Negative, neutral, and positive interactions among nonnative plants: patterns, processes, and management implications

SARA E. KUEBBING[1*] and MARTIN A. NUÑEZ[2]

[1]*Department of Ecology and Evolutionary Biology, University of Tennessee, 569 Dabney Hall, Knoxville, TN 37996-1610, USA,*
[2]*Laboratorio Ecotono, INIBIOMA, CONICET, Universidad Nacional del Comahue, Quintral 1250, San Carlos de Bariloche, CP 8400, Argentina*

Abstract

The movement of species is one of the most pervasive forms of global change, and few ecosystems remain uninvaded by nonnative species. Studying species interactions is crucial for understanding their distribution and abundance, particularly for nonnative species because interactions may influence the probability of invasion and consequent ecological impact. Interactions among nonnatives are relatively understudied, though the likelihood of nonnative species co-occurrence is high. We quantify and describe the types of interactions among nonnative plants and determine what factors affect interaction outcomes for ecosystems globally. We reviewed 65 studies comprising 201 observations and recorded the interaction type, traits of the interacting species, and study characteristics. We conducted a census of interaction types and a meta-analysis of experiments that tested nonnative competition intensity. Both methods showed that negative and neutral interactions prevailed, and a number of studies reported that the removal of a dominant nonnative led to competitive release of other nonnatives. Positive interactions were less frequently reported and positive mean effect sizes were rare, but the plant characteristics nitrogen fixation, life cycle (annual or perennial), and functional group significantly influenced positive interactions. Positive interactions were three times more frequent when a neighboring nonnative was a nitrogen fixer and 3.5 times lower when a neighboring nonnative was an annual. Woody plants were two or four times more likely to have positive interactions relative to grasses or herbs, respectively. The prevalence of negative interactions suggests that managers should prepare for reinvasion of sites when treating dominant nonnatives. Though positive interactions were infrequent, managers may be able to anticipate positive interactions among nonnatives based upon traits of the co-occurring invaders. Predicting positive nonnative interactions is an important tool for determining habitat susceptibility to a particular invasion and for prioritizing management of nonnatives with a higher likelihood of positive interactions.

Keywords: invader interactions, invasional meltdown, level of invasion, nonnative interactions, plant communities, positive interactions

Received 4 June 2014 and accepted 30 July 2014

Introduction

The anthropogenic movement of species is one of the most pervasive forms of global change, and few ecosystems remain uninvaded by nonnative species. Nonnative species impact native populations, communities, and ecosystems globally (Vilà *et al.*, 2011; Pyšek *et al.*, 2012), and understanding the drivers of invasion and the impacts of nonnative species are critical for effective conservation. The likelihood that a nonnative species will establish, spread, or have an impact in its new range can be modulated by interactions with neighbor-

ing species. The importance of interactions between nonnatives and the resident species they encounter are central components of many invasion biology hypotheses. For example, the biotic resistance hypothesis predicts that negative interactions between resident species and nonnatives can prevent invasion (Elton, 1958; Levine & D'Antonio, 1999). Alternatively, the absence of negative interactions could promote nonnative spread and growth as when nonnatives are released from above- and belowground herbivores or pathogens (Keane & Crawley, 2002; Klironomos, 2002). Neutral interactions between nonnatives and potential enemies could stimulate the evolution of increased competitive ability in nonnatives as they reallocate resources from traits conferring protection to those promoting competition (Blossey & Nötzold, 1995). Most recently, the Pathogen-Accumulation-Infection-Decline hypothesis predicts

*Present address: School of Forestry and Environmental Studies, Yale University, 195 Prospect Street, New Haven, CT 06511, USA

Correspondence: S. E. Kuebbing, tel. +1 203 436 9148, fax +1 203 432 3123, e-mail: sara.kuebbing@yale.edu

that the relative frequency of negative interactions between nonnatives and potential enemies should increase with nonnative residence time as local enemies adapt to nonnatives (Mitchell *et al.*, 2010; Flory & Clay, 2013). Altogether, approximately 18 hypotheses establish that species interactions are important mechanisms for understanding establishment and persistence patterns of nonnatives (Catford *et al.*, 2009; Lamarque *et al.*, 2011).

Yet, only one invasion biology hypothesis, invasional meltdown, explicitly considers the implications of interactions among co-occurring nonnatives (Catford *et al.*, 2009). This hypothesis emphasizes the significance of positive nonnative interactions, suggesting that facilitation between nonnative species can increase population expansion or the per capita effect of each species (Simberloff & Von Holle, 1999). Many invasional meltdown examples involve interactions between plants and other trophic levels, and there are few examples of plant–plant invasional meltdown (Simberloff & Von Holle, 1999; Simberloff, 2006). Here, we focus on understanding interactions among nonnative plant species, which should be as important as understanding interactions among native and nonnative plants because it is becoming more common for many habitats to have high nonnative plant species richness (Chytrý *et al.*, 2008; Catford *et al.*, 2012; Kuebbing *et al.*, 2013). Predicting when positive interactions between nonnative species are more likely to occur is important for predicting the impacts or likelihood of establishment of nonnative species.

