). Indicating additional variance in the effect sizes may be explained by the continuous predictors. Meta-regression showed that the overall effect sizes were positively correlated to absolute latitude. In turn, growth and overall effect sizes were negatively related to experimental duration (Table 3, Fig. S3; for detailed comparisons among phyla, climatic regions and other factors see Fig. 2 and Appendix S1).

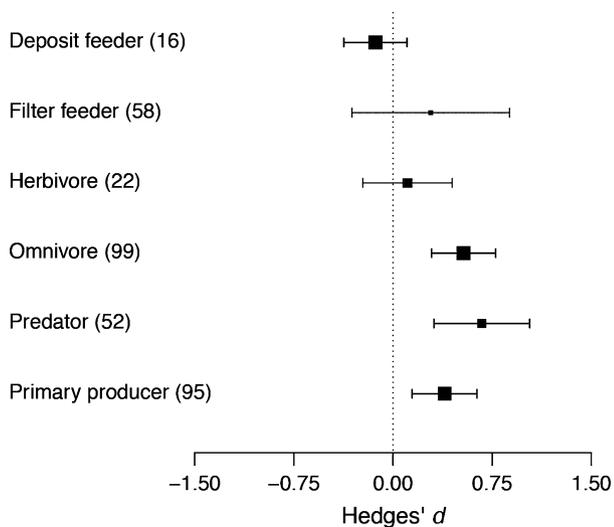
When we compared different functional feeding groups, three of the six groups (omnivores, predators, and primary producers) performed better as NIS than native species, with mean effect sizes all significantly higher than zero (Fig. 3). Although the mean effect size for filter feeders and herbivores was not significantly different from zero, the heterogeneity was significant and high (Table S5).



**Fig. 2** Mean effect sizes ( $d$ ) of trait comparisons illustrating the groups of explanatory variables: experimental design, habitat, confamilial comparisons, and history of introductions elsewhere. Sample sizes shown in parentheses. Positive mean effect sizes indicate a better performance by nonindigenous species. Significance occurs when 95% CI bars do not include zero.

## Discussion

A crucial puzzle in ecology surrounds understanding the role of species traits in shaping recent range shifts (Pyšek *et al.*, 2008). Studies focussing on terrestrial taxa (Blackburn *et al.*, 2009; van Kleunen *et al.*, 2010b;



**Fig. 3** Mean effect sizes ( $d$ ) of trait comparisons illustrated by functional feeding groups. Sample sizes shown in parentheses. Positive mean effect sizes indicate a better performance by nonindigenous species. Significance occurs when 95% CI bars do not include zero.

Estrada *et al.*, 2016) or ecological impacts (Ward & Ricciardi, 2007; Gallardo *et al.*, 2016) of NIS have provided invaluable insights into possible links between species traits and invasiveness. Our study provides the first comprehensive meta-analysis of trophic trait differences between nonindigenous and native aquatic species, covering a wide range of taxa and scenarios. We found evidence of enhanced consumption and growth in NIS, especially when newly introduced species have no close relatives in the local biota. These results indicate that these trophic traits are a significant determinant of potentially hazardous aquatic NIS. In addition, we found a bias towards studies conducted in temperate regions, suggesting that more studies in other climatic regions are needed. Overall, we identified a set of trophic traits that facilitate the colonization and establishment of aquatic NIS and that are thus key for understanding and predicting future species invasions.

