Reports

Interactions among multiple invasive animals

M. C. Jackson[1]

Centre for Invasion Biology, Department of Zoology and Entomology, University of Pretoria, Hatfield 0028 South Africa

Abstract. With accelerating rates of invasion being documented in many ecosystems, communities of interacting invasive species are becoming increasingly common. Opposing theories predict that invaders can either hinder or promote one another's success. Additionally, evidence suggests that co-occurring invaders can interact to amplify or mitigate one another's impacts on ecosystems. However, there has not been a quantitative review on interactions among multiple invasive animals. Here I use a meta-analysis approach to show that, across a global scale, the mean interaction among invaders was to reduce one another's performance. This pattern was consistent when considering interactions between marine animals but interactions were neutral overall in terrestrial and freshwater ecosystems. Crucially, individual studies showed that neutral interactions were the most common interaction type. Further, I demonstrate that the combined ecological impacts of multiple invaders were frequently the sum of their independent effects (additive) but the mean effect was non-additive and less than predicted (antagonistic). In both meta-analyses, the disparity between the most frequent and mean interaction type indicates that case studies of multiple invasions commonly have different outcomes to global trends. These results will help predict how co-occurring invasive animals interact and assist in developing management strategies for problematic invaders in our changing world.

Key words: biotic resistance; invasional meltdown; invasive species; meta-analyses; multiple invasions; non-additive effects; species interactions.

INTRODUCTION

Invasive species have adverse consequences for biodiversity and ecosystem processes and, with accelerating rates of invasion (Cohen and Carlton 1998, Jackson and Grey 2013), it is becoming increasing important to understand how multiple invaders interact (Kuebbing et al. 2013). The patterns, processes and impacts of plant invasions have been extensively reviewed (e.g., Powell et al. 2011, Vila et al. 2011, Bradley et al. 2012, Pysek et al. 2012) and, overall, the evidence indicates that interactions among multiple nonnative plants are most commonly negative or neutral (Kuebbing and Nuñez 2015). In contrast, animal invasions are less well studied (Lowry et al. 2013) and there has not been a quantitative review on the interactions and impacts of multiple animal invasions despite their prevalence, particularly on oceanic islands and in freshwater ecosystems (Ricciardi 2001, Ricciardi and MacIsaac 2011, Jackson and Grey 2013).

Interactions among invaders can be neutral, negative, or positive (Kuebbing and Nuñez 2015). In the absence of negative interactions, a novel nonnative animal can rapidly spread and reproduce as they are released from their natural enemies, including predators and pathogens (Enemy Release Hypothesis; Colautti et al. 2004). However, classic ecological theory predicts that resident nonnative species will negatively impact potential invaders and prevent establishment by occupying any vacant niches (Biotic Resistance Model; Elton 1958, Levine and D'Antonio 1999). A more recent and opposing hypothesis suggests that established invaders will pave the way for further invasions because of the ecosystem changes they instigate (Invasion Meltdown Model; Simberloff and Von Holle 1999, Simberloff 2006). There is evidence to support both these theories (e.g., Ricciardi 2001, DeVanna et al. 2011, Green et al. 2011), however there is little information on how invader identity and environmental context influence invasive animal interactions and no effort has been made to detect global trends.

Recent meta-analyses have revealed that multiple stressors frequently cause non-additive ecological effects (Crain et al. 2008, Darling and Cote 2008, Tylianakis et al. 2008, Ban et al. 2014) rendering their combined impacts difficult to predict. Similarly, much of the concern over multiple invaders arises from their potential to interact, with net effects that may be greater than (synergistic) or less than (antagonistic) the sum of their independent effects (Preston et al. 2012, Kuebbing et al. 2013, Jackson et al. 2014). However, despite the increasing interest in multiple stressors (Ormerod et al. 2010, Staudt et al. 2013), there is little information on how co-occurring invasive animals interact (Kuebbing et al. 2013, Kueffer et al. 2013). Here, I use a meta-analysis approach to answer two key questions: (1) Are interactions among paired nonnative animals neutral, negative, or positive? (2) What are the combined impacts of paired nonnative animals on ecosystem properties?