The consequences and significance of nonnative interactions is not wholly absent from the literature. Many authors have introduced terminology relating to the oft-noted phenomenon that the decline in one nonnative leads to a rapid increase in another, which indicates competition among nonnative plants may be common. This phenomenon has earned many titles including: 'invasion treadmill' (Thomas & Reid, 2007), 'secondary invasion' (Pearson *et al.*, 2009), and 'surprise effects' (Caut *et al.*, 2009). Other authors have coined terms to describe differences in the competitive ability of co-occurring nonnatives, including 'strong' (Ortega & Pearson, 2005) and 'dominant' (MacDougall & Turkington, 2005) plants. Likewise, the term 'invasional interference' is the antithesis of 'invasional meltdown' and describes scenarios when the performance of a nonnative is reduced when it co-occurs with another nonnative (Yang *et al.*, 2011; Rauschert & Shea, 2012). Though this terminology is dispersed throughout the literature and no single term or set of terms has yet to gain traction, these authors highlight the importance of nonnative species interactions.

To date, there has not been a comprehensive assessment of the relative frequency of interaction types

among nonnative species since the original invasional meltdown publication (Simberloff, 2006). The traits of the environment, the species, or the individual are expected to influence the type of interactions among plants (Callaway & Walker, 1997). Plant interaction theory predicts that interactions should change along stress gradients (Wilson & Keddy, 1986b; Bertness & Callaway, 1994; Brooker, 2006) and productivity gradients (Grime, 1973; Wilson & Keddy, 1986a). More stressful environments, like deserts or alpine tundras, are expected to promote positive interactions (Callaway *et al.*, 2002), while more productive environments are predicted to promote negative interactions (Wilson & Keddy, 1986b; Rees, 2013). Interaction type may also vary based upon characteristics of the species or individual. Plants may have a positive interaction with neighboring plants when they are seedlings, but this interaction may become negative once they are adults (Callaway & Walker, 1997; Wright *et al.*, 2014). Likewise, interactions can change depending on a plant's functional group (Gaudet & Keddy, 1988), leaf nitrogen levels (Wardle *et al.*, 1998), or life cycle (Fowler, 1986; Crawley & May, 1987). Whether these models apply to nonnative plant interactions has rarely been tested, and three current unknowns in invasion biology include: (i) the overall frequency of nonnative interaction types (i.e. negative, neutral, and positive), (ii) the overall magnitude and direction of plant interactions, and (iii) whether the frequency, magnitude, or direction of interaction type is affected by traits of the interacting nonnative species or the habitats in which they co-occur. This manuscript aims to assemble and synthesize the research to date on nonnative plant interactions. We focus on plants due to the importance of plant invasions and the availability of data. We conducted a comprehensive literature search to find studies that explicitly test nonnative plant interactions and ask the following questions: (i) What is the relative frequency of negative, positive, or neutral interactions among nonnative plant species? (ii) What is the direction and magnitude of mean effect sizes in plant competition intensity experiments? and (iii) Are there any traits of nonnatives that cause deviations in overall interaction patterns among nonnative species?

Materials and methods

Literature search

We searched the database Web of Science (v. 5.2 Thomson Reuters 2011) in June 2013 using the search terms invas* OR introduced OR alien OR exotic OR non-native OR non-indigenous AND plant* AND interact* OR compet* OR facilit* OR meltdown, which produced 12488 citations. We did not

include any starting date restrictions for this search. We culled this initial list to 5538 citations by selecting the following Web of Science Categories: ecology, plant sciences, biodiversity conservation, environmental sciences, and forestry. For each citation, we reviewed abstracts and selected articles that dealt with nonnative plant interactions. In addition, we screened the reference list of the retrieved articles to find other relevant publications that we missed in the initial search. Our final number of studies was 65 articles (Appendix S1).

Data collection

Some articles contained multiple experiments or observations, either considering more than two nonnative plants or comparing interactions in different environments (e.g. soil nutrient or water availability). We considered an observation to be the outcome of a single plant–plant interaction or the effect of species A (neighbor species) on species B (focal species) in a particular environment. Therefore, if a study compared two nonnative plants, we considered the effect of species A on B as a separate observation from the impact of species B on A.

