**META-
ANALYSIS**

Global meta-analysis of the impacts of terrestrial invertebrate invaders on species, communities and ecosystems

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ABSTRACT

Aim Terrestrial invertebrates comprise a large proportion of alien species world-wide, yet a quantitative global synthesis of their effects on native species and ecosystems has not been explored. We conducted a meta-analysis to examine the ecological impacts of terrestrial invertebrate invaders and to test how impacts are modulated by the invader's trophic position, habitat attributes (i.e. insularity and disturbance) and the study methodology (observational versus experimental).

Location Global.

Methods We investigated the effects of terrestrial invertebrate invaders on populations, communities and ecosystems by conducting a random effects meta-analysis using 112 articles reporting data from 710 field and laboratory studies. The analysis included 16 insect, 11 earthworm, 7 slug and 1 nematode invaders.

Results On average, across invaders, the presence of invaders reduced plant fitness (52%), animal diversity (33%) and animal abundance (29%). Leaf litter decomposition was 41% higher in the presence of invaders, while other ecosystem-level variables such as nutrient cycling were not affected in a consistent direction. Invasive predators and detritivores decreased animal abundance, whereas herbivores and omnivores had limited impacts. Single invaders increased soil nitrogen pools while multiple species did not. Insularity and disturbance did not affect the magnitude of the impacts significantly, mainly because there was a large variation among studies.

Main conclusions Overall, our study indicates that terrestrial invertebrate invaders have significant consistent effects on populations, communities and ecosystems, with islands and disturbed sites not being more prone to impacts. However, effects vary considerably depending on the type of impact being examined and the trophic position of the invader. There is no evidence that invaders cause larger impacts when multiple species of invaders, rather than single invaders, are involved.

Keywords
Alien, arthropods, biological invasions, ecosystem functioning, effect size, insects, non-native, systematic review, trophic position.

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INTRODUCTION

Biological invasions are recognized as key drivers of global change that pose substantial threats to biodiversity and ecosystem functioning (Parker *et al.*, 1999; Ehrenfeld, 2010; Simberloff, 2011). A large number of case studies have been conducted to examine the impacts of invasions, and recent meta-analyses synthesizing this research have provided consid-erable insight into general trends on the impacts of terrestrial plant invaders on species, communities and ecosystems (Liao *et al.*, 2008; Vilà *et al.*, 2011; Castro-Díez *et al.*, 2014; van Hengstum *et al.*, 2014), as well as the impacts of aquatic invaders on species and communities (Thomsen *et al.*, 2014; Maggi *et al.*, 2015; Gallardo *et al.*, 2016). Yet our general understanding of patterns of impacts and the processes determining these patterns remains limited (Blackburn *et al.*, 2014; Jeschke *et al.*,

2014), with most studies failing to test specific hypotheses that could help to disentangle the context-specific nature of major impacts (Ricciardi *et al.*, 2013).

Terrestrial invertebrates comprise a large number of alien species world-wide (Pimentel *et al.*, 2005); for example, in Europe 2481 species of alien terrestrial invertebrates are present, making them the second largest group of alien taxa after alien plants (5789 species) (Vilà *et al.*, 2010). In Canada, there are even more alien terrestrial invertebrates (1658 species) than alien plants (1229 species) (Langor *et al.*, 2014). Terrestrial invertebrates can have significant ecological and economic impacts when they invade, for instance as crop or forest pests, as predators of native organisms or as vectors of wildlife and human diseases (Roques *et al.*, 2009; Vaes-Petignat & Nentwig, 2014). Moreover, ranges of the top invertebrate invaders are projected to increase substantially in the future with climate change and land-use change (Bellard *et al.*, 2013). Despite their prevalence, impacts and increasing numbers with global change (Roques *et al.*, 2009), there has yet to be a quantitative synthesis of their ecological impacts.

We conducted a global meta-analysis of the ecological impacts of terrestrial invertebrate invaders to investigate how the magnitude and direction of impacts vary across levels of ecological complexity and to test key factors that could influence the variability in the ecological changes they inflict. In particular, we tested if differences in impact are modulated by invader characteristics, main habitat attributes and study methodology. We tested the following hypotheses:

1. The trophic level of the invader affects the magnitude and direction of the impact, with predators having the strongest negative impacts on animals but weaker effects on plants. The trophic position of invaders has been suggested to strongly influence their impacts on communities and ecosystems (Elton, 1958; Clavero & García-Berthou, 2005; Strayer, 2010). It has also been proposed that the effect of an invader may vary depending on the trophic position of the native species in the recipient community being invaded. For example, invasive predators are expected to have negative effects on other consumers but may have indirect positive effects on primary producers due to trophic cascades (Schmitz *et al.*, 2000). In particular we examined whether impacts on plants versus animals differed and whether the trophic position of the invader influenced the strength of the impact.

2. Invasions of multiple species result in larger impacts than invasions involving a single invader. Invasive species often interact with other invaders and may facilitate each other's spread or establishment, leading to an acceleration in the magnitude of effects on invaded systems (Simberloff & Von Holle, 1999; Simberloff, 2006).

3. Impacts are larger on islands than on mainland. Islands often have fewer species and differ in community composition from mainland habitats (Whittaker & Fernandez-Palacios, 2006), which results in greater opportunities for invaders to be functionally distinct and thus to have larger impacts.

4. Invaders have greater impacts in disturbed areas. Disturbances that remove native species or shift habitat conditions away

from those to which the native community is adapted may lead to larger impacts of invaders that lose native competitors (Byers, 2002; Lockwood *et al.*, 2013).

We also tested the effects of study methodology. A previous meta-analysis on marine systems found that the effects of invaders differed for experimental versus observational studies (Maggi *et al.*, 2015). Although observational studies of uninvaded or lightly invaded versus heavily invaded plots can allow data to be collected relatively easily, effects may be confounded with differences between sites that are due to factors other than the presence of alien species. Conversely, experiments might have a disadvantage over observational studies, as the effects of invader removal might be confounded with disturbance effects (Kumschick *et al.*, 2015).