METHODS

I searched Web of Science and Google Scholar in September 2014 (see Appendix A for full search terms and selection of papers) and selected articles that examined nonnative animal interactions, resulting in a total of 74 papers. From these papers, I collected information to complete two meta-analyses in order to examine my two key questions. Data were acquired directly from text and tables or from figures using Data Thief software (Tummers et al. 2010).

Interactions among invasive animals

To examine if co-occurring nonnative animals have neutral, negative, or positive impacts on one another, I considered studies that examined the performance of a nonnative animal in the absence and presence of a second nonnative animal. Where articles contained multiple observations, experiments or pairs of nonnative species, I considered each separately. Additionally, if a study examined the effect of a impacting species A on a focal species B and of impacting species B on focal species A, these were considered as two distinct observations. Performance endpoints were split into five categories to examine any variation between them: growth, diet, abundance/biomass, behavior, and survival. For each impact of species A on B, I extracted the mean performance endpoint when species B was alone and when species B was together with species A. In order to calculate effect sizes, I also extracted standard deviation and sample size. I used the effect size Hedge's d, an estimate of the standardized mean difference not biased by small sample (Gurevitch and Hedges 2001, Rosenberg et al. 2000). For each mean response variable (X) from the two treatment groups (invader alone [a] and in combination with a second invader [c]), the individual effect size Hedge's d (Rosenberg et al. 2000) was calculated as

$$\frac{X_a - X_c}{S} j$$

where j is a weighting factor based on the number of replicates (n) per treatment, calculated as:

$$1 - \frac{3}{4(n_a + n_c - 2) - 1}$$

and S is the pooled standard deviation, calculated as

$$\sqrt{\frac{(n_a - 1)\sigma_a^2 + (n_c - 1)\sigma_c^2}{n_a + n_c - 2}}.$$

Finally, variance of d (V_d) was calculated as:

$$\frac{n_a + n_c}{n_a n_c} + \frac{d^2}{2(n_a + n_c)}.$$

A positive individual effect size indicates that the impacting invader has a positive effect on the focal invader's performance. Likewise, a negative individual effect size indicates that the impacting invader has a negative effect on the focal invader's performance. Bootstrapped 95% confidence intervals were calculated for each effect size and used to assess their significance; if the confidence intervals cross zero, the performance of the focal invader was not significantly different when alone and in combination with a second invader (i.e., a neutral interaction).

For each study, I also recorded ecosystem (freshwater, marine, terrestrial) and the functional feeding group (omnivore, herbivore, predator) of the impacting species to investigate the influence of these variables on the interactions. Mean effect sizes were calculated for these broad classifications using a mixed-effects meta-analytic model (Gurevitch and Hedges 2001). The data were then analyzed within each ecosystem across different study types (field, in situ experiments and field observations; and experiment, controlled laboratory or mesocosm experiments) and phyla using the same approach (where $n > 3$).

