**REVIEW AND SYNTHESIS**

## Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems

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### Abstract

Biological invasions cause ecological and economic impacts across the globe. However, it is unclear whether there are strong patterns in terms of their major effects, how the vulnerability of different ecosystems varies and which ecosystem services are at greatest risk. We present a global meta-analysis of 199 articles reporting 1041 field studies that in total describe the impacts of 135 alien plant taxa on resident species, communities and ecosystems. Across studies, alien plants had a significant effect in 11 of 24 different types of impact assessed. The magnitude and direction of the impact varied both within and between different types of impact. On average, abundance and diversity of the resident species decreased in invaded sites, whereas primary production and several ecosystem processes were enhanced. While alien N-fixing species had greater impacts on N-cycling variables, they did not consistently affect other impact types. The magnitude of the impacts was not significantly different between island and mainland ecosystems. Overall, alien species impacts are heterogeneous and not unidirectional even within particular impact types. Our analysis also reveals that by the time changes in nutrient cycling are detected, major impacts on plant species and communities are likely to have already occurred.

### Keywords

Biological invasions, bottom-up effects, diversity, ecological complexity, ecosystem functioning, effect size, exotic species, island, N-fixing, weeds.

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## INTRODUCTION

Given the increasing pace of global change, it is becoming more important than ever to understand how human activities are altering biodiversity and ecosystem functioning (Tylianakis *et al.* 2008). A key driver of change is the invasion of ecosystems by alien species, many of which attain sufficiently high abundance to influence biodiversity. In contrast to the extensive literature and syntheses on the processes leading to biological invasions (Jeschke & Strayer 2005; LePrieur *et al.* 2008; Van Kleunen *et al.* 2010a,b), a robust framework to understand impacts has yet to be developed (Parker *et al.* 1999). For example, various invasive plants are known to decrease local plant species diversity (Vilà *et al.* 2006; Gaertner *et al.* 2009; Hejda *et al.* 2009; Powell *et al.* 2011), increase ecosystem productivity and alter the rate of nutrient cycling (Liao *et al.* 2008; Ehrenfeld 2010), and hence impact upon ecosystem services and human well-being (Pejchar & Mooney 2009). However, while there are a growing number of studies reporting impacts of alien plants, we still lack broad quantitative syntheses of how impacts vary depending on the attributes of recipient ecosystems and of the invaders themselves (Levine *et al.* 2003). This absence of a broad-scale assessment limits our ability to generalize and predict when and where impacts might be most deleterious.

To address this key issue in invasion biology, we undertake a quantitative synthesis on the effects of alien plant species on a wide range of ecological response variables using a meta-analytical approach (Rosenberg *et al.* 2000). Meta-analysis provides an opportunity to explore heterogeneity among studies and identify large-scale patterns across species and geographic regions (Steward 2010). Our goal was to determine how the magnitude and direction of alien species impacts vary across levels of ecological complexity. An alien plant species that reaches a high abundance and dominates an ecosystem will potentially influence the performance of individual resident species and their population dynamics (Vilà & Weiner 2004), and as a consequence, it will have both direct and indirect effects on plant community structure and ecosystem functioning (Levine *et al.* 2003). In this study, we assess how impacts on species compare with those on community properties and ecosystem processes.

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*Nomenclature as in Weber (2003).*

We focus on two aspects that have for long been pivotal in the biological invasion literature. First, do N-fixing alien species exert greater ecological impacts than non-N-fixing species? Although there has been considerable research examining how species traits might influence plant invasiveness (Daehler 2003; Pyšek & Richardson 2007; Van Kleunen *et al.* 2010a,b), the effect of particular plant traits on the type of impact is unclear with the exception of studies reporting N-fixing alien species having a significant impact on N-cycling (Vitousek 1990; Ehrenfeld 2003, 2010; Liao *et al.* 2008). As strong impacts on nutrient cycling subsequently affect plant performance (e.g. plant resource allocation, plant competitive ability, plant resistance to herbivory, etc.) and hence community structure, we assumed N-fixing plants to have greater community impacts than non-N-fixing species.