To investigate if there were any species or habitat characteristics that affected the type of interaction, we extracted the following information for each experiment: location of study, habitat type (aquatic, desert, disturbed, dune, fern-sedge, old field, temperate forest, tropical forest, grassland, riparian, sparse, shrubland, wetland), species studied, life stage of each species (seed, seedling, sapling, adult), life cycle of each species (annual, biennial, perennial), functional group of each species (herbaceous, graminoid, shrub, tree, vine), whether the species was a nitrogen fixer, experiment type (observation, greenhouse, field, lab), and whether the experiment was a removal experiment (i.e. if the experiment monitored the effects of the removal of a target nonnative plant on other nonnative species). We also assessed whether the native range of each nonnative pair overlapped, which might suggest some degree of coevolution between the species. We used the USDA Germplasm Resources Information Network Database (GRIN; http://www.ars-grin.gov/) as a standardized account of the native range for all nonnative species reviewed in our study. The GRIN database provides a coarse list (continental region and country) of the native range of these species, but does not provide information on habitat types or specific locations within the native range. Therefore, our method for accounting whether two nonnative species co-occur in their native ranges is limited to assessing the potential for co-occurrence because it does not determine whether species are found in similar habitats (i.e. two species may both be reported as native to a specific country, but one may occur in upland forests and one in riparian forests).

Data analysis

To provide the most comprehensive assessment of nonnative plant interaction studies, we implement two analyses. First, we census all 201 observational and experimental studies and record the frequency of interaction types reported. We then use a meta-analysis on those studies that experimentally test for competition intensity among nonnative plants. Meta-analyses are beneficial because they provide a quantitative measure of overall effect size and account for variation among sample sizes across studies (Gurevitch & Hedges, 2001; Stewart, 2010), but can be limiting when the reviewed studies do not implement similar experimental approaches or do not report necessary statistics for calculating effects sizes (i.e. variable reporting, Gurevitch & Hedges, 2001). We had to exclude over two-thirds of the reviewed studies because they did not experimentally manipulate nonnative species (e.g. observational studies), the experiments did not directly test for competition intensity (e.g. tested for indirect effects or built competition models), or they did not provide the necessary data. Therefore, our meta-analysis is restricted to 22 of the published studies and 124 of the observations. While we recognize the limitations of a census-based method (Stewart, 2010), we consider the information contained within the studies excluded from the meta-analysis as valuable additions to this review. We report results from both techniques because these two analyses, given their differences, provide complimentary evidence of nonnative plant interaction patterns.

For all 201 observations, we evaluated whether the interaction between the species pair was positive, negative, or neutral. Examples of positive interactions included statistically significant ($\alpha \leq 0.05$) increased growth or fitness or decreased rates of herbivory or disease. Neutral interactions occurred when the presence of plant A had no significant effect ($\alpha > 0.05$) on plant B. We used the statistical analysis provided in each manuscript to evaluate statistical significance. We did not weight particular response variables (i.e. aboveground biomass, belowground biomass, plant height, number of flowers or fruit, percent cover) as 'greater' or 'lesser' importance; however, the majority of studies reported plant biomass as the response variable. We used Fisher's Exact Test to investigate if the frequency of interactions was affected by species or habitat characteristics (Crawley, 2012).

For the meta-analysis, we included studies that tested for competition intensity between nonnative plants. These studies employed two different experimental methods: measurements of relative neighbor effects (RNE) or relative competition effects (RCE). In both experiment types, the competition treatment consists of an individual focal species grown with a heterospecific neighbor. In RNE experiments, the competition treatment was compared to the growth of the focal species grown alone (i.e. without a neighbor), which tests for the total competition intensity with a neighboring species. In RCE experiments, the competition treatment was compared to the growth of the focal species with a conspecific neighbor (i.e. with a neighbor), which tests for the relative importance of intra- and interspecific competition. Because different experimental designs can influence the interpretation of competition intensity (Weigelt & Jolliffe, 2003), we calculated the overall effect size across all studies as well as effect sizes for each experimental design.

We estimated mean effect sizes using Hedges' $d+$, which measures the difference between treatment groups (i.e. growth of a nonnative with a second nonnative) and control groups

(i.e. growth or performance of a nonnative alone or with a conspecific neighbor). This method corrects for small sample size bias and avoids overestimating effect sizes when study sample size is low (Gurevitch & Hedges, 2001; Lajeunesse & Forbes, 2003). We extracted the sample size, mean, and variance of treatment and control groups, and if the necessary data were only reported in figures, we extracted data with extraction software (Plot Digitizer v. 2.6.4, © 2014 Joseph A. Huwaldt). If studies reported more than one response variable, we only used a single response variable to avoid issues of independence between the data (Gurevitch & Hedges, 2001). We calculated the grand mean effect size across studies and 95% confidence intervals, and analyzed how species and habitat characteristics and experimental methods influenced mean effect sizes. We also calculated the mean effect size for each of our census interaction type (i.e. negative, neutral, positive) to compare the two methods and to compare the magnitude of negative and positive effects. We consider a mean effect size to be significant when its 95% confidence intervals do not overlap zero. In this review, positive mean effect sizes indicate that nonnative plant performance increases in the presence of another nonnative plant species.