Although many studies in my original database considered interactions among co-occurring nonnative species, relatively few compared how their interaction differed when the species occurred alone and were therefore not suitable for our meta-analysis (e.g., Platvoet et al. 2009, O'Connor 2014). Therefore, to extend my database, I obtained information from these papers to include in the review. Papers were included if the authors concluded that the impact of one nonnative species on the other (and/or vice versa) was considered to be neutral, negative, or positive. Using the full data set, I also examined how interactions differed between invader pairs categorized by class (where $n \geq 8$). In total, I collected 179 observations of which 57 were used in the meta-analysis (see Appendix B: Tables B1 and B2).
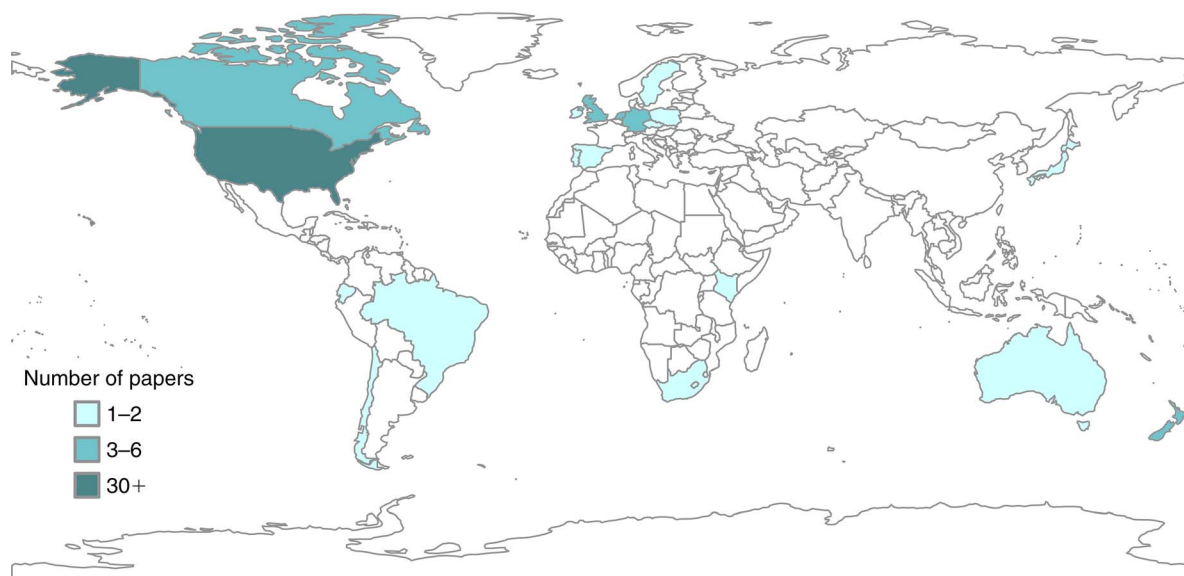
Fig. 1. The global distribution of papers from which data was extracted for both meta-analyses.

The combined impact of multiple invasive animals

To examine how interactions among nonnative species influence one another's ecological impacts on ecosystems I selected studies that used a fully factorial design to measure the impact of species A and species B, in combination and alone, compared to an un-invaded control. If a paper studied different nonnative animal combinations, these were considered as separate observations. To calculate effect sizes, I extracted the mean, standard deviation, and sample size of the response endpoint in the presence of species A, species B, species A and B, and the control for each study. Similar to my interaction meta-analysis, I also recorded study type, ecosystem, the taxonomic class and phylum of each nonnative animal, response level (community or population), and response group (autotroph or heterotroph) to investigate the influence of these variables on the outcome of interactions. Where studies examined multiple different response endpoints, only the most inclusive was used to avoid replication (e.g., community abundance over population abundance) unless the study measured the impact of the invasive animals on different populations (e.g., both an autotroph and heterotroph population) but did not give a total community response, in which both were included in the analysis. Reponses were always native abundance, survival, or diversity. In total, 45 responses (from 15 papers) to multiple animal invasions were included in the meta-analysis (see Appendix B: Table B3).

For each mean response variable (X) from the four treatment groups (i.e., control [u], invader A, invader B, and both invaders A and B [AB]), I calculated the predicted additive effect of the two invaders (p) as

$$(X_A - X_u) + (X_B - X_u) + X_u.$$

Predicted standard deviations were calculated by pooling σ_A and σ_B and sample sizes were calculated as $n_A + n_B$. I then compared the predicted effect to the observed effect of invaders A and B (o) to calculate Hedge's d (Rosenberg et al. 2000) effect size

$$\frac{X_p - X_o}{S} j$$

where j, S, and V_d were calculated as above. Bootstrapped 95% confidence intervals were calculated for each interaction effect size and used to assess their significance. For these interaction effect sizes, a positive d reflects an amplified effect (synergistic interaction) and a negative d reflects a mitigated effect (antagonistic interaction) of the paired invaders compared to the sum of the independent impacts (represented by a 0 effect size). If the confidence intervals cross zero, the interaction was deemed to be additive.

Both meta-analyses were deemed robust and free of publication bias (see Appendix A). All analyses were carried out in MetaWin 2.0 (Rosenberg et al. 2000) and figures were made using R (R Core Team 2014).