METHODS

Literature search

On 8 May 2014 we searched the ISI Web of Science database for articles on impacts of terrestrial invertebrate invaders, using a combination of search terms for invertebrate groups and ecological effects. We searched using the names of all major phyla of terrestrial invertebrates, as well as search terms for insects, earthworms, snails and slugs, as these groups are often not referred to by their taxonomic classification. We focused on 19 impact types (Table 1) relating to the performance of individual species, characteristics of communities and ecosystem properties or processes. The search term combinations used were: ((invader OR exotic OR alien OR invas* OR non-native) AND (invert* OR annelid* OR arthropod* OR platyhelminth* OR nematod* OR nematomorph* OR tardigrad* OR onychophor* OR priapulid* OR nemert*OR mollus* OR insect* OR earthworm* OR snail* OR slug*) AND (ecosystem* OR structure OR function OR nutrient* OR carbon OR nitrogen OR phosphorus OR decomposition OR soil OR hydrolog* OR water OR community* OR diversity* OR compet* OR herbivor* OR predat* OR prey) AND (impact* OR effect*)) NOT (marine or freshwater). No restriction was placed on publication year.

We scanned the titles of articles obtained in this search (3469 articles in total) to remove those that addressed unrelated topics. For example, articles involving biological control, other purposeful introductions or expansions of native species were excluded. We also did not include alien species which were parasites, nor did we include effects of alien species on other alien species. We read the abstracts and, if necessary, the full text of the remaining articles to assess their suitability. We also examined the reference lists of the articles selected using these criteria for additional suitable papers. Further, we obtained additional articles by searching the references listed in two previous reviews (Kenis *et al.*, 2009; Gandhi & Herms, 2010) that reviewed studies on invasions of terrestrial insects.

We then applied the following criteria to select case studies for analysis:

1. Studies that quantitatively compared either invaded versus uninvaded treatments, or heavily versus lightly invaded treat-

Table 1 Ecological variables corresponding to the 19 impact types classified into three levels of organization (species, community, ecosystem) following Vilà *et al.* (2011). The sign of the effect sizes (–) for mortality was changed because an increase in mortality corresponds to a decrease in survival. Likewise, the signs of the effect sizes for mass remaining, depth and cover of litter were changed because an increase corresponds to a decrease in decomposition rate.

Level	Impact type	Variables
Species	Plant fitness	Seedling establishment, fruit set, seed set, flowering, mortality (–), herbivore damage
Species	Plant growth	Population growth
Species	Animal fitness	Fledging success, hatching success, juvenile recruitment, survival, mortality (–), reproduction
Species	Animal growth	Population growth
Communities	Animal production	Biomass
Communities	Animal abundance	Density, number, volume, cover
Communities	Animal diversity	Richness, diversity
Communities	Plant production	Biomass
Communities	Plant abundance	Density, cover, number
Communities	Plant diversity	Richness, diversity
Ecosystems	Microbial activity	Respiration, enzyme activity
Ecosystems	P pools	Soil P
Ecosystems	pH	Soil pH, litter pH
Ecosystems	Litter decomposition	Decomposition rate, mass remaining (–), mass lost, litter depth (–), litter cover (–)
Ecosystems	C pools	Litter C, soil C, plant C
Ecosystems	C/N	Litter C/N, plant C/N, soil C/N
Ecosystems	N pools	Soil $N/NO_3/NH_4$, litter N, plant N
Ecosystems	N fluxes	N mineralization/nitrification rate
Ecosystems	Soil moisture	Soil moisture

ments. Articles lacking appropriate controls or replication were excluded.

2. Studies reporting the mean values of variables, number of replicates and a measure of variability around the mean. However, if these data could not be obtained from a paper but did appear to have been recorded, we contacted the authors of the original study to request either the raw data or relevant information.

3. When multiple ecosystem types, species or response variables were examined separately within the same article they were treated as separate case studies. This approach has been used in previous meta-analyses (e.g. Liao *et al.*, 2008; Vilà *et al.*, 2011; van Hengstum *et al.*, 2014). Nevertheless, case studies from the same article may lack independence; therefore, we included a random effect for article identity in all analyses.

4. If an article included studies conducted on the same species and ecosystem type but located in two or more distinct regions we also considered the studies independently.

5. When more than two treatment levels were examined in a study, only the putative largest contrast was included (Vilà *et al.*, 2011). Thus, if the degree of invasion varied, we examined the least invaded versus the most invaded sites. If the time of residence of the invader varied, we examined the sites that had been invaded for longest.

6. If response variables were measured at multiple time points, we included only the longest time step. In some cases, studies examined responses across seasons; in these cases, we selected the season in which the impact is most commonly examined. For example, most studies measure arthropod abundance in summer, and thus we used estimates of abundance from that season.

7. If multiple sampling techniques were used to estimate impacts within one area, only results from the most efficient sampling method were included. For example, if a study used both pitfall traps and sweep nets to sample insect communities, we chose the method that captured a greater number of individuals.

Data extraction and effect sizes

We recorded means, measures of variability and sample sizes for each response variable. Data from graphs were extracted using the image analysis software IMAGEJ (Schneider *et al.*, 2012). We classified case studies based on whether impacts related to populations, communities or ecosystems. These levels of ecological complexity were further divided into 19 impact types (Table 1), following Vilà *et al.* (2011). We also collected data on the trophic position of the invader (i.e. detritivore, herbivore, omnivore, predator); whether single or multiple invasive species were present; whether the invasion occurred on an island; whether the invaded area was intact or disturbed; and whether the study was observational or experimental.

For each response variable, we calculated the Hedges' *d* effect size to estimate the difference in impacts between invaded sites

(i) and uninvaded/lightly invaded sites (ni). Hedges' d weighs cases by their sample size and the inverse of their variance, and it was calculated as follows (Hedges & Olkin, 1985):

$$d = \frac{(\bar{X}_i - \bar{X}_{ni})}{\mathrm{SD}_{\mathrm{pooled}}} J \qquad (1)$$

where $\bar{X}_i$ and $\bar{X}_{ni}$ are the sample means of the two groups (invaded and uninvaded/lightly invaded, respectively), $\mathrm{SD}_{\mathrm{pooled}}$ is their pooled standard deviation, and J is a weighting factor based on the number of replicates per group. $\mathrm{SD}_{\mathrm{pooled}}$ was calculated as:

$$\mathrm{SD}_{\mathrm{pooled}} = \sqrt{\frac{\mathrm{SD}_i^2(n_i - 1) + \mathrm{SD}_{ni}^2(n_{ni} - 1)}{n_i + n_{ni} - 2}} \qquad (2)$$

where n_i and n_{ni} are the number of observations in the two groups, and SD_i^2 and SD_{ni}^2 are their standard deviations.