Second, we assess whether island ecosystems are more vulnerable to impacts than mainland ecosystems. Islands often support large regional pools of alien species (Lonsdale 1999; Pyšek *et al.* 2010) and are often considered to be highly impacted by invaders (but see Diez *et al.* 2009). Certainly, introduced predators can trigger strong trophic cascades on islands and these indirect effects can importantly influence primary production and plant community structure (Croll *et al.* 2005). However, doubts have been expressed about the relative vulnerability of island ecosystem to the impacts of alien plants (Sax & Gaines 2008) but as yet no formal assessment of the vulnerability of island ecosystems to impacts has been undertaken.

## METHODS

### Literature search

We used several data sources to gather quantitative evidence from the literature on the ecological impacts of alien plants upon: (1) individual plant and animal species performance, (2) characteristics of the recipient community and (3) ecosystem processes (see Table 1 for definitions and examples of these measures). We searched for relevant articles on the ISI Web of Knowledge (http://apps.isiknowledge.com) database on 11 March 2009 with no restriction on publication year, using the following search term combinations: (plant invader OR exotic plant OR alien plant OR plant invasion*) AND (impact* OR effect*) AND (community structure* OR diversity* OR ecosystem process* OR competition*). As the next step, we also screened the reference lists from all retrieved articles for other relevant publications. As some of those articles were reviews (e.g. Levine *et al.* 2003) that were also based on the 'grey literature', we achieved a reasonably good coverage of the literature on impacts of alien plants, not restricted to that indexed in Web of Science.

We examined each article to assess their potential for meeting the selection criteria for inclusion in the review. The main selection criterion required studies to compare quantitatively any ecological pattern or process in both invaded and uninvaded plots in natural or semi-natural ecosystems. We did not include studies conducted in agricultural systems as this topic has been reviewed elsewhere (Vilà *et al.* 2004). This resulted in an initial set of 515 articles from which the following criteria for data inclusion were adopted:

(1) Replicated field studies that were either observational (i.e. comparing non-manipulated invaded and uninvaded sites) or experimental (i.e. removal or addition of target plants) were included where they explicitly mentioned the identity of the alien

plant taxon causing impact. We only selected studies focusing on the impact of a single alien species rather than that of multispecies alien assemblages. We also excluded all studies addressing the effects of expanding or colonizing native species such as 'shrub encroachment' (the review of Liao *et al.* 2008 included many studies on native species).

(2) Where the same article examined different alien species, several ecosystems and/or more than one response variable, we considered each of these separately as they represented different examples of ecological impacts. A possible criticism is that using all measures represents a form of pseudo-replication in the meta-analysis. However, the same approach has previously used in meta-analysis (Liao *et al.* 2008; Rey-Benayas *et al.* 2009). The influence of pseudo-replication was tested with a randomly selected single effect size per article for impact types with large sample sizes (see next section).

(3) When a response variable was measured at different times (e.g. sampling at different seasons or years), we made an informed decision on whether to take the mean value across times or consider each measure as independent. In some instances, we only used the final measurement (see Criterion 5).

**Table 1** Summary of the ecological impacts due to alien plant species classified by levels of ecological complexity, impact types and response variables examined in the meta-analysis