RESULTS

Interactions among invasive animals

The papers used in the meta-analysis covered a global range, but the majority of studies were conducted in North America, followed by New Zealand, Great Britain, and Canada (Fig. 1). Overall, the mean effect of invaders on one another's performance was negative (Hedges' $d = -0.69$, CI -1.19 to -0.21; $n = 57$; Table A1). The mean effect sizes varied between methodologies,

TABLE 1. The impact of an invasive species on a second invasive species across different ecosystems, phyla, and study types.

| | | All studies | | | Meta-analysis only | | | |
| | | Impact in individual studies (%) | | | | | Lower to upper confidence intervals | |
Ecosystem, impacting species, and study type	n	+	0	−	n	d		Mean effect
Freshwater								
Arthropoda								
Field	17	11.8	52.9	35.3	1			
Experiment	34	2.9	52.9	44.1	18	−1.46	−2.26 to −0.79	negative
Chordata								
Field	24	8.3	54.2	37.5	5	0.7	−0.47 to 2.02	neutral
Experiment	10	20.0	70.0	10.0	4	1.35	−1.57 to 4.05	neutral
Mollusca								
Field	9	44.4	44.4	11.1	0			
Experiment	9	66.7	22.2	11.1	5	0.99	−1.17 to 3.44	neutral
Marine								
Arthropoda								
Field	14	7.1	42.9	50.0	8	−1.03	−1.91 to −0.38	negative
Experiment	5	0.0	20.0	80.0	4	−2.94	−5.17 to −2.03	negative
Chordata								
Field	6	0.0	66.7	33.3	0			
Experiment	1	0.0	0.0	100.0	0			
Mollusca								
Field	4	75.0	25.0	0.0	1			
Experiment	1	0.0	100.0	0.0	1			
Echinodermata								
Field	1	0.0	0.0	100.0	0			
Terrestrial								
Arthropoda								
Field	12	41.7	33.3	25.0	6	0.15	−0.12 to 0.73	neutral
Experiment	2	0.0	0.0	100.0	2			
Chordata								
Field	26	7.7	38.5	53.8	0			
Experiment	2	0.0	0.0	100.0	2			
Annelida								
Experiment	2	0.0	100.0	0.0	0			

Note: Results are given as the percentage of positive (+), neutral (0), or negative (−) impacts in all individual studies and as the mean effect size (Hedge's d) when $n > 3$.

with neutral and negative impacts occurring in field studies ($d = -0.27$, CI −0.98 to 0.31; $n = 21$) and controlled experiments ($d = -0.97$, CI −1.61 to −0.29; $n = 36$), respectively. However, in most cases there was no difference in the mean effect size in each ecosystem and feeding group category when considering field and controlled experiments separately because the different types of studies were evenly distributed throughout the data set (Tables 1 and A1; the one exception is outlined in the next paragraph). Further, when phyla were grouped within ecosystems (where $n > 3$), the mean effect size did not change interaction type when considered controlled experiments and field studies separately (Table 1).

When considering interactions across major ecosystem types, the mean effect size remained negative between marine animals ($d = -1.37$, CI −2.25 to −0.62; $n = 14$) but was neutral between freshwater ($d = -0.53$, CI −1.29 to 0.26; $n = 33$) and terrestrial ($d = -0.34$, CI −0.98 to 0.41; $n = 10$) animals (Fig. 2a). However in terrestrial laboratory studies, there was a mean negative effect size, however sample size was low (two papers) and therefore this result is unreliable. If the impacting

invader was an omnivore ($d = -1.49$, CI −2.74 to −1.20; $n = 15$) the mean effect size was negative; however predators ($d = -0.48$, CI −1.17 to 0.25; $n = 30$) and herbivores ($d = 0.03$, CI −0.59 to 0.83; $n = 14$) had neutral mean effects overall (Fig. 2b). Where phyla were grouped within ecosystems, the overall effect of chordates and molluscs in freshwaters was neutral while arthropods had a negative effect (Table 1). Likewise, arthropods had negative mean effects in marine ecosystems but neutral effects in terrestrial ecosystems (Table 1).