Consumption was the most commonly measured trait in the studies considered. This was in accordance with many comparative analyses investigating impacts or effects of biological invasions that report the negative impacts of alien consumers on recipient communities. For example, Paolucci *et al.* (2013) found alien consumers (predators and herbivores) were associated with negative effects on native populations. Similar findings have been described for non-native crayfish (Twardochleb *et al.*, 2013), terrestrial mammals and birds (Salo *et al.*, 2007), and dreissenid mussel species (Higgins & Vander Zanden, 2010). Conversely, a meta-analysis on biotic resistance suggested that consumptive biotic resistance appears to limit the success of

freshwater, marine, and terrestrial invaders (Alofs & Jackson, 2014). Our study suggests that nonindigenous consumers are more likely to outcompete or damage native prey populations via their higher predatory/feeding rate. Community assemblages may suffer major changes if native consumers are replaced by non-native consumers, contrary to the notion that NIS can beneficially fill vacancies created by native extirpations (Schlaepfer *et al.*, 2011). Furthermore, the addition of invading consumers may exacerbate local extinction rates of native species by rendering them more vulnerable to anthropogenic stressors and stochastic extinction dynamics.

Growth had the greatest positive effect size and magnitude among the traits. Growth has been documented to play an important role on physiology in many comparative reviews involving trait comparisons (Pyšek & Richardson, 2007; Blackburn *et al.*, 2009; van Kleunen *et al.*, 2010a,b, 2015). However, equivocal results are heavily reported in other studies, for example, in a native–invasive plant comparison by Daehler (2003), which found that NIS did not have higher growth rates compared to natives. A meta-analysis by Leffler *et al.* (2014) quantified the difference between native and NIS for various traits and found no differences when compared to differences among native species reported in the same studies. A meta-analysis of growth rates for invasive freshwater fishes by Rypel (2014) found that not all species gain apparent growth rate advantages in invasive populations, and in the majority of cases, growth rates were unchanged or significantly slower when measured using validated ageing structures (e.g. otoliths). Similarly, Pintor & Sih (2009) studied behavioural and growth rates across native and introduced populations of crayfish and found higher growth rates in the introduced than the native range. Overall, this evidence suggests that NIS with enhanced growth have the ability to transcend and outcompete native species.

When analysing all the studied traits together, there was a negative trend of effect size with increasing experimental duration indicating that as time extends native species become more inclined to survive or reestablish. It was anticipated that experimental duration may be important for native species, because biotic resistance effects tend to accrue over time (Stachowicz *et al.*, 2007). However, studies by Kimbro *et al.* (2013) and Alofs & Jackson (2014) found that biotic resistance was not significantly related to experimental duration. Our results suggest that NIS may be ephemeral (Pedersen *et al.*, 2005) as shown by the significant negative correlation of effect sizes on growth. NIS growth may occur exponentially from the offset, or there may be a time lag period where organisms may grow slowly. These lags may depend on local adaptation to novel

environments, adaptation of native communities to the NIS, or environmental changes in the invaded habitat (Crooks, 2005). A study by Gurevitch *et al.* (1992) found experimental duration had significant effects on the strength of species interactions and that short-duration experiments included more variation in environmental conditions and the strength of species interactions, which caused greater variability in their results. A meta-analytical study of NIS impacts (Kulhanek *et al.*, 2011) reported that many experiments had been conducted over relatively short time spans, and their results may not reflect the potential variation of impacts that may occur under natural conditions. Furthermore, studies often measure growth at a single or a few life-history stages, while the effects of biotic interactions on growth may be important across the entire life cycle (Rius *et al.*, 2014). Future studies should further explore experimental duration dynamics and life history to understand how time influences the outcome of species' interactions.