| Level | Impact type | Variables |
|---|---|---|
| Plant species | Fitness | Seed set, germination rate, seedling establishment, survival, mortality (−) |
| | Growth | Increase in size of whole plants or plant parts |
| Plant communities | Production | Biomass, NPP |
| | Abundance | Plant number, density, cover |
| | Diversity | Alpha diversity, richness, evenness |
| Animal species | Fitness | Egg production, adult emergence, survival, mortality (−) |
| | Growth | Increase in size of whole animals at any life stage |
| Animal communities* | Production | Biomass |
| | Abundance | Density, visits, counts |
| | Diversity | Alpha diversity, richness |
| | Behaviour | Grazing, predation, mobility, activity |
| Ecosystems | Soil OM | Soil organic matter |
| | C pools | Soil, litter, plant C |
| | N pools | Soil, litter, plant N |
| | N available | $NO_3$ and/or $NH_4$ in soil |
| | N mineralization | N mineralization rate |
| | N nitrification | N nitrification rate |
| | P pools | Soil, litter, plant P |
| | C/N | Soil, litter, plant C/N |
| | Microbial activity | Activity of soil bacteria, fungi or enzymes |
| | pH | pH |
| | Litter decomposition | Litter decomposition rate |
| | Salinity | Soil Na, electrical conductivity |
| | Soil moisture | Soil water content |

As low mortality indicates high survival, the sign of the effect sizes of the former variable was changed (−).

*Although they refer mostly to animals, they also include impacts on micro-organisms (e.g. bacteria, fungi and protozoa).

(4) There were also studies conducted on the same species in similar ecosystems but at different locations. We made an informed decision whether to consider studies as independent if locations were from clearly distinct regions (e.g. different islands, different countries) and considered the effects across locations if they represented similar ecosystems under the influence of the same environmental conditions. If the study manipulated other ecological factors (e.g. N-addition, disturbance levels) only results from non-manipulated plots were considered.

(5) When the study investigated the effects of different degrees of invasion (e.g. heavily vs. less invaded sites) and different residence times (i.e. old vs. recent invasions) we only considered the putative largest contrast. That is, we examined differences between the least invaded sites (i.e. often uninvaded) and the most invaded sites, or differences between uninvaded sites and sites with the longest time since invasion.

## Data extraction

A total of 199 articles representing 1041 cases of invasion across 135 taxa (all at the species level except four hybrids and one subspecies) met our criteria (Appendix S1). In the vast majority of studies, invaded sites had high alien abundance and although the measures of plant abundance were not always given, the study sites were usually described as having high or > 50% cover. Furthermore, the alien species considered were in many cases explicitly described as invasive in the study region. Thus, our results summarize the impact of invasive alien plant species.

Among the alien plant species investigated, perennial herbs (344 cases) and trees (202 cases) were more often represented than other life-forms and there were only 18 N-fixing species (156 cases). Almost half of the studies (478) have been conducted in temperate regions and one-third (340) in grasslands. Twenty-four per cent of studies (245) were conducted on islands.

In most cases, field assessments of impact were based on comparisons of several ecological variables in long-standing invaded vs. uninvaded sites nearby. Only 14% of the studies involved manipulative experiments (i.e. removal or addition of species). The impact variables measured most frequently concerned N pools (103 cases), plant species diversity (136), animal abundance (94) and plant biomass and production (90). Individual response variables were related to species performance, community structure and ecosystem processes in invaded and uninvaded plots. These levels of ecological complexity were further classified into 24 types of impact (Table 1). Many impact types contain different variables and sometimes the same variable has been estimated by using different methods. However, using different variables to estimate effect sizes within a category is intrinsic to meta-analysis (e.g. Cardinale *et al.* 2006; Winfree *et al.* 2009; Van Kleunen *et al.* 2010b). Although the inclusion of heterogeneous data has prompted some criticism of meta-analytical methods, they provide the opportunity to quantitatively identify large-scale patterns (Steward 2010) as the effect size is a unit-free metric that accounts for sample size bias (see below).

We extracted mean, statistical variation (usually SE or SD) and sample size values for invaded and uninvaded plots for each response variable. These data were extracted directly from tables or from graphs using the DATATHIEF II software (B. Thumers; http://www.datat-hief.org) or, in some cases, also by measuring mean and statistical variation 'manually' using a ruler. For other studies, we obtained data directly from the corresponding authors.