A further 122 scenarios (Table A2; total of $n = 179$) were used in the vote-counting analysis and this revealed that interactions among co-occurring nonnative animals are frequently neutral (46%) or negative (39%). Positive or facilitative interactions among invasive animals were the least common (16%) in all ecosystems. The frequencies of interaction type were similar between field studies and controlled experiments within each ecosystem and impacting species phylum (Table 1). Positive effects were most commonly caused by a mollusc invader (Table 1). For instance, bivalves frequently had positive effects on other invaders (10
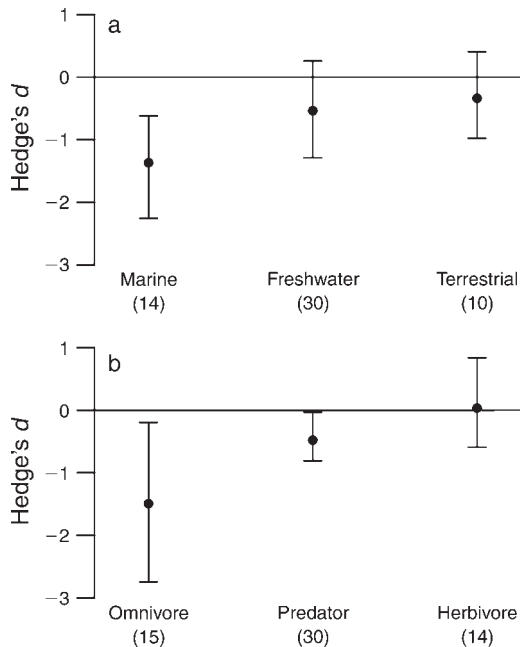
FIG. 2. The effect of an invasive animal (impacting species) on the performance of a second invasive animal (focal species) species (a) in different ecosystems and (b) across different impacting species' trophic feeding groups. A positive d indicates a positive effect on performance and a negative d indicates a negative effect on performance. Values are means with 95% CI. Where confidence intervals cross zero, the effect is considered neutral.

out of 18 observations). Arthropods commonly had negative effects on other invaders (Table 1) with interactions among invasive paired malacostraca (decapods and amphipods) being frequently either neutral (24 out of 50 observations) or negative (25 out of 50 observations). Neutral interactions were also common when the impacting species was a chordate (Table 1), for instance interactions between paired invasive fish (actinopterygii; 8 out of 10 observations).

The combined impact of multiple invasive animals

Overall, my second meta-analysis revealed that invasive animals interact to mediate one another's impacts on ecosystems (Table A3). This means their combined impacts were antagonistic ($d = -0.80$, CI -1.21 to -0.44; $n = 45$; Fig. 3) and therefore less than predicted based on their individual effects. The majority of the studies were in aquatic ecosystems ($n = 43$) and when considering the combined impacts of invaders in freshwater and marine ecosystems separately, the mean remained significantly antagonistic for both. Similarly, the result was antagonistic when considering impacts measured across different levels of biological organization (community and population), response groups (survival, abundance, growth, diet, and behavior) and study types (in situ or mesocosm/laboratory). However, when the impact of multiple invaders on autotrophs was

examined it became additive ($d = 0.08$, CI -0.40 to 0.52, $n = 9$) while remaining antagonistic for heterotrophs ($d = -1.03$, CI -1.51 to -0.64, $n = 36$; Fig. 3). Additive interactions were the most frequent in individual studies (58%) with non-additive effects being less common (antagonistic 38%, synergistic 4%; Table A3).

DISCUSSION

Study of the impacts of invasions has produced a wealth of knowledge on their environmental impacts (Simberloff et al. 2013), yet the combined effects of multiple invaders are rarely considered. Here, I have shown that invasive animals generally have neutral or negative impacts on one another and their combined adverse impacts on native biodiversity, abundance, or survival are often less than predicted by an additive response and were rarely synergistic.