J was calculated as:

$$J = 1 - \frac{3}{4(n_i + n_{ni} - 2) - 1}. \qquad (3)$$

The variance of Hedges' d was calculated using the following equation:

$$\mathrm{Var}\, d = \frac{n_i + n_{ni}}{n_i n_{ni}} + \frac{d^2}{2(n_i + n_{ni})} \qquad (4)$$

Hedges' d ranges from $-\infty$ to $+\infty$. A negative value indicates a decrease while a positive value indicates an increase in species, communities or ecosystem properties with invasion. Larger effect sizes indicate a greater difference between invaded and uninvaded treatments, whereas a Hedges' d of zero indicates that there is no difference between treatments for the variable being examined. The magnitude of Hedges' d can be interpreted using the following rule of thumb (Cohen, 2013): 0.2 is considered to be a small effect, 0.5 is a medium effect, 0.8 is a large effect and $d > 1.0$ is a very large effect. We calculated a grand mean effect size (d^+) for each impact type by combining effect sizes of all relevant comparisons using a random effects model (Koricheva *et al.*, 2013). Random effects models include two components of variance around the mean, a within-study variance (sampling error) and a between-study variance (τ^2). We also included a random effect in our model to account for a potential lack of independence among case studies from the same article (e.g. due to a shared study location or similar experimental design). The SE of the mean effect was used to calculate 95% confidence intervals, and mean effect sizes were considered significantly different from 0 if their confidence intervals did not include 0.

The mean percentage of change in response variables between invaded and uninvaded treatments was estimated as:

$$(e^{R^+} - 1) \times 100 \qquad (5)$$

where R^+ is the weighted mean response ratio (R) across studies. The natural logarithm of R was calculated as (Koricheva *et al.*, 2013):

$$\ln R = \ln \left(\frac{\bar{X}_i}{\bar{X}_{ni}} \right). \qquad (6)$$

For each weighted mean effect size, we calculated the total heterogeneity (Q_t) to test whether effect sizes across case studies were heterogeneous (Koricheva *et al.*, 2013). A significant Q_t value (assessed using a chi-square distribution) indicates that the individual effect sizes used to calculate the weighted mean effect size (d^+) are heterogeneous, and the variance among them is greater than would be expected due to sampling error alone. This suggests that there may be some additional unexamined factor influencing the effect sizes. We calculated between-group heterogeneity (Q_b) to investigate whether mean effect sizes differed among impact types and within-group heterogeneity (Q_w) to assess whether effect sizes differed within each impact type.

We also calculated between-group heterogeneity to investigate differences between levels of categorical explanatory variables. Specifically, analyses were conducted to examine if main effect sizes differed with the trophic position of the invader, between single and multiple invasive species, between islands and mainlands, between disturbed and intact sites, as well as between experimental and observational studies. For the test examining effects of disturbance, we restricted our analysis to field studies as no laboratory experiments examined intact systems. We calculated Q_b for all impact types that had at least two case studies per category. The proportion of observed variance explained by the model (i.e. a given explanatory variable) can be calculated by determining the ratio of Q_b to Q_t (Koricheva *et al.*, 2013). Analyses were performed in R v.3.1.2 (R Core Team, 2014) using the metafor package (Viechtbauer, 2010).

To examine whether the results of our meta-analysis may be affected by publication bias, we examined the correlation between sample size and standardized effect sizes across studies and created funnel plots (Koricheva *et al.*, 2013).

RESULTS

Database characteristics

After applying the selection criteria, our dataset consisted of a total of 710 case studies from 112 articles (see Appendix S1 in the Supporting Information). The articles examined the effects of 35 species of alien terrestrial invertebrates belonging to four classes (Fig. S1, Table 2). The majority of the studies assessed the impacts of ants, oligochaetes and hemipterans. The ant *Linepithema humile* was the most frequently investigated species (30%). Most studies focused on impacts on animal abundance (44%). Global coverage was highly uneven, with 56% of case studies being conducted in North America. Most of the studies were conducted in the field (86%) rather than in the laboratory, and more were observational (62%) than experimental. Experimental studies were conducted in both the field and laboratory, whereas all observational studies were field-based.

Table 2 List of species included in the meta-analysis, their trophic position, taxonomic group (order for the class Insecta and class for other taxa) and the number of case studies examining each species. Some case studies involved multiple species and are therefore included more than once.

Species	Trophic position	Taxonomic group	Number of case studies
Adelges tsugae	Herbivore	Hemiptera	80
Amynthas hawayanus	Detritivore	Oligochaeta	12
Amynthas rodercensis	Detritivore	Oligochaeta	6
Amynthas hilgendorfi	Detritivore	Oligochaeta	6
Anoplolepis gracilipes	Omnivore	Hymenoptera	56
Aporrectodea caliginosa	Detritivore	Oligochaeta	5
Aporrectodea longa	Detritivore	Oligochaeta	3
Aporrectodea tuberculate	Detritivore	Oligochaeta	5
Arion circumscriptus	Herbivore	Gastropoda	5
Arion rufus	Herbivore	Gastropoda	8
Bursaphelenchus xylophilus	Herbivore	Nematoda	2
Coccinella septempunctata	Predator	Coleoptera	9
Dendrobaena octaedra	Detritivore	Oligochaeta	37
Deroceras leave	Herbivore	Gastropoda	6
Deroceras reticulatum	Herbivore	Gastropoda	5
Earthworms (species not specified)	Detritivore	Oligochaeta	56
Fiorinia externa	Herbivore	Hemiptera	4
Harmonia axyridis	Predator	Coleoptera	2
Limacus flavus	Herbivore	Gastropoda	6
Limax maximus	Herbivore	Gastropoda	6
Linepithema humile	Omnivore	Hymenoptera	214
Lumbricus rubellus	Detritivore	Oligochaeta	34
Lumbricus terrestris	Detritivore	Oligochaeta	83
Lymantria dispar	Herbivore	Lepidoptera	7
Meghimatium striatum	Herbivore	Gastropoda	6
Myrmica rubra	Omnivore	Hymenoptera	8
Octolasion tyrtaeum	Detritivore	Oligochaeta	7
Polistes chinensis	Predator	Hymenoptera	2
Pheidole megacephala	Predator	Hymenoptera	12
Pontoscolex corethrurus	Detritivore	Oligochaeta	12
Solenopsis invicta	Predator	Hymenoptera	58
Uroleucon nigrotuberculatum	Herbivore	Hemiptera	7
Vespula germanica	Omnivore	Hymenoptera	10
Vespula pensylvanica	Omnivore	Hymenoptera	3
Wasmannia auropunctata	Predator	Hymenoptera	15

Effect sizes

There was a large amount of heterogeneity in effect sizes across all studies ($Q_t = 3383.70$, d.f. = 709, $P < 0.0001$) and considerable variability among impact types ($Q_b = 86.06$, d.f. = 18, $P < 0.0001$). In addition, effect sizes varied substantially within impact types ($Q_w = 2876.91$, d.f. = 691, $P < 0.0001$; see Table S1 for Q_t values for each impact type). In invaded treatments, plant fitness declined by 52%, animal abundance by 29% and animal diversity by 33% (Fig. 1). In contrast, litter decomposition was 41% higher in the presence of invasive terrestrial invertebrates (Fig. 2). For the remaining 15 of the 19 impact types examined, the 95% confidence intervals overlapped zero, indicating that effect sizes were not significant in many impact types due to large variability among studies.