## Response ratios

For each pair of invaded (*i*) and uninvaded (*ni*) sites per case study, we calculated Hedges' *d* as a measure of effect size. Hedges' *d* is an estimate of the standardized mean difference that is not biased by small sample sizes (Rosenberg *et al.* 2000). From each pair of mean values $(\overline{X})$ the individual effect size *d* was calculated as:

$$d = \frac{\left(\overline{X}^i - \overline{X}^{ni}\right)}{S} J,$$

where *S* is the pooled standard deviation and *J* a weighting factor based on the number of replicates (*N*) per treatment. *J* was calculated as:

$$J = 1 - \frac{3}{4(N^{ni} + N^i - 2) - 1}.$$

The variance of Hedges' *d*, *Vd* was calculated as:

$$Vd = \frac{N^{ni} + N^i}{N^{ni} N^i} + \frac{d^2}{2(N^{ni} + N^i)}.$$

Hedges' *d* is a unit-free index which ranges from $-\infty$ to $+\infty$ and estimates the size of the impact and its direction. As in classical statistical analysis, the highest effect sizes are from those studies showing large differences between invaded and uninvaded plots when the plots have low variability. Zero *d* values signify no difference in the variable measured between invaded and uninvaded plots; positive and negative *d* values imply a general trend following invasion for an increase and decrease, respectively. Hedges' *d* calculations and statistical analysis were conducted with the MetaWin v2.1 Software (Rosenberg *et al.* 2000).

For each impact type, we calculated the weighted mean effect size $(d^+)$ across the sample of studies with information on the relevant response variable. To test whether $d^+$ differed significantly from zero (i.e. no change with invasion), we assessed whether the bias-corrected 95% bootstrap-confidence interval (CI) of $d^+$ did not overlap zero based on 999 iterations (Rosenberg *et al.* 2000). We also tested whether effects sizes across studies were homogeneous, using the $Q_{total}$ statistic based on a chi-squared test ($Q_t$ hereafter). A significant $Q_t$ indicates that the variance among effect sizes is greater than that expected by sampling error alone (i.e. effect sizes are not equal across studies). The mean percentage of change in a response variable was estimated as $(e^{R+} - 1) \times 100$ where $R^+$ is the weighted mean response ratio (*R*) across studies (Rosenberg *et al.* 2000). The natural logarithm of *R* is calculated as:

$$\ln R = \ln\left(\frac{\overline{X}^i}{\overline{X}^{ni}}\right).$$

For categorical comparisons (e.g. N-fixing vs. non-N-fixing), we examined $P_{random}$ values associated to $Q_{between}$ statistic ($Q_b$ hereafter), which describe the variation in effect sizes that can be ascribed to differences between categories. We also tested whether the remaining within-group heterogeneity ($Q_w$) was significant using a chi-squared test. Data were analysed using random-effects models which are

preferable in ecological data synthesis because their assumptions are more likely to be satisfied (Rosenberg *et al.* 2000).

Many studies reported data on the effect of the same alien species on different response variables or in different ecosystems. To avoid pseudoreplication, we also ran the analyses with a randomly selected single effect size per article, for three response variables with the largest sample sizes: plant diversity, animal abundance and N pools. The mean effect sizes for each of these types of impact were similar to those obtained for all studies and the bias-corrected 95% bootstrap-confidence interval (CI) overlapped between the whole dataset and the reduced dataset (Appendix S2). As a consequence, we felt confident to include all the data in our analyses. The inclusion of all case studies enabled us to screen for differences in impact within levels of ecological complexity in a manner similar to the amalgamated meta-analysis performed by Rey-Benayas *et al.* (2009) or Liao *et al.* (2008).