My results support the Biotic Resistance Model and correlative evidence on invasive plants (Kuebbing and Nuñez 2015), suggesting that it is unusual for invasive species to facilitate one another in a "meltdown" scenario. Instead, the mean negative effect of invaders on one another adds support to the idea of "serial replacement." This theory, which has also been termed the "invasion treadmill," suggests that, over time, different invasive species might come to dominate a community by out-competing other invaders (Lohrer and Whitlatch 2002, Thomas and Reid 2007). A recent paper suggested that in the Laurentian Great Lakes, where the sheer number of invasions seemed to have lent the Invasion Meltdown model support, it is actually a strongly interacting invasive mussel promoting population-level changes in both native and nonnative species rather than meltdown per se (DeVanna et al. 2011). My meta-analysis supports this idea since 47% of the positive interactions I found in freshwater communities involved a positive effect of the invasive zebra mussel (*Dreissena polymorpha*) on other invasive benthic invertebrates. Consequently, I suggest that ecosystems with numerous invasive species are a result of multiple
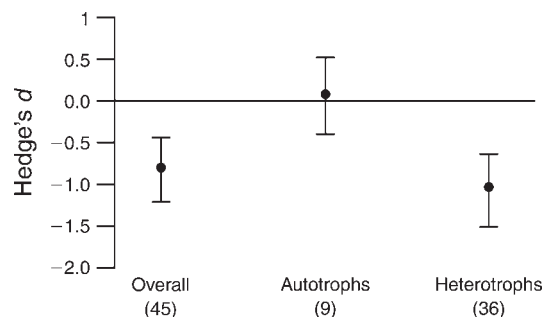

FIG. 3. The interactive effect of paired invaders on ecosystem properties measured overall, in autotrophs and in heterotrophs. A positive d indicates a synergistic effect and a negative d indicates an antagonistic effect. Values are means with 95% CI. Where confidence intervals cross zero, the effect is considered additive.

Reports

introductions and correlations in invasion pathways (such as ballast water), rather than facilitative interactions among invaders (Ricciardi 2006, Adebayo et al. 2014, Bobeldyk et al. 2015).

The dominance of antagonistic effects of co-occurring invasive animals can be explained by co-tolerance of individuals or taxa to different invaders (Vinebrooke et al. 2004). Sensitive native species are likely to be negatively affected by a single invasive animal species and therefore, when additional invasions occur they are often already locally extinct or significant reduced in abundance. For instance, if both invasive species have similar feeding strategies, the same native taxa are likely to be consumed by either invader, whether the invasion is single- or multi-species (Jackson et al. 2014). Therefore, antagonistic interactions are of concern from a conservation perspective, since both invasive animals may need to be controlled to produce ecological recovery. Alternatively, antagonistic interactions can occur when the combined effect of invaders reflects that of the most damaging invader, masking the impact of the second invader (Nyström et al. 2001).

Mean and frequencies of interaction type varied between ecosystems, phyla and functional feeding groups, indicating the importance of context in predicting future interactions among invasive animals. For instance arthropods, which were the most sampled group in all ecosystems, generally had neutral or negative effects in aquatic ecosystems and neutral or positive effects in terrestrial ecosystems. In fact, although the mean effect of invaders on one another was negative, the frequency of interactions between invasive animals was dominated by neutral interactions in individual studies. Similarly, despite the detection of an overall mean antagonistic effect of paired invasive animals, additive interactions were more frequent in individual studies and interaction type differed when impact was measured on heterotrophs or autotrophs. Case studies of multiple invaders may differ from the overall global trend of negative invader interactions and antagonistic invader impacts because of the utility of meta-analyses in detecting patterns and significant results (e.g., Crain et al. 2008, Hillebrand and Gurevitch 2014). However, these global trends can hide the huge variability present at a more local scale in the natural world (Ives and Carpenter 2007). Certainly, no universal explanation will describe interactions between invasive animals due to the complexity of the mechanisms and interactions involved in biological invasions (Kueffer et al. 2013). Alternatively, the predominance of neutral interactions and additive impacts in individual studies may indicate that study durations were not long enough to detect effects, however this was not assessed. I emphasize that my findings are broad generalizations based on the current literature and therefore, a sensitive interplay between local case studies and global trends is required to fully understand interactions among invasive animals and to direct research and management towards realistic conservation goals.