The trophic position of the invader strongly affected impacts of invasions on animal abundance (Fig. 3, Table S2). Predators and detritivores had significant negative effects, while omnivores and herbivores did not significantly affect animal abundance. Trophic position also affected impacts on nitrogen (N) pools (Fig. 3, Table S2). N pools were larger when herbivores invaded, whereas no significant effects were observed when the invaders were detritivores or omnivores. When a single species invaded (compared with multiple species) N pools were significantly larger but no other impact types were affected (Fig. 4, Table S3).

Insularity and disturbance had no effects on any of the impact types examined (Table S4). The influence of methodological differences on effect size was limited (Table S5). Impacts on animal abundance and animal diversity differed between observational and experimental studies, with stronger negative effects occurring in observational than experimental studies. For animal abundance, no significant effect was observed for experimental studies. No effects of study methodology were observed for any of the other impact types.

The Spearman's correlation coefficient between effect size and sample size across studies was non-significant (Spearman
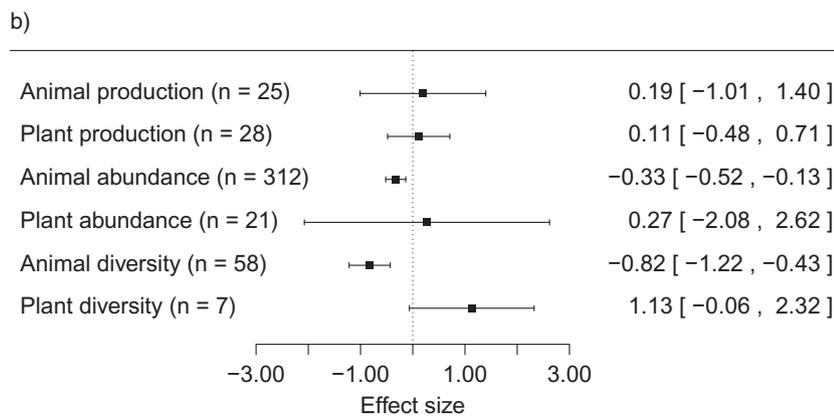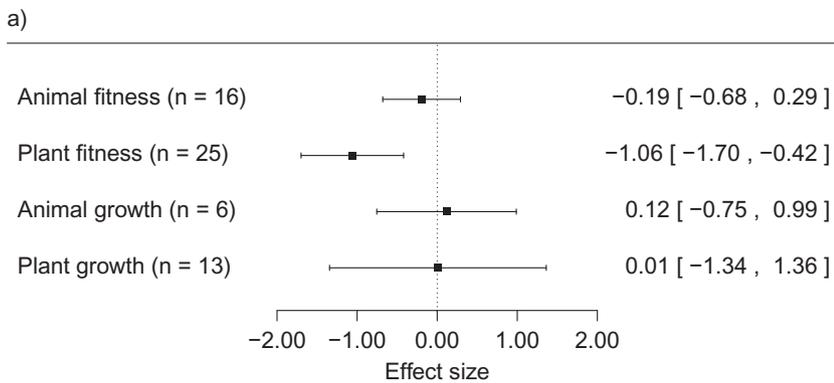
a)

Animal fitness (n = 16)	−0.19 [−0.68 , 0.29]
Plant fitness (n = 25)	−1.06 [−1.70 , −0.42]
Animal growth (n = 6)	0.12 [−0.75 , 0.99]
Plant growth (n = 13)	0.01 [−1.34 , 1.36]

−2.00 −1.00 0.00 1.00 2.00
Effect size

b)

Animal production (n = 25)	0.19 [−1.01 , 1.40]
Plant production (n = 28)	0.11 [−0.48 , 0.71]
Animal abundance (n = 312)	−0.33 [−0.52 , −0.13]
Plant abundance (n = 21)	0.27 [−2.08 , 2.62]
Animal diversity (n = 58)	−0.82 [−1.22 , −0.43]
Plant diversity (n = 7)	1.13 [−0.06 , 2.32]

−3.00 −1.00 1.00 3.00
Effect size

Figure 1 Mean effect size (Hedges' *d*) of impacts of terrestrial invertebrate invasions on plants and animals for (a) species-level variables and (b) community-level variables. Lines indicate 95% confidence intervals. Sample sizes are indicated in parentheses next to the name of each impact type. Values of mean effect size and 95% confidence intervals in brackets are shown on the right-hand side of the figure.
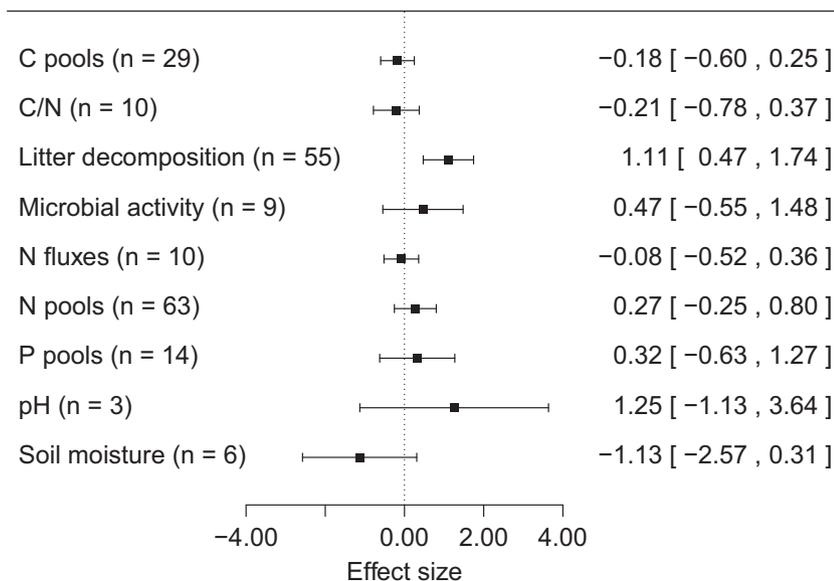