Results

Literature demographics

We studied a total of 87 species spanning 58 genera and 26 families. The species varied in functional group (37 herbs, 33 graminoids, 9 trees, 7 shrubs, and 1 woody vine), life cycle (19 annuals, 3 biennials, 65 perennials), and nitrogen-fixing ability (8 nitrogen fixers). We combined the trees, shrubs, and vines into a single functional group (i.e. woody species) and excluded biennials from our life cycle analysis because the numbers of each group individually were too low. The most frequently studied species were the annual grass *Bromus tectorum* L. (six studies comprising 16 experiments), the perennial herb *Centaurea stoebe* L. (two studies comprising nine experiments), and the succulent shrub *Carpobrotus edulis* (L.) L. Bolus (two studies comprising nine experiments). In over half of the experiments, the nonnative species had overlapping native ranges ($n = 118$).

Grasslands and prairies were the most frequently studied habitat type (34.6%, $n = 75$) and all the remaining habitat types had less than 10% frequency. Eighty-four percent of the experiments were conducted in North America [($n = 169$; Canada ($n = 2$), United States of America ($n = 167$)], 16% were conducted in Europe [$n = 32$; Czech Republic ($n = 20$), France ($n = 10$), United Kingdom ($n = 2$)], and less than 5% were conducted in Africa [Seychelles ($n = 3$)], Asia [$n = 4$; China ($n = 2$), Japan ($n = 2$)], Australasia [New Zealand ($n = 2$)], and South America [$n = 7$; Argentina ($n = 5$), Chile ($n = 1$), Ecuador ($n = 1$)]. Experiments were infrequently con-

ducted on islands ($n = 25$, 12%). The majority of tests worked with seedlings (45.2%, $n = 98$) or adults (53.0%, $n = 115$), while less than 1% worked with saplings ($n = 1$) or seeds ($n = 2$). Over half of the tests were greenhouse studies (56.7%, $n = 123$). The remaining tests were field studies (29.5%, n = 64), observational studies (11.1%, $n = 24$), or lab studies (0.03%, $n = 6$; n.b., all lab studies were performed in a wind tunnel to test effects of sand deposition on plant growth and competition, Zarnetske *et al.*, 2013). Fifteen studies experimentally manipulated environmental conditions (i.e. soil nutrient availability, water availability, shade levels, allelochemical leachate, or sand deposition). Sixteen of the studies were nonnative removal experiments, where a single nonnative was removed from a community. In all 16 cases, the removal led to the invasion of at least one other nonnative species, and in 13 studies, the nonnative species response (relative cover or biomass) was proportionally greater than the native species response. Because the nonnative removal experiments were not specifically testing for interactions between nonnative plants (i.e. they were focused on the efficacy of removal techniques or on overall plant community response to invader removal), we excluded them from analyses, but consider their implications.

Nonnative interactions

Of the 201 nonnative plant interactions, 39.8% ($n = 80$) were negative, 18.9% ($n = 38$) were positive, and 41.3% ($n = 83$) were neutral (Fig. 1a). The overall mean effect size of plant competition intensity studies ($N = 124$) was negative, and the type of competition experiment affected the mean effect size. Experiments testing for relative neighbor effects (RNE) had a mean effect size 71 times more negative than experiments testing for relative competition effects (RCE), which had a slightly negative, but not significant, mean effect size (Fig. 1c). When the data were split by interaction type, the direction of the effect size was consistent with the reported interaction type, and the magnitude of the mean effect size for positive and negative interactions were equally large (Fig. 1b). The mean effect size for reported neutral interactions was negative, but was five times lower than that of negative interactions (Fig. 1b).

Three plant characteristics – nitrogen-fixing ability, life cycle, and functional group – significantly affected the proportion of interaction outcomes and the direction or magnitude of the mean effect size. Positive interactions were three times more frequent and negative interactions 2.5 times less frequent when the neighbor was a nitrogen fixer compared to a non-nitrogen species that did not fix nitrogen (Fig. 2a). Likewise, the mean effect size was significantly positive when the
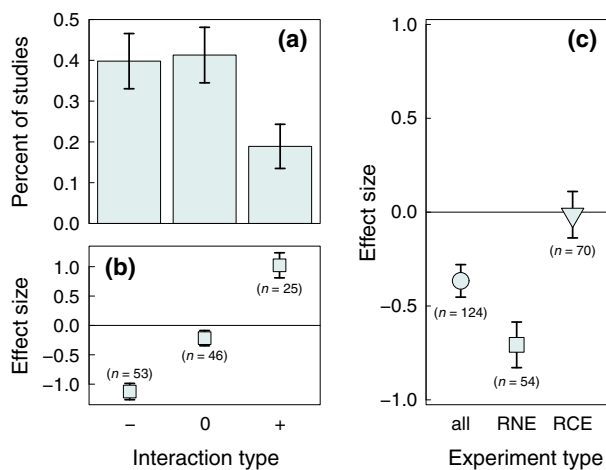
Fig. 1 Negative and neutral interactions among nonnative plants were common, in terms of frequency of reports (a) and mean effect size (*Hedges d+*) of plant competition studies (c). The magnitude of mean effect sizes of reported positive and negative interactions were equally large (b). Relative neighbor experiments (RNE) compare the growth of an individual nonnative alone to the growth of an individual nonnative with a heterospecific neighbor and relative competitive experiments (RCE) compare the growth of two conspecific nonnatives with the growth of two heterospecific nonnatives. Error bars represent 95% confidence intervals of the mean, and positive mean effect sizes indicate that nonnative plants performed better in the presence of another nonnative plant species.