Invasive species interact with one another and native species in ecological networks, which means they have a wide variety of direct and indirect impacts (Tylianakis et al. 2008, Simberloff et al. 2013). In my meta-analysis, the detected combined effect of multiple invaders was measured across a wide variety of ecosystem properties, from population abundance to community diversity. Consequently, more research is needed to draw precise conclusions on the combined impact of specific invasive species pairs on specific ecological receptors (Kuebbing et al. 2013, Kueffer et al. 2013). Further, despite the clear trends detected here, few studies have examined the impact of multiple invaders, especially in terrestrial ecosystems and in countries outside of the United States, where 43% of the papers used in this report conducted their research. More research is therefore needed to address unanswered questions, such as, how do interactions among invasive animals vary across different habitats and continents? Does the evolutionly history (i.e., native co-occurrence) of invaders influence their interactions? Research on the specific interaction types between different invader pairs and the subsequent consequences on ecosystem properties is a critical area of ecology that requires more attention.

Literature Cited

Adebayo, A. A., A. Zhan, S. A. Bailey, and H. J. MacIsaac. 2014. Domestic ships as a potential pathway of nonindigenous species from the Saint Lawrence River to the Great Lakes. Biological Invasions 16:793–801.

Ban, S. S., N. A. Graham, and S. R. Connolly. 2014. Evidence for multiple stressor interactions and effects on coral reefs. Global Change Biology 20:681–697.

Bobeldyk, A. M., J. Rüegg, and G. A. Lamberti. 2015. Freshwater hotspots of biological invasion are a function of species–pathway interactions. Hydrobiologia 746:363–373.

Bradley, B. A., et al. 2012. Global change, global trade, and the next wave of plant invasions. Frontiers in Ecology and the Environment 10:20–28.

Cohen, A. N., and J. T. Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. Science 279:555–558.

Colautti, R. I., A. Ricciardi, I. A. Grigorovich, and H. J. MacIsaac. 2004. Is invasion success explained by the enemy release hypothesis? Ecology Letters 7:721–733.

Crain, C. M., K. Kroeker, and B. S. Halpern. 2008. Interactive and cumulative effects of multiple human stressors in marine systems. Ecology Letters 11:1304–1315.

Darling, E. S., and I. M. Cote. 2008. Quantifying the evidence for ecological synergies. Ecology Letters 11:1278–1286.

DeVanna, K. M., B. L. Bodamer, C. G. Wellington, E. Hammer, C. M. Mayer, and J. M. Bossenbroek. 2011. An alternative hypothesis to invasional meltdown in the Laurentian Great Lakes region: general facilitation by Dreissena. Journal of Great Lakes Research 37:632–641.

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

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

Gurevitch, J., and L. V. Hedges. 2001. Meta-analysis: combining the results of independent experiments. Pages 347–369 in S. M. Scheiner and J. Gurevitch, editors. Design

Reports

and analysis of ecological experiments. Second edition. Oxford University Press, New York, New York, USA.

Hillebrand, H., and J. Gurevitch. 2014. Meta-analysis results are unlikely to be biased by differences in variance and replication between ecological lab and field studies. Oikos 123:794–799.

Ives, A. R., and S. R. Carpenter. 2007. Stability and diversity of ecosystems. Science 317:58–62.

Jackson, M. C., and J. Grey. 2013. Accelerating rates of freshwater invasions in the catchment of the River Thames. Biological Invasions 15:945–951.

Jackson, M. C., T. Jones, M. Milligan, D. Sheath, J. Taylor, A. Ellis, J. England, and J. Grey. 2014. Niche differentiation among invasive crayfish and their impacts on ecosystem structure and functioning. Freshwater Biology 59:1123–1135.

Kuebbing, S. E., and M. A. Nuñez. 2015. Negative, neutral, and positive interactions among nonnative plants: patterns, processes and management implications. Global Change Biology 21:926–934.

Kuebbing, S. E., M. A. Nuñez, and D. Simberloff. 2013. Current mismatch between research and conservation efforts: the need to study co-occurring invasive plant species. Biological Conservation 160:121–129.

Kueffer, C., P. Pysek, and D. M. Richardson. 2013. Integrative invasion science: model systems, multi-site studies, focused meta-analysis and invasion syndromes. New Phytologist 200: 615–633.