The Darwin naturalization hypothesis (Daehler, 2001) predicts that species that are introduced in communities where closely related species or species that share phenotypic traits are present will experience competitive exclusion, higher vulnerability to predation and/or parasites. Relatedness between introduced and native species can be an important factor predicting which introduced species will become high-impact invaders in both aquatic (Ricciardi & Atkinson, 2004; Ricciardi & Mottiar, 2006) and terrestrial ecosystems (Strauss *et al.*, 2006). Our study showed that feeding traits that enhance consumption and growth are key for aquatic species invasions, particularly when newly introduced NIS interact with taxonomically distinctive taxa. Growth was a significant trait when we compared dissimilar marine habitats and familial taxa, indicating that an invading marine species entering a community, in which it is distinct from the native assemblage, may be more capable of colonizing if it has traits that enhance growth. A study of lake species by Hall & Mills (2000) attributed successful NIS colonization to species belonging to a novel genus. Furthermore, a study by Ricciardi & Atkinson (2004) found that greater impacts came from NIS that were not represented in the native fauna or flora. However, contradictory evidence has been reported in a recent terrestrial study by Li *et al.* (2015) who examined invasion dynamics over 40 years. This study showed that NIS more closely related to native species were more likely to establish and dominate resident communities, and the native residents more likely to go locally extinct. Genetic divergence among NIS may confer novel ways to use available resources, such as gaining novel traits that increase the competitive ability of individuals. As a

large range of mechanisms may underlie invasiveness, ecological novelty may be partially gauged by relatedness and is a general metric that may not necessarily require knowledge of specific traits. In our study, growth was significant when compared to dissimilar familial taxa; these results coupled with findings in other systems (Strauss *et al.*, 2006) suggest that particular attention should be paid to newly introduced species for which there are no close relatives in the local biota. Consequently, relatedness of NIS to natives may provide a method for identifying threats to native communities.

Despite our initial efforts to include studies focussing on nontrophic traits, only a few studies compared behavioural responses of native vs. NIS, mainly focusing on the response of prey to the presence of predators. It is well established that novel antipredator behavioural traits can facilitate species invasions (Holomuzki & Biggs, 2012). In addition, Holway & Suarez (1999) made a compelling case regarding the need to further understand behaviours of species to predict the outcome of species introductions. However, species behavioural responses can often be context specific (e.g. Keller & Moore, 2000) differing under a given set of organism conditions (e.g. hunger state, size, age, physiological condition) or environmental conditions (e.g. temperature, light intensity, water velocity, substrate complexity). Future studies should carefully study interacting aquatic native and NIS in common environments to understand how behavioural variation determines colonization and establishment of NIS.

A critical consideration when comparing native and NIS is that the studied native species may also have successfully colonized and established elsewhere, implying that studies may have inherently compared NIS with NIS. Thus, including comparisons of NIS to native species that are themselves not known to have NIS populations elsewhere increases the power of detecting trophic traits which are consistently associated with NIS (van Kleunen *et al.*, 2010b). In line with this, our results showed that consumption and growth were consistently significant when comparing NIS to native species without known NIS populations elsewhere (Fig. S6).

Large alterations in ecosystem functioning occur when dramatic changes arise in the composition of functional feeding groups within a community (Pratt *et al.*, 2015). The introduction of species of novel feeding types may have profound effects on recipient communities. Generalist feeding (omnivory or predatory) was an expected characteristic due to its key role in the ecology of invasive species (Twardochleb *et al.*, 2013) and negative impacts that can transpire (Dick *et al.*, 2002). Thus, the ability to have flexibility or dietary

breadth favours species entering new and unknown surroundings, which can generate ecological impacts across the food web, producing trophic cascade effects in ecosystems. A meta-analysis by Gallardo *et al.* (2016) found both positive and negative effects of invaders upon varying trophic positioning. For example, non-indigenous aquatic plants have the capacity to transform food webs and ultimately alter communities (Thomsen *et al.* 2014). Another example is that the presence of novel predators can reduce the abundance of benthic invertebrates and fish but promote plankton species through grazer release (Gallardo *et al.*, 2016). Conversely, the establishment of nonindigenous suspension feeders can strengthen coastal biofilters and increase benthic biomass production (Reise *et al.*, 2006). The precise effect of a NIS may depend on its own trophic position, and the degree of trait difference between native and NIS may be more important in determining the influence of NIS on ecosystem functioning rather than predicting invasion (Strayer, 2012). With strong trophic links that characterize aquatic ecosystems in the presence of invasive species, there may be a widespread effect on the structure and ecological function of aquatic ecosystems.