In studies on ecological impact, there might be a bias against publishing negative results and studies with larger sample sizes might have more power to detect significant impacts. We examined standardized effect sizes of the raw data to test these potential biases and found that they were slightly negatively (Spearman $r = -0.099$) but significantly ($P = 0.001$) associated with sample size. This might suggest that studies with small sample sizes are slightly more likely to be published when they found bigger differences between invaded and uninvaded sites (Rosenberg *et al.* 2000). However, a plot of the effect sizes against the sample size revealed a funnel-shaped distribution of the data points (Appendix S3), as would be expected in the absence of a sampling bias (Palmer 1999).

Following Rosenthal (1979), we estimated the fail-safe number, that is, the number of studies that would have to be added to change the results of the meta-analysis from significant to non-significant, to be 37 689. As this value is larger than $5N + 10 = 5215$ where $N =$ number of case studies in our dataset, we are confident that the observed results can be treated as a reliable estimate of the true effect (Rosenberg 2005). Moreover, a plot of the standardized effect sizes against the normal quantiles revealed a straight line (Appendix S3) indicating that the effect sizes are normally distributed (Wang & Bushman 1998). Overall, this indicates that there was only a mild publication bias unlikely to change the overall meaning of the results.

## RESULTS

Averaged across all studies, there was considerable variability in the effect sizes ($Q_t = 2257.36$, d.f. = 1039, $P < 0.0001$) ranging over 5 orders of magnitude. Mean effect sizes differed significantly among the impact types examined ($Q_b = 316.78$, d.f. = 23, $P = 0.001$) not only in magnitude but also in direction (Figs 1 and 2; Appendix S4).

The mean effect size within impact types was also heterogeneous ($Q_w = 1940.57$, d.f. = 1016, $P < 0.0001$; see Appendix S4 for $Q_t$ of each impact type). This result indicates that even for particular impact types the magnitude and direction of the effect size varied significantly across studies. For 11 of the 24 impact types examined, the CI of the mean effect size overlapped zero (Figs 1 and 2). Therefore, for these impact types, we could not support the hypothesis that the variables examined changed uniformly with invasion, due to heterogeneity in the direction of effects found for different studies (Appendix S4).

Alien plants significantly reduced fitness and growth of resident plant species by 41.7 and 22.1%, respectively, and changed plant community structure by decreasing species' abundance (43.5%) and diversity (50.7%). However, total community production increased by
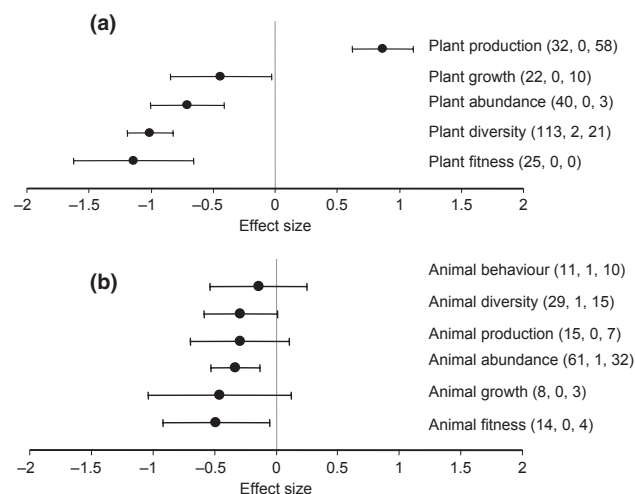