neighboring plant was a nitrogen fixer in RCE experiments (Fig. 2b). When the focal species was a nitrogen fixer, there was no effect on the frequency of interaction types (Fig. 2c), and the mean effect size was significantly negatively for focal nitrogen-fixing plants (Fig. 2d).

When the neighboring plant was an annual, negative interactions were 1.7 times more frequent and positive interactions were 3.5 times less frequent compared to when a neighbor was a perennial. Perennials were two times more likely to have negative interactions when their neighbor was an annual compared to a perennial (Fig. 3c), and the mean effect of an annual nonnative on a perennial nonnative was significantly negative in RCE experiments (Fig. 3d). The mean effect size of annual plants on other annuals and the mean effect size of a perennial plant on other annuals or perennials did not differ from zero (Fig. 3b,f,h).

Positive interactions were three times more common when the focal species was a woody plant than when the focal species was an herb (Fig. 4a). In contrast, the mean effect size of competition on a woody plant was significantly negative, while the mean effect size on grasses and herbaceous nonnatives did not differ from zero in RCE experiments (Fig. 4b). Positive interactions were two times more common when the neighboring
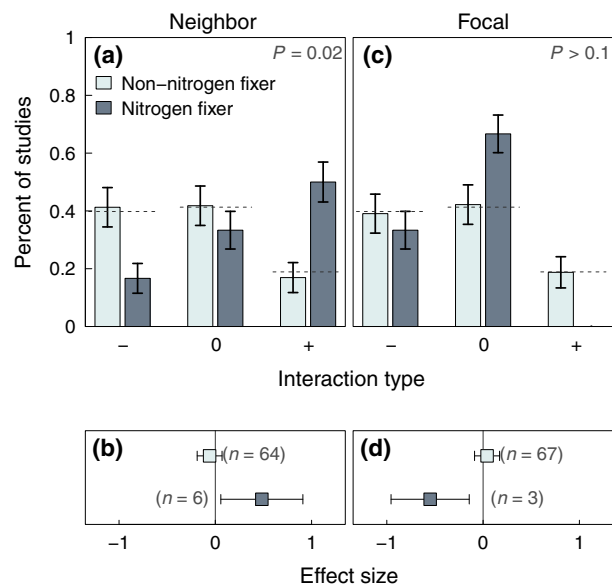

Fig. 2 When the neighboring nonnative plant was a nitrogen fixer, positive interactions were more frequent and negative interactions less frequent (a) and the mean effect size (Hedges' *d+*) was significantly positive (b). Interaction frequency did not vary depending on whether the focal nonnative was a nitrogen fixer (c) although the mean effect of relative competition on focal nitrogen fixers was significantly negative (d). Dashed lines indicate the interaction frequencies for all nonnative interaction studies, and error bars represent 95% confidence intervals of the mean. Positive mean effect sizes indicate that nonnative plants performed better in the presence of another nonnative plant species.

species was a woody plant compared to an herb or grass, although this difference was not significant (Fig. 4c). The mean effect size of competition when a nonnative had a woody neighbor was significantly positive in RCE experiments (Fig. 4d).

We did not detect deviations in nonnative interaction type frequencies when we considered the type of experiment ($P = 0.09$), whether species pairs had overlapping native ranges ($P = 0.60$), the habitat type of the nonnatives ($P = 0.30$), or the life stage of either the focal or neighboring nonnative ($P = 1$). Likewise, mean effect sizes across these treatments were predominantly negative or did not differ from zero (Table S1). The type of competition experiment impacted the mean effect size across nearly all plant traits and habitat characteristics. Mean effect sizes of RNE experiments were consistently lower than mean effect sizes of RCE experiments (Table S1).