C pools (n = 29)	−0.18 [−0.60 , 0.25]
C/N (n = 10)	−0.21 [−0.78 , 0.37]
Litter decomposition (n = 55)	1.11 [0.47 , 1.74]
Microbial activity (n = 9)	0.47 [−0.55 , 1.48]
N fluxes (n = 10)	−0.08 [−0.52 , 0.36]
N pools (n = 63)	0.27 [−0.25 , 0.80]
P pools (n = 14)	0.32 [−0.63 , 1.27]
pH (n = 3)	1.25 [−1.13 , 3.64]
Soil moisture (n = 6)	−1.13 [−2.57 , 0.31]

−4.00 0.00 2.00 4.00
Effect size

Figure 2 Mean effect size (Hedges' *d*) of impacts of terrestrial invertebrate invasions on ecosystems. Lines indicate 95% confidence intervals. Sample sizes are indicated in parentheses next to the name of each impact type. Values of mean effect size and 95% confidence intervals in brackets are shown on the right-hand side of the figure.

r = −0.012, *P* = 0.75), suggesting that studies with larger effect sizes are no more likely to be published than those with smaller effect sizes (Koricheva *et al.*, 2013). In addition, a plot of effect sizes against the inverse of the standard error (Fig. S2) showed a funnel-shaped distribution, as expected when no sampling bias is present (Palmer, 1999).

DISCUSSION

Impacts across levels of ecological complexity

Terrestrial invertebrates had negative effects on species and communities, including decreases of 52% in plant fitness, 29%
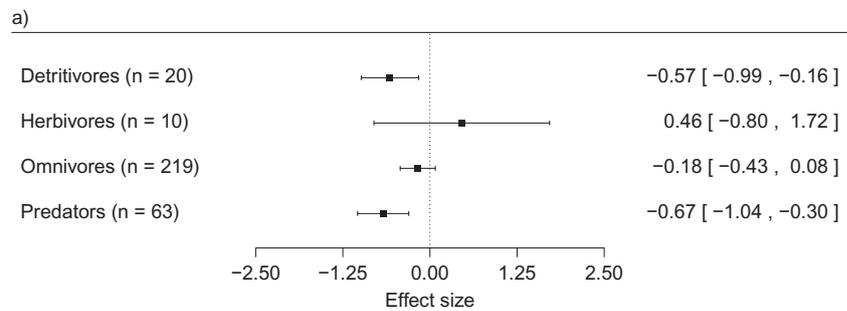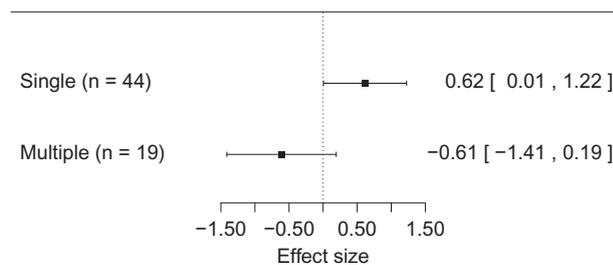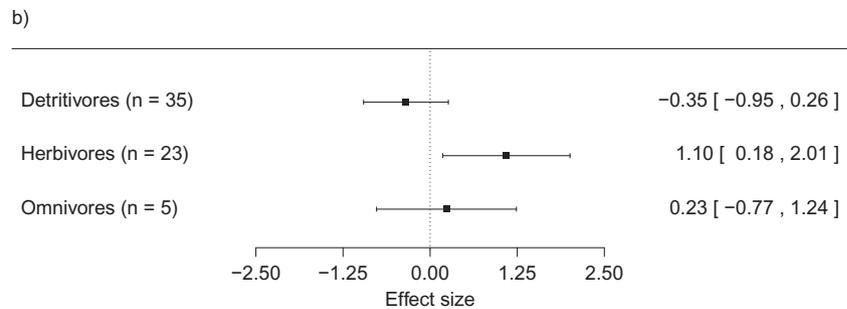
Figure 3 Mean effect size (Hedges' *d*) due to invaders from different trophic levels (detritivores, herbivores, omnivores, predators) for (a) animal abundance and (b) N pools. Lines indicate 95% confidence intervals. Sample sizes are indicated in parentheses next to the name of each impact type. Values of mean effect size with 95% confidence intervals in brackets are shown on the right-hand side of the figure.

Figure 4 Mean effect size (Hedges' *d*) for N pools due to single versus multiple invasive species. Lines indicate 95% confidence intervals. Sample sizes are indicated in parentheses next to the name of each impact type. Values of mean effect size with 95% confidence intervals in brackets are shown on the right-hand side of the figure.

in animal abundance and 33% in animal diversity in response to invasions. At the ecosystem level, litter decomposition was 41% higher in the presence of invaders compared with uninvaded locations. Most of the studies examining litter decomposition focused on alien earthworms, which fragment and consume leaf litter rapidly when introduced to ecosystems with no native earthworms (e.g. Alban & Berry, 1994). No other significant trends were observed at the ecosystem level when all trophic levels were considered together, although N pools were significantly larger in the presence of invasive herbivores. Effects on ecosystems may take longer to become evident than those on species and communities, as has been suggested for plant invasions (Vilà *et al.*, 2011). However, we were unable to test the influence of time since invasion on impacts as most studies did not report the initial date of invasion, and many only reported results for a few impacts at one level of ecological complexity. Overall, the magnitude and direction of effects varied across impact types and many were not significantly affected.

Consistent with our finding that terrestrial invertebrate invaders increased or had neutral effects on ecosystem variables, previous syntheses indicate that plant invasions also typically cause increases in nutrient fluxes and rates of transformation of materials within ecosystems (Liao *et al.*, 2008; Vilà *et al.*, 2011; Castro-Díez *et al.*, 2014). Plants influence ecosystem processes through resource acquisition and growth, while animals may have effects via both direct trophic and non-trophic interactions (Ehrenfeld, 2010). Consequently, invasive animals can impact ecosystem processes through a greater number of mechanistic pathways (e.g. involving consumption, excretion, ecosystem engineering), which remain poorly understood or unmeasured (Ehrenfeld, 2010).