**Figure 1** Mean effect size (Hedges' *d*) of differences between alien plant species impacts to (a) plant species and communities and (b) animal species and communities. The bars around the means denote bias-corrected 95%-bootstrap confidence intervals. A mean effect size is significantly different from zero when its 95% confidence interval do not bracket zero. Positive mean effect sizes indicate that the invaded plots had on average greater values for variables describing a particular impact type. The sample sizes with Hedges' *d* < 0, Hedges' *d* = 0 and Hedges' *d* > 0 are given next to the bars.
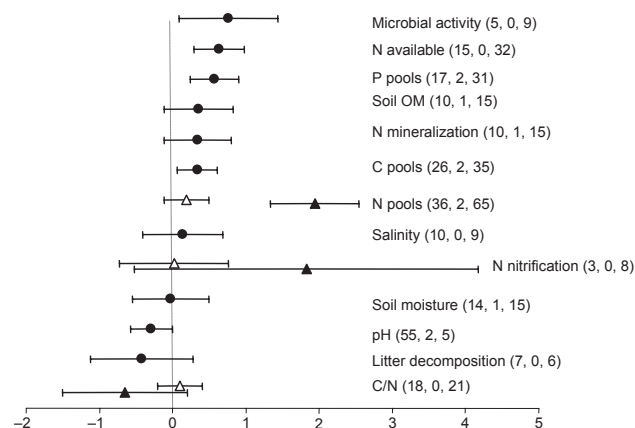


**Figure 2** Mean effect size (Hedges' *d*) of differences between ecosystem impacts with indication of significant differences between N-fixing (closed triangles) and non-N-fixing (open triangles) alien plant species. Otherwise as in Figure 1.

56.8% following invasion (Fig. 1a). Alien plants also significantly decreased animal species' fitness by 16.5% and abundance by 17.3% (Fig. 1b). For the other variables related to animal species performance and animal community structure the CI of the mean effect size overlapped zero. Thus, although the trend was towards a decrease in the other variables with invasion, the direction of effect sizes were not uniform across studies.

With regard to ecosystem impacts, alien plants enhanced microbial activity by 32.3%, available N (53.7%), N, P and C pools (22.1, 19.7 and 11.6%, respectively), and decreased pH (3%), but for the impacts on the other variables, the CI of the mean effect size overlapped zero (Fig. 2; Appendix S4). For instance, on average, invasion decreased litter decomposition by 15.6% but there was a significant heterogeneity among studies ($Q_t = 24.14$, d.f. = 12, $P = 0.02$) with almost as

many studies showing increases as decreases in litter decomposition due to invasion (Fig. 2).

Compared with non-N-fixing species, the alien N-fixing species increased the impact on N pools and N nitrification significantly ($d^+ = 1.94$ vs. $d^+ = 0.19$; $d^+ = 1.83$ vs. $d^+ = 0.02$, respectively). By contrast, while N-fixing species decreased C/N, non-N-fixing species increased the value of this variable ($d^+ = -0.65$ vs. $d^+ = 0.10$). The impact of N-fixing alien plants was not significantly different from that of non-N-fixing species for any of the other impact type addressed in this study (Table 2).

There were no significant differences in the mean effect sizes between studies conducted on islands and on the mainland (Table 2).

## DISCUSSION

Our analysis provides rigorous evidence that alien plant species exert significant impacts on many ecological variables. However, the magnitude and direction of these impacts vary among different levels of ecological complexity. In absolute terms, impacts on plant species and communities were substantial whereas those on nutrient cycling were relatively minor. This indicates that by the time impacts on nutrient cycling are detected, plant species and communities are likely to have already been affected by invasion. Nevertheless, the causal

**Table 2** Heterogeneity between ($Q_b$) the impact of N-fixing and non-N-fixing alien plant species and for studies conducted in islands and in mainland ecosystems with indication of sample sizes and *P*-values (significant results are in **bold**)