Discussion

Negative and neutral interactions were twice as common as positive interactions between nonnative plants,
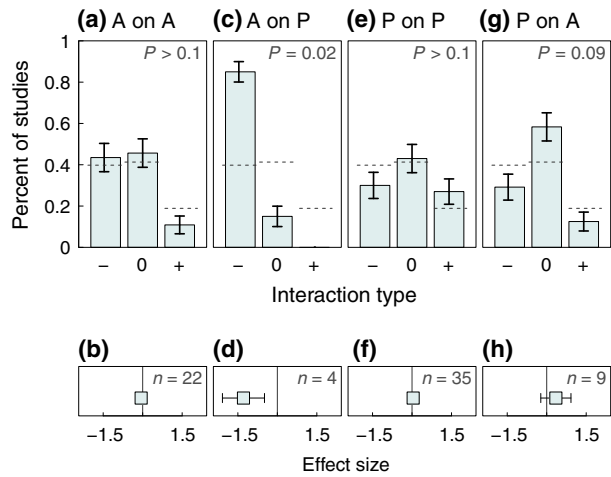
Fig. 3 Perennial plants with annual neighbors (A on P) were more frequently reported to have negative interactions (c) and had significantly negative mean effect size (Hedges' *d+*; d). The frequency of reported interactions for annual plants with annual neighbors (A on A), perennial plants with perennial neighbors (P on P), and annual plants with perennial neighbors (P on A) did not differ from overall interaction frequencies (a, e, g) and the mean effect size of these combinations was not significant. Dashed lines indicate the interaction frequencies for all nonnative interaction studies, and error bars represent 95% confidence intervals of the mean. Positive mean effect sizes indicate that nonnative plants performed better in the presence of another nonnative plant species.
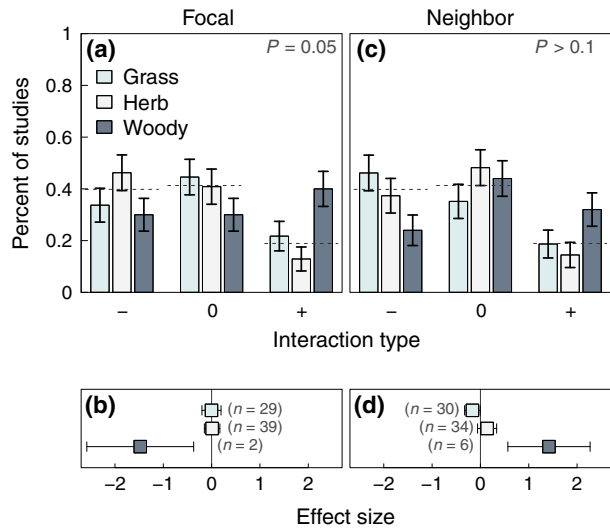

Fig. 4 Positive interactions were more frequent when a focal species was a woody plant (a), but there was no difference in interaction frequencies when the neighbor was a woody plant (c). Conversely, the mean effect size (Hedges' *d+*) when the focal species was a woody plant was negative (b), and the mean effect size when a neighboring plant was a woody was positive (d) in relative competition experiments. Dashed lines indicate the interaction frequencies for all nonnative interaction studies, and error bars represent 95% confidence intervals of the mean. Positive mean effect sizes indicate that nonnative plants performed better in the presence of another nonnative plant species.

and in plant competition studies, the mean effect size was negative. The relative frequency of interaction types and direction and magnitude of effect sizes shifted when a neighboring nonnative was a nitrogen fixer or an annual, and when the focal nonnative was a woody plant. Importantly, when a neighboring nonnative was a nitrogen fixer or a woody plant, positive interactions were more frequent and mean effect sizes were positive compared to nonnitrogen-fixing plants and nonwoody plants, respectively. This information is helpful for predicting when nonnative plants are likely to compete and for prioritizing management toward nonnatives with a higher likelihood of positive interactions.

Implications of negative interactions

Negative interactions indicate that nonnative species may be preventing or retarding the spread of other nonnatives into ecosystems, and they could be an unexplored kind of biotic resistance that results in failed invasions (Zenni & Nuñez, 2013). These negative interactions (i.e. suppression of subdominant nonnative populations) present a concern for managing invaders (Hulme & Bremner, 2006; Kuebbing *et al.*, 2013)

because they imply that a conservation practitioner must plan for the management of a dominant nonnative plant species and for 'secondary invasions' by subdominant nonnatives that are present or are likely to become present at a site (Pearson *et al.*, 2009). In some cases, the promotion of desired vegetation through direct seeding or planting may be necessary (Kettenring & Adams, 2011). In extreme instances, when managers know that the likelihood of reinvasion of a site by another nonnative is high and they do not have the resources to undergo monitoring or vegetation restoration, they may decide to delay or discontinue management in lieu of triggering an 'invasion treadmill' (Thomas & Reid, 2007).