Effects of trophic position

In addition to the impact of an invader being affected by its trophic position, it has been proposed that the effect of an invader may vary depending on the trophic position of the native species in the recipient community being invaded. For example, invasive predators are expected to have negative effects on other consumers but may have indirect positive effects on primary producers due to trophic cascades (Schmitz *et al.*, 2000). In particular we examined whether impacts on plants versus animals differed and whether the trophic position of the invader influenced impact strength.

We hypothesized that terrestrial invertebrates would have greater impacts on animals (i.e. other consumers) than on primary producers. On average, abundance and diversity of animals, but not of plants, decreased due to terrestrial invertebrate invasions. This effect may be driven by competition between alien and native species within a trophic level (Thomsen *et al.*, 2014; Maggi *et al.*, 2015). This appears to be the case for fire ant (*Solenopsis invicta*) invasions in Texas, where

competitive displacement by fire ants is probably the primary mechanism behind declines in the native ant community (Porter & Savignano, 1990).

The trophic position of the invasive species significantly affected the strength of impacts on animal abundance. As predicted, predators had stronger negative impacts than invasive omnivores and herbivores. For instance, the seven-spotted ladybird beetle (*Coccinella septempunctata* L.) greatly reduced the abundance of one of its key prey species, pea aphids (*Acrythosiphum pisum* [Harris]), as well as the abundance of other native ladybirds that also prey upon pea aphids (Evans, 2004). Detritivores also had large negative effects on animal abundance. Many of the studies on detritivores examined earthworm invasions into areas where native earthworms were absent (e.g. hardwood forests in the north-eastern United States) and thus their functional uniqueness as ecosystem engineers in these systems may have contributed to their large effects (Frelich *et al.*, 2006). Ecosystem engineers can strongly influence other species by causing large-scale changes in ecosystem processes or structures, in addition to having direct trophic effects (Jones *et al.*, 1994). In a recent meta-analysis on aquatic invasions, indirect changes due to ecosystem engineering similarly caused substantial changes in invaded communities; for example, filter collectors had an especially negative impact on planktonic communities and positive effects on benthic invertebrates and macrophytes due to a combination of direct filtering activity and indirect alteration of habitat conditions (Gallardo *et al.*, 2016).

We were not able to examine effects on specific trophic levels, as the studies in our analysis that examined responses at the community level often grouped multiple trophic levels of animals together. However, organisms at higher trophic levels may benefit from habitat formation or the provision of food by invaders (Rodriguez, 2006; Thomsen *et al.*, 2014). For example, the abundance of eastern towhees (*Pipilo erythrophthalmus*) increased following a gypsy moth (*Lymantria dispar*) outbreak in West Virginia, presumably because defoliation by gypsy moths created more early successional forests, which are the preferred habitat of eastern towhees (Bell & Whitmore, 1997).

Effects on N pool size also varied depending on the trophic position of the invader, with herbivores leading to larger increases in N pools than invasions by detritivores or omnivores. It is not clear why effects would be larger for herbivores, but most (87%) of the case studies on the effects of herbivores on N pools involved hemlock woolly adelgids (*Adelges tsugae*), which appear to strongly affect N pools via a combination of mechanisms including increased decomposition, reduced uptake of N by declining trees, decreased understorey vegetation and N-enriched throughfall from invaded canopies (Orwig *et al.*, 2008).

Effects of other explanatory variables

There was a large amount of heterogeneity in effect sizes within impact types and the other explanatory variables we tested explained little of this variability. We predicted that multiple species invasions would lead to larger impacts due to facilitation among invaders (Simberloff & Von Holle, 1999; Simberloff, 2006) but N pool size was the only impact type affected by the presence of multiple versus single invaders. N pools increased when a single invader was present, but not when multiple species invaded. In our analysis, studies examining the effects of multiple species of invaders on N pools more frequently involved invasive detritivores (89%) compared with those examining single species (41%), and therefore the effect of multiple versus single invaders was confounded with trophic level. A recent meta-analysis on single versus multiple invaders concluded that invasive animals most often have neutral or negative impacts on each other, with terrestrial arthropod invaders having neutral effects on each other overall (Jackson, 2015). Further, consistent with our results, the Jackson (2015) meta-analysis found that the combined impacts of multiple animal invaders are generally antagonistic, although only two studies on terrestrial invertebrates were included in that analysis (Jackson, 2015). Rather than facilitating each other in an invasional meltdown scenario, it was suggested that invasive species may serially replace each other by out-competing other invaders, with different species dominating a community over time (Lohrer & Whitlatch, 2002; Thomas & Reid, 2007; Jackson, 2015). As most studies in our analysis were conducted over short time frames, it is not clear whether this replacement is occurring for terrestrial invertebrate invaders. Longer-term studies are needed to understand the dynamics of the interaction among multiple invaders.

Although especially large impacts have been observed in some cases on islands, such as the invasional meltdown caused by the yellow crazy ant (*Anoplolepis gracilipes*) on Christmas Island (Green *et al.*, 2011), we found no evidence overall to support our prediction that impacts would be stronger on islands. However, with the exception of animal abundance on islands, there were relatively few case studies that examined impacts on islands, and therefore this result should be viewed with caution.

Similarly, the results did not support our prediction that invasive terrestrial invertebrates would have large impacts in disturbed areas. While disturbances and invasion impacts can be strongly related, their relationship appears to be context dependent, and disturbances are likely to have a positive affect on invasive species mainly in situations where the disturbance produces conditions that differ substantially from those to which the native community is adapted (Lockwood *et al.*, 2013). However, some studies in our analysis provided limited information about the presence of anthropogenic or natural disturbances and thus they may have been misclassified as intact when disturbances were in fact present.

Finally, unexpectedly, our results were generally robust to effects of methodological differences, except that stronger negative effects were seen in observational studies on animal abundance and animal diversity than in experimental studies. Although the most appropriate method for assessing impacts of invaders will vary depending on the taxon of the invader and the type of impact (Kumschick *et al.*, 2015), impacts of invaders may be confounded with between-site differences in observational studies, whereas experimental studies can demonstrate

causality (Kumschick *et al.*, 2015). However, experimental studies are often less realistic than observational studies and may be more likely to be conducted over spatial or temporal scales that are too small to allow accurate assessment of the impacts (Krushelnycky & Gillespie, 2010). Despite the well known context dependence in the direction and magnitude of impacts, the factors that influence variability in effect sizes within impact types remain poorly understood (Hulme *et al.*, 2013).