| Level | Impact type | N-fixing | | | Insularity | | |
|---|---|---|---|---|---|---|---|
| | | $Q_b$ | $N_{yes}, N_{no}$ | P | $Q_b$ | $N_{yes}, N_{no}$ | P |
| Plant species | Fitness | 1.31 | 8, 18 | 0.29 | 0.77 | 2, 23 | 0.46 |
| | Growth | – | – | – | 1.08 | 8, 46 | 0.37 |
| Plant communities | Production | 7.25 | 4, 86 | 0.06 | 4.74 | 13, 77 | 0.14 |
| | Abundance | 1.92 | 11, 42 | 0.17 | 0.66 | 4, 49 | 0.45 |
| | Diversity | 3.60 | 15, 121 | 0.09 | 1.03 | 25, 111 | 0.34 |
| Animal species | Fitness | – | – | – | – | – | – |
| | Growth | – | – | – | – | – | – |
| Animal communities* | Production | 0.00 | 4, 18 | 1 | 0.45 | 3, 19 | 0.46 |
| | Abundance | 4.45 | 11, 83 | 0.06 | 0.00 | 34, 60 | 0.97 |
| | Diversity | 0.12 | 3, 42 | 0.74 | 1.19 | 12, 33 | 0.30 |
| | Behaviour | – | – | – | – | – | – |
| Ecosystems | Soil OM | 1.31 | 8, 18 | 0.29 | 0.34 | 3, 23 | 0.60 |
| | C pools | 2.62 | 7, 56 | 0.14 | 0.46 | 3, 19 | 0.46 |
| | N pools | 28.21 | 25, 78 | **0.001** | 0.04 | 34, 69 | 0.87 |
| | N available | 1.96 | 13, 34 | 0.22 | 0.17 | 10, 37 | 0.71 |
| | N mineralization | 0.19 | 7, 18 | 0.71 | 0.08 | 4, 21 | 0.82 |
| | N nitrification | 8.35 | 3, 8 | **0.01** | 0.96 | 2, 9 | 0.35 |
| | P pools | 4.33 | 13, 37 | 0.06 | 4.25 | 12, 38 | 0.10 |
| | C/N | 3.99 | 7, 32 | **0.05** | 0.73 | 20, 19 | 0.42 |
| | Microbial activity | 0.86 | 3, 11 | 0.39 | – | – | – |
| | pH | 0.14 | 11, 51 | 0.77 | 0.00 | 25, 37 | 0.96 |
| | Litter decomposition | 0.01 | 2, 11 | 0.97 | 2.30 | 3, 10 | 0.27 |
| | Salinity | 0.11 | 5, 14 | 0.75 | 0.17 | 4, 15 | 0.69 |
| | Soil moisture | 0.23 | 3, 17 | 0.66 | 0.73 | 3, 17 | 0.41 |

Significance values of $Q_b$ are based on randomization tests. Empty cells denote the analysis could not be conducted due to the lack of replicates.
*Although they refer mostly to animals, they also include impacts on micro-organisms (e.g. bacteria, fungi and protozoa).

links between plant community and ecosystem impacts remain largely unexplored (Levine *et al.* 2003). There are only a few experiments that teased apart the direct impacts on nutrient cycling from the indirect impacts via changes in community structure (but see Belnap *et al.* 2005; Allison *et al.* 2006 for exceptions).

Our analysis also shows that alien plants have bottom-up impacts on higher trophic levels, although on average these effects are of lower magnitude than those within the same trophic level. The effect of alien plants on taxa at higher trophic levels might depend on the degree of their dependence on alien plants as a food resource (de Groot *et al.* 2007; Gerber *et al.* 2008) but indirect effects may occur when alien plants increase habitat heterogeneity (Pearson 2009). Studies which have simultaneously investigated the impacts of alien plants on primary producers and on other trophic levels are scarce (Valtonen *et al.* 2006; de Groot *et al.* 2007; Gerber *et al.* 2008) and more are needed to understand how frequent feedback impacts occur across trophic levels.

One of the most striking findings of our study is that alien plant species reduced local plant species diversity and increased plant production of the invaded community. This is contrary to what diversity-ecosystem functioning experiments would predict and supports the importance of sampling effects in the patterns observed in such studies (Cardinale *et al.* 2006). Experimental work has shown that a strong invader can essentially reverse the positive diversity–productivity relationship in a manner consistent to what we have found (Zavaleta & Hulvey 2004; Maron & Marler 2008). Our analysis suggests that alien plant invasions may result in a sampling effect where ecosystem production is driven by the addition of a single highly productive species, even if overall species diversity declines.