The heterogeneity in effect sizes was considerable throughout our analysis, as indicated by significant  $Q_E$  values. Even when attempts were made to reduce heterogeneity by performing tests on the subsets of data,  $Q_E$  was still significant. This indicates that aspects such as highly dissimilar traits, design of the studies, and species and environments studied contributed to this heterogeneity. Despite a steady increase in recent years, the number of studies comparing traits of native and NIS under common conditions is still relatively low and thus reducing this heterogeneity remains challenging.

Although our analysis found clear trophic trait differences between native and NIS, this could partly reflect a bias towards finding more studies that investigated species that are known to be high performers (van Kleunen *et al.*, 2015). Alternatively, there may be a publication bias towards studies that find significant values for NIS over native species. Results of asymmetry for the funnel plot were as a consequence of some data with large values and high variances. Distribution of studies is extensively biased towards temperate regions, thus potentially vital areas are going unexamined. Thus, more research is needed in understudied regions to provide a holistic understanding on how species traits may influence species invasions. Furthermore, a highly informative method for detecting trait differences includes examining unsuccessful NIS; however, this comparison is not always possible due to the challenges in detecting species that have overcome initial

introduction barriers but nevertheless fail to establish. Future studies should tackle these limitations to estimate more robust effects.

As meta-analyses consider many concurrent, synergistic, and antagonist factors, disentangling the relative importance of species traits, experimental design, ecosystem type, and phylogenetic relatedness is essential for building hypotheses to identify and predict species invasions. Our study suggests that future studies should consider trophic traits of aquatic NIS, as these traits are indicative of multiple interacting mechanisms involved in promoting species invasions.

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## Supporting Information

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

**Table S1.** The studies and data included in the meta-analysis: Trait differences between native and non-indigenous species.

**Table S2.** Non-indigenous species (ordered by the number studies that investigated the species) included in the present meta-analysis.

**Table S3.** Traits measured in the meta-analysis and number of studies per trait.

**Table S4.** Residual heterogeneity ( $Q_E$ ) and moderators ( $Q_M$ ) between the groups of variables, sample size ( $k$  = number of case studies), and residual heterogeneity ( $I^2$ : percentage of total variance across studies due to heterogeneity).

**Table S5.** Mean effect sizes ( $d$ ), 95% confidence intervals (CI; significant results are in bold), heterogeneity across studies ( $Q$ ) produced from random-effects models, sample size ( $k$  = number of case studies), and residual heterogeneity ( $I^2$ : percentage of total variance across studies due to heterogeneity) for each taxonomic, functional feeding and climatic groups.

**Table S6.** Mean effect sizes ( $d$ ), 95% confidence intervals (CI, significant results are in bold), heterogeneity across studies ( $Q$ ) produced from random-effects model, sample size ( $k$  = number of case studies), and residual heterogeneity ( $I^2$ : percentage of total variance across studies due to heterogeneity) for each subset of the study variable.

**Figure S1.** Geographical distribution of studies used in the meta-analysis.

**Figure S2.** Mean effect sizes ( $d$ ) of the growth trait category by functional group.

**Figure S3.** Meta-regression for effects sizes of overall dataset influenced by: (A) absolute latitude, and (B) experimental duration and type.

**Figure S4.** Mean effect sizes ( $d$ ) of trait comparisons by phyla. Sample sizes shown in parentheses.

**Figure S5.** Mean effect sizes ( $d$ ) of the trait categories showing differences between: Left) experimental design, and Right) habitat.

**Figure S6.** Mean effect sizes ( $d$ ) of the trait categories showing differences between: Left) confamilial species, and Right) species with or without NIS elsewhere.

**Figure S7.** Mean effect sizes ( $d$ ) of trait comparisons by climate.

**Figure S8.** Mean effect sizes ( $d$ ) by temperate and Mediterranean climates.

**Appendix S1.** Supplementary results surrounding the different factors analysed.