Data limitations and concluding remarks

Although our systematic review of articles on terrestrial invertebrate invasions was extensive, much of the published literature has focused on a small subset of invasive species, impact types and geographical locations. In our analysis, studies focused predominantly on impacts on animal abundance, and most ecosystem processes were poorly studied. Moreover, studies on Hymenoptera and Oligochaeta conducted in North America were over-represented, and this bias limits our ability to reach general conclusions about the impacts of terrestrial invertebrates globally.

Another key issue is that quantitative meta-analysis cannot accommodate cases without controls, which are required to calculate effect sizes. However, extreme impact cases often lack controls. For example, for some invaders such as the gypsy moth (*L. dispar*) which cause almost complete defoliation in forests, there are rarely sites available with zero or little defoliation and thus these species could not be included in the meta-analysis.

We found few differences in island and disturbed areas compared with continental and undisturbed areas, respectively. Many studies lacked detailed information on the invasion or habitat examined, which restricted the types of explanatory factors that could be examined. Impacts can differ greatly across spatial and temporal scales (Gaertner *et al.*, 2009; Jeschke *et al.*, 2014), but in many cases the spatial extent of the study and time since initial invasion were not reported. There were also limited data available on densities of invaders, which prevented us from examining how impacts might vary in response to invader density. Few experimental studies appear to have investigated the density–impact relationship for terrestrial invertebrate invaders, but observational studies indicate that ecological impacts can be either linearly (e.g. Porter & Savignano, 1990) or nonlinearly (e.g. Hoffmann *et al.*, 1999) related to invader density.

In sum, our results show that terrestrial invertebrate invaders have substantial effects on populations, communities and ecosystems, but effects vary depending on the type of impact being examined and the trophic position of the invader. Because impacts are often highly context dependent, repeated observations and experiments at multiple sites differing in abundance of invader species across broad spatial scales could help to improve our knowledge about how impacts of terrestrial invertebrate invaders are modulated. More experimental studies, for example using a four-way experimental design with invaded, uninvaded, native species removal and alien species removal treatments (Kumschick *et al.*, 2015), would provide greater information on the impacts of invaders on ecosystem processes and the links between impacts on communities and ecosystem processes. Also, few studies have examined the mechanisms, such as competition, predation and ecosystem engineering, through which impacts occur but this information is critical for effective management of invasions.

REFERENCES

Alban, D.H. & Berry, E.C. (1994) Effects of earthworm invasion on morphology, carbon, and nitrogen of a forest soil. *Applied Soil Ecology*, **1**, 243–249.

Bell, J.L. & Whitmore, R.C. (1997) Eastern towhee numbers increase following defoliation by gypsy moths. *The Auk*, **114**, 708–716.

Bellard, C., Thuiller, W., Leroy, B., Genovesi, P., Bakkenes, M. & Courchamp, F. (2013) Will climate change promote future invasions? *Global Change Biology*, **19**, 3740–3748.

Blackburn, T.M., Essl, F., Evans, T. *et al.* (2014) A unified classification of alien species based on the magnitude of their environmental impacts. *PLoS Biology*, **12**, e1001850.

Byers, J.E. (2002) Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos*, **97**, 449–458.

Castro-Díez, P., Godoy, O., Alonso, A., Gallardo, A. & Saldaña, A. (2014) What explains variation in the impacts of exotic plant invasions on the nitrogen cycle? A meta-analysis. *Ecology Letters*, **17**, 1–12.

Clavero, M. & García-Berthou, E. (2005) Invasive species are a leading cause of animal extinctions. *Trends in Ecology and Evolution*, **20**, 110.

Cohen, J. (2013) *Statistical power analysis for the behavioral sciences*. Routledge Academic, London.

Ehrenfeld, J.G. (2010) Ecosystem consequences of biological invasions. *Annual Review of Ecology, Evolution, and Systematics*, **41**, 59–80.

Elton, C.S. (1958) *The ecology of invasions by animals and plants*. Methuen, London.

Evans, E.W. (2004) Habitat displacement of North American ladybirds by an introduced species. *Ecology*, **85**, 637–647.

Frelich, L.E., Hale, C.M., Scheu, S., Holdsworth, A.R., Heneghan, L., Bohlen, P.J. & Reich, P.B. (2006) Earthworm invasion into

previously earthworm-free temperate and boreal forests. *Biological Invasions*, **8**, 1235–1245.

Gaertner, M., Breeyen, A.D., Hui, C. & Richardson, D.M. (2009) Impacts of alien plant invasions on species richness in Mediterranean-type ecosystems: a meta-analysis. *Progress in Physical Geography*, **33**, 319–338.

Gallardo, B., Clavero, M., Sanchez, M.I. & Vilà, M. (2016) Global ecological impacts of invasive species in aquatic ecosystems. *Global Change Biology*, **22**, 151–163.

Gandhi, K.J.K. & Herms, D.A. (2010) Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. *Biological Invasions*, **12**, 389–405.

Green, P.T., O'Dowd, D.J., Abbott, K.L., Jeffery, M., Retallick, K. & MacNally, R. (2011) Invasional meltdown: invader–invader mutualism facilitates a secondary invasion. *Ecology*, **92**, 1758–1768.

Hedges, L.V. & Olkin, I. (1985) *Statistical methods for meta-analysis*, 1st edn. Academic Press, Orlando, FL.

van Hengstum, T., Hooftman, D.A.P., Oostermeijer, J.G.B. & van Tienderen, P.H. (2014) Impact of plant invasions on local arthropod communities: a meta-analysis. *Journal of Ecology*, **102**, 4–11.

Hoffmann, B.D., Andersen, A.N. & Hill, G.J.E. (1999) Impact of an introduced ant on native rain forest invertebrates: *Pheidole megacephala* in monsoonal Australia. *Oecologia*, **120**, 595–604.

Hulme, P.E., Pyšek, P., Jarošík, V., Pergl, J., Schaffner, U. & Vilà, M. (2013) Bias and error in understanding plant invasion impacts. *Trends in Ecology and Evolution*, **28**, 212–218.

Jackson, M.C. (2015) Interactions among multiple invasive animals. *Ecology*, **96**, 2035–2041.

Jeschke, J.M., Bacher, S., Blackburn, T.M., Dick, J.T.A., Essl, F., Evans, T., Gaertner, M., Hulme, P.E., Kühn, I., Mrugała, A., Pergl, J., Pyšek, P., Rabitsch, W., Ricciardi, A., Richardson, D.M., Sendek, A., Vilà, M., Winter, M. & Kumschick, S. (2014) Defining the impact of non-native species. *Conservation Biology*, **28**, 1188–1194.