The coexistence of co-occurring nonnative plants may still be commonplace, despite the high frequency of negative interactions. Generally, ecological theory favors the notion that competition structures communities (Callaway & Walker, 1997; Brooker *et al.*, 2008), and our findings suggest that competition may be common between nonnative plants. However, if nonnative plant interactions are less competitive than native-nonnative interactions, then the presence of one nonnative may indirectly promote a second nonnative (Brooker *et al.*, 2008; Flory & Bauer, 2014). The prevalence of neutral

mean effect sizes in RCE experiments indicates that intra- and interspecific competition intensity between nonnative plants is generally equivalent. In contrast, interspecific competition between nonnative and native plants generally favors nonnative species (Vilà & Weiner, 2004). However, the increased performance of nonnatives is usually associated with changes in resource availability or disturbance regimes (Daehler, 2003), which may explain why we found many studies that reported that the removal of nonnative species led to competitive release of other nonnatives. In a few instances, the percent increase in the nonnative species was equivalent to the release of neighboring native species (Alvarez & Cushman, 2002; Truscott et al., 2008; Stephens et al., 2009), but in most cases, the increase in nonnative cover significantly exceeded that of native species (Adler et al., 1998; Brooks, 2000; Allen et al., 2005; MacDougall & Turkington, 2005; Ogden & Rejmánek, 2005; Hulme & Bremner, 2006; Story et al., 2006; Bush et al., 2007; Cox & Allen, 2008, 2011; Ortega & Pearson, 2010; Bahm et al., 2011; Skaer et al., 2013).

An obvious question regarding these findings is why subdominant nonnatives, but not subdominant natives, are responding to removal of the competitive dominant in the system? This could be due to a reporting bias in the literature, although many of the publications describing this phenomenon were interested in the response of the entire plant community to nonnative plant control and thus are unlikely to report only the release of the nonnatives. Alternatively, the number of propagules of nonnatives could be higher than that of native species, which could happen if the site was degraded or disturbed prior to invasion (MacDougall & Turkington, 2005; Kettenring & Adams, 2011). Taken together, the long-term repercussions of negative nonnative interactions on plant community dynamics are not necessarily straightforward because they will hinge upon the strength of interactions within the plant community and the environmental conditions of the ecosystem.

Implications of positive interactions

Although positive interactions were infrequent, they remain an important consideration for prioritization of management efforts. As predicted in plant ecology theory, we found evidence that certain plant traits increased the frequency of positive interactions and caused positive mean effect sizes (Callaway, 1995; Brooker et al., 2008). Nonnative plants benefited when their neighbor was a nitrogen fixer, and this may be because nitrogen-fixing plants tend to increase available soil nitrogen, which is typically considered a limiting soil resource (Vitousek & Howarth, 1991; Vitousek

et al., 2010). Nonnative woody species were also more likely to have positive associations, which are common across ecosystems globally (Gómez-Aparicio, 2009). Woody plants frequently act as nurse plants, and if nonnative woody shrubs create novel and favorable microenvironments, they may promote the establishment of other nonnatives that may otherwise not invade an ecosystem (Tecco et al., 2007; Giantomasi et al., 2008).

Positive interactions are understudied (Callaway, 1995; Brooker et al., 2008), but we do not think a publication bias skewed our results toward finding a higher frequency of negative interactions. We found no indication that negative effect sizes were more common than positive effect sizes (i.e. funnel plot analysis, Palmer, 1999; Figure S1). Although general plant ecology studies may systematically favor competition as the driving mechanism structuring native plant communities, an important motivation for nonnative interaction studies is to test the invasional meltdown hypothesis (Simberloff & Von Holle, 1999), which has stimulated research on positive interactions among nonnative species (Simberloff, 2006).

Future research directions

We still require a better understanding of how nonnative plant interactions will change with shifting environments, particularly in the context of other global change drivers, such as changes in climate and nitrogen deposition (Tylianakis et al., 2008). We found that interactions among nonnative plants shifted in studies that altered resource availability, which aligns with predictions that changing environmental conditions alters interactions (Bertness & Callaway, 1994; Callaway, 1995; Callaway et al., 2002; Brooker et al., 2008). However, the direction of the interaction shift was study- and species-specific (D'Antonio et al., 2001; Thomsen et al., 2006; Mony et al., 2007; Pfeifer-Meister et al., 2008; Besaw et al., 2011; Mangla et al., 2011; Metlen et al., 2013; Zarnetske et al., 2013), and this inconsistency likely influenced the change in mean effect sizes from significantly negative in "ambient" conditions to neutral in manipulated conditions in the meta-analysis (Table S1). How to merge plant interaction theory with invasion biology theory is still in early stages (Bruno et al., 2003). More explicit research testing how nonnative interactions change across stress and productivity gradients may improve our understanding of how both native and nonnative plants will respond to future environmental changes (Brooker et al.,2008).

We have provided an initial assessment of the frequency, direction, and magnitude of interactions among nonnative plant species based on a diffuse

literature examining nonnative species interactions. We have found negative and neutral interactions prevailed and that certain plant traits can alter the relative frequency, magnitude, and direction of interactions. We see this assessment as a foundation for further empirical studies on nonnative plant interaction hypotheses. Overall, our study suggests that studying interactions among nonnative can be key to predicting their nonnative potential and impacts and for planning their management.