Levine, J. M., and C. M. D'Antonio. 1999. Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87:15–26.

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

Lowry, E., E. J. Rollinson, A. J. Laybourn, T. E. Scott, M. E. Aiello-Lammens, S. M. Gray, J. Mickley, and J. Gurevitch. 2013. Biological invasions: a field synopsis, systematic review, and database of the literature. Ecology and Evolution 3:182–196.

Nyström, P., O. Svensson, B. Lardner, C. Bronmark, and W. Graneli. 2001. The influence of multiple introduced predators on a littoral pond community. Ecology 82:1023–1039.

O'Connor, N. J. 2014. Invasion dynamics on a temperate rocky shore: from early invasion to establishment of a marine invader. Biological Invasions 16:73–87.

Ormerod, S. J., M. Dobson, A. G. Hildrew, and C. R. Townsend. 2010. Multiple stressors in freshwater ecosystems. Freshwater Biology 55:1–4.

Platvoet, D., J. T. A. Dick, C. MacNeil, M. C. van Riel, and G. van der Velde. 2009. Invader–invader interactions in relation to environmental heterogeneity leads to zonation of two invasive amphipods, *Dikerogammarus villosus* (Sowinsky) and *Gammarus tigrinus* Sexton: amphipod pilot species project (AMPIS) report 6. Biological Invasions 11:2085–2093.

Powell, K. I., J. M. Chase, and T. M. Knight. 2011. A synthesis of plant invasion effects on biodiversity across spatial scales. American Journal of Botany 98:539–548.

Preston, D. L., J. S. Henderson, and P. T. J. Johnson. 2012. Community ecology of invasions: direct and indirect effects of multiple invasive species on aquatic communities. Ecology 93:1254–1261.

Pysek, P., V. Jarosik, P. E. Hulme, J. Pergl, M. Hejda, U. Schaffner, and M. Vila. 2012. A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. Global Change Biology 18:1725–1737.

R Core Team. 2014. R: a language and environment for statistical computing. Version 3.0.3. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Ricciardi, A. 2001. Facilitative interactions among aquatic invaders: is an invasional meltdown occurring in the Great Lakes? Canadian Journal of Fisheries and Aquatic Sciences 58:2513–2525.

Ricciardi, A. 2006. Patterns of invasion in the Laurentian Great Lakes in relation to changes in vector activity. Diversity and Distributions 12:425–433.

Ricciardi, A., and H. J. MacIsaac. 2011. Impacts of biological invasions on freshwater ecosystems. Pages 211–224 in D. M. Richardson, editor. Fifty years of invasion ecology: the legacy of Charles Elton. Wiley-Blackwell, Chichester, UK.

Rosenberg, M. S., D. C. Adams, and J. Gurevitch. 2000. MetaWin: statistical software for meta-analysis: Version 2.1. Sinauer, Sunderland, Massachusetts, USA.

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

Simberloff, D., et al. 2013. Impacts of biological invasions: what's what and the way forward. Trends in Ecology & Evolution 28:58–66.

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

Staudt, A., A. K. Leidner, J. Howard, K. A. Brauman, J. S. Dukes, L. J. Hansen, C. Paukert, J. Sabo, and L. A. Solorzano. 2013. The added complications of climate change: understanding and managing biodiversity and ecosystems. Frontiers in Ecology and the Environment 11:494–501.

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

Tummers, B., J. van der Laan, and K. Huyser. 2010. Data Thief III: Version 1.6. http://www.datathief.org

Tylianakis, J. M., R. K. Didham, J. Bascompte, and D. A. Wardle. 2008. Global change and species interactions in terrestrial ecosystems. Ecology Letters 11:1351–1363.

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

Vinebrooke, R. D., K. L. Cottingham, J. Norberg, M. Scheffer, S. I. Dodson, S. C. Maberly, and U. Sommer. 2004. Impacts of multiple stressors on biodiversity and ecosystem functioning: the role of species co-tolerance. Oikos 104:451–457.

Reports

Supplemental Material

Ecological Archives

Appendices A and B are available online: http://dx.doi.org/10.1890/15-0171.1.sm