Jones, C.G., Lawton, J.H. & Shachak, M. (1994) Organisms as ecosystem engineers. *Oikos*, **69**, 373–386.

Kenis, M., Auger-Rozenberg, M.-A., Roques, A., Timms, L., Pere, C., Cock, M.J.W., Settele, J., Augustin, S. & Lopez-Vaamonde, C. (2009) Ecological effects of invasive alien insects. *Biological Invasions*, **11**, 21–45.

Koricheva, J., Gurevitch, J. & Mengersen, K. (2013) *Handbook of meta-analysis in ecology and evolution*. Princeton University Press, Princeton, NJ.

Krushelnycky, P.D. & Gillespie, R.G. (2010) Sampling across space and time to validate natural experiments: an example with ant invasions in Hawaii. *Biological Invasions*, **12**, 643–655.

Kumschick, S., Gaertner, M., Vilà, M., Essl, F., Jeschke, J.M., Pyšek, P., Ricciardi, A., Bacher, S., Blackburn, T.M., Dick, J.T.A., Evans, T., Hulme, P.E., Kuhn, I., Mrugala, A., Pergl, J., Rabitsch, W., Richardson, D.M., Sendek, A. & Winter, M. (2015) Ecological impacts of alien species: quantification, scope, caveats, and recommendations. *Bioscience*, **65**, 55–63.

Langor, D.W., Cameron, E.K., MacQuarrie, C.J.K., McBeath, A., McClay, A., Peter, B., Pybus, M., Ramsfield, T., Ryall, K., Scarr, T., Yemshanov, D., DeMerchant, I., Foottit, R. & Pohl, G.R. (2014) Non-native species in Canada's boreal zone: diversity, impacts, and risk. *Environmental Reviews*, **22**, 372–420.

Liao, C., Peng, R., Luo, Y., Zhou, X., Wu, X., Fang, C., Chen, J. & Li, B. (2008) Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytologist*, **177**, 706–714.

Lockwood, J.L., Hoopes, M.F. & Marchetti, M.P. (2013) *Invasion ecology*, 2nd edn. Wiley-Blackwell, Chichester.

Lohrer, A.M. & Whitlatch, R.B. (2002) Interactions among aliens: apparent replacement of one exotic species by another. *Ecology*, **83**, 719–732.

Maggi, E., Benedetti-Cecchi, L., Castelli, A., Chatzinikolaou, E., Crowe, T.P., Ghedini, G., Kotta, J., Lyons, D.A., Ravaglioli, C., Rilov, G., Rindi, L. & Bulleri, F. (2015) Ecological impacts of invading seaweeds: a meta-analysis of their effects at different trophic levels. *Diversity and Distributions*, **21**, 1–12.

Orwig, D.A., Cobb, R.C., D'Amato, A.W., Kizlinski, M.L. & Foster, D.R. (2008) Multi-year ecosystem response to hemlock woolly adelgid infestation in southern New England forests. *Canadian Journal of Forest Research*, **38**, 834–843.

Palmer, A.R. (1999) Detecting publication bias in meta-analyses: a case study of fluctuating asymmetry and sexual selection. *The American Naturalist*, **154**, 220–233.

Parker, I.M., Simberloff, D., Lonsdale, W.M., Goodell, K., Wonham, M., Kareiva, P.M., Williamson, M.H., Holle, B.V., Moyle, P.B., Byers, J.E. & Goldwasser, L. (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, **1**, 3–19.

Pimentel, D., Zuniga, R. & Morrison, D. (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, **52**, 273–288.

Porter, S.D. & Savignano, D.A. (1990) Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology*, **71**, 2095–2106.

R Core Team (2014) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

Ricciardi, A., Hoopes, M.F., Marchetti, M.P. & Lockwood, J.L. (2013) Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs*, **83**, 263–282.

Rodriguez, L.F. (2006) Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur. *Biological Invasions*, **8**, 927–939.

Roques, A., Rabitsch, W., Rasplus, J.-Y., Lopez-Vaamonde, C., Nentwig, W. & Kenis, M. (2009) Alien terrestrial invertebrates of Europe. *Handbook of alien species in Europe*, pp. 63–79. Springer, Berlin.

Schmitz, O.J., Hambäck, P.A. & Beckerman, A.P. (2000) Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. *The American Naturalist*, **155**, 141–153.

Schneider, C.A., Rasband, W.S. & Eliceiri, K.W. (2012) NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, **9**, 671–675.

Simberloff, D. (2006) Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? *Ecology Letters*, **9**, 912–919.

Simberloff, D. (2011) How common are invasion-induced ecosystem impacts? *Biological Invasions*, **13**, 1255–1268.

Simberloff, D. & Von Holle, B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, **1**, 21–32.

Strayer, D.L. (2010) Alien species in fresh waters: ecological effects, interactions with other stressors, and prospects for the future. *Freshwater Biology*, **55**, 152–174.

Thomas, M.B. & Reid, A.M. (2007) Are exotic natural enemies an effective way of controlling invasive plants? *Trends in Ecology and Evolution*, **22**, 447–453.

Thomsen, M.S., Byers, J.E., Schiel, D.R., Bruno, J.F., Olden, J.D., Wernberg, T. & Silliman, B.R. (2014) Impacts of marine invaders on biodiversity depend on trophic position and functional similarity. *Marine Ecology Progress Series*, **495**, 39–47.

Vaes-Petignat, S. & Nentwig, W. (2014) Environmental and economic impact of alien terrestrial arthropods in Europe. *NeoBiota*, **22**, 23–42.

Viechtbauer, W. (2010) Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, **36**, 1–48.

Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., Nentwig, W., Olenin, S., Roques, A., Roy, D., Hulme, P.E. & DAISIE Partners (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in Ecology and the Environment*, **8**, 135–144.

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

Whittaker, R.J. & Fernandez-Palacios, J.M. (2006) *Island biogeography: ecology, evolution, and conservation*, 2nd edn. Oxford University Press, Oxford.

SUPPORTING INFORMATION

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

Appendix 1 Data sources.
Figure S1 Number of case studies by taxonomic group.
Figure S2 Funnel plot.
Table S1 Overall meta-analysis of 19 impact types.
Table S2 Invader trophic position results.
Table S3 Single versus multiple species results.
Table S4 Disturbance and insularity results.
Table S5 Methodological approach results.
Appendix S1 Data sources. List of articles in the meta-analysis.

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