A prediction which our analysis did not support is generally greater impact of alien N-fixing species compared with alien non-N-fixing species. Seminal work on the impact of *Myrica faya*, an N-fixing introduced tree in Hawaii, on early stages of primary succession (Vitousek *et al.* 1987) motivated the idea that alien N-fixing species can exert large impacts on recipient ecosystems. Current evidence suggests that compared with non-N-fixing species, N-fixing alien species more strongly affect N and C cycling (Liao *et al.* 2008), but our results indicate that no such differences are found for impacts on other ecosystem processes or on community structure.

Another unexpected result is that we did not find greater impacts on islands than on mainland ecosystems. The generally accepted assumption that islands are more threatened by plant invaders than the mainland is largely drawn form the fact that their floras are proportionally more dominated by alien species and ecosystems are more disturbed (D'Antonio & Dudley 1994). Indeed, compared with corresponding mainland ecosystems, islands often harbour more alien species (Lonsdale 1999) and individual alien plants can often be more widespread (Gimeno *et al.* 2006). This might suggest greater impacts but our results indicate that the magnitude of the impact is not significantly greater than in mainland ecosystems and imply that invasion success does not necessarily translate into greater impacts at a local scale (Parker *et al.* 1999).

Our results summarize the impacts of strongly dominating alien plant species prone to cause changes in species, communities or ecosystems (Vilà *et al.* 2010). The data available did not allow us to determine how impacts might increase as a function of alien plant abundances. This seems to be a major gap in our understanding of biological invasion regarding whether the relationship between alien plant abundance and impact is saturating, sigmoid or linear (Ehrenfeld

2010). It is of interest to know whether there are thresholds or 'breakpoints' where impacts of alien plants may not scale linearly with their abundances, and how this relationship may vary among invading species (Andreu *et al.* 2009) and the spatial scale of study (Powell *et al.* 2011). The experimental studies examining this relationship found it to either scale linearly (Maron & Marler 2008) or not at all (Meffin *et al.* 2010) with invader abundance. Thus, additional experiments are needed before we can make generalizations about the nature of this relationship (Parker *et al.* 1999; Levine *et al.* 2003). This topic remains at the core of whether the impact of alien species is related to their ecological success.

In conclusion, our analyses have highlighted that alien plants pose significant impacts at the species, community and ecosystem level. Current understanding of invasive plant impacts is restricted to relatively few dominant alien species (Pyšek *et al.* 2008). However, possibly because our database had different representation of alien plant life forms and ecosystems, the magnitude of the impacts was very variable and even for a given impact type, the direction of the ecological change was context-dependent. Our quantitative approach to value impacts could be further developed as the basis for scoring alien species and recipient ecosystems for risk assessment of invasions (Nentwig *et al.* 2009). We hope this article helps to re-invigorate this area of research by highlighting the association among impacts at several levels of ecological complexity and also the links between invasion success and invasion impacts.

## ACKNOWLEDGEMENTS

## AUTHOR CONTRIBUTIONS

MV, PP, US and PEH designed research; MV, JLE, MH, JP and YS prepared the database; MV and VJ analysed data; and MV, PP, VJ, JLM, US and PEH wrote the article.

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## SUPPORTING INFORMATION

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

**Appendix S1** List of studies for meta-analysis on alien plant species impact on species, communities and ecosystems.

**Appendix S2** Total heterogeneity ($Q_t$) with indication of sample size, effect sizes ($d^+$) and 95% CI for three impact types of alien plant species when considering all case studies (whole) and only one study per article (reduced).

**Appendix S3** MetaWin output for (a) normal quartile plot and (b) funnel-plot of effect sizes (Hedges' *d*) of the raw data vs. sample size.

**Appendix S4** Total heterogeneity ($Q_t$) with indication of *P*-values, mean effect sizes ($d^+$), degrees of freedom (d.f.) and 95% CI for different impact types of alien plant species.

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