Acknowledgements

References

Adler PB, D'Antonio CM, Tunison JT (1998) Understory succession following a dieback of *Myrica faya* in Hawai'i Volcanoes National Park. *Pacific Science*, **52**, 69–78.

Allen EB, Cox RD, Tennant T, Kee SN, Deutschman DH (2005) Landscape restoration in southern California forblands: response of abandoned farmland to invasive annual grass control. *Israel Journal of Plant Sciences*, **53**, 237–245.

Alvarez ME, Cushman JH (2002) Community-level consequences of a plant invasion: effects on three habitats in coastal California. *Ecological Applications*, **12**, 1434–1444.

Bahm MA, Barnes TG, Jensen KC (2011) Restoring native plant communities in smooth brome (*Bromus inermis*)-dominated grasslands. *Invasive Plant Science and Management*, **4**, 239–250.

Bertness MD, Callaway R (1994) Positive interactions in communities. *Trends in Ecology & Evolution*, **9**, 191–193.

Besaw LM, Thelen GC, Sutherland S, Metlen K, Callaway RM (2011) Disturbance, resource pulses and invasion: short-term shifts in competitive effects, not growth responses, favour exotic annuals. *Journal of Applied Ecology*, **48**, 998–1006.

Blossey B, Nötzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology*, **83**, 887–889.

Brooker RW (2006) Plant-plant interactions and environmental change. *New Phytologist*, **171**, 271–284.

Brooker RW, Maestre FT, Callaway RM *et al.* (2008) Facilitation in plant communities: the past, the present, and the future. *Journal of Ecology*, **96**, 18–34.

Brooks ML (2000) Competition between alien annual grasses and native annual plants in the Mojave Desert. *American Midland Naturalist*, **144**, 92–108.

Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution*, **18**, 119–125.

Bush RT, Seastedt TR, Buckner D (2007) Plant community response to the decline of diffuse knapweed in a Colorado grassland. *Ecological Restoration*, **25**, 169–174.

Callaway RM (1995) Positive interactions among plants. *Botanical Review*, **61**, 306–349.

Callaway RM, Walker LR (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, **78**, 1958–1965.

Callaway RM, Brooker R, Choler P *et al.* (2002) Positive interactions among alpine plants increase with stress. *Nature*, **417**, 844–848.

Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions*, **15**, 22–40.

Catford JA, Vesk PA, Richardson DM, Pyšek P (2012) Quantifying levels of biological invasion: towards the objective classification of invaded and invasible ecosystems. *Global Change Biology*, **18**, 44–62.

Caut S, Angulo E, Courchamp F (2009) Avoiding surprise effects on Surprise Island: alien species control in a multitrophic level perspective. *Biological Invasions*, **11**, 1689–1703.

Chytrý M, Maskell LC, Pino J, Pyšek P, Vilà M, Font X, Smart SM (2008) Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. *Journal of Applied Ecology*, **45**, 448–458.

Cox RD, Allen EB (2008) Stability of exotic annual grasses following restoration efforts in southern California coastal sage scrub. *Journal of Applied Ecology*, **45**, 495–504.

Cox RD, Allen EB (2011) The roles of exotic grasses and forbs when restoring native species to highly invaded southern California annual grassland. *Plant Ecology*, **212**, 1699–1707.

Crawley MJ (2012) *The R Book*. John Wiley & Sons, West Sussex, UK.

Crawley M, May R (1987) Population dynamics and plant community structure: competition between annuals and perennials. *Journal of Theoretical Biology*, **125**, 475–489.

Daehler C (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annual Review of Ecology, Evolution, and Systematics*, **34**, 183–211.

D'Antonio CM, Hughes RF, Vitousek PM (2001) Factors influencing dynamics of two invasive C4 grasses in seasonally dry Hawaiian woodlands. *Ecology*, **82**, 89–104.

Elton CS (1958) *The Ecology of Invasions by Animals and Plants*. Methuen & Co. Ltd, London, UK.

Flory SL, Bauer JT (2014) Experimental evidence for indirect facilitation among invasive plants. *Journal of Ecology*, **102**, 12–18.

Flory SL, Clay K (2013) Pathogen accumulation and long-term dynamics of plant invasions. *Journal of Ecology*, **101**, 607–613.

Fowler N (1986) The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics*, **17**, 89–110.

Gaudet CL, Keddy PA (1988) A comparative approach to predicting competitive ability from plant traits. *Nature*, **334**, 242–243.

Giantomasi A, Tecco PA, Funes G, Gurvich DE, Cabido M (2008) Canopy effects of the invasive shrub *Pyracantha angustifolia* on seed bank composition, richness and density in a montane shrubland (Córdoba, Argentina). *Austral Ecology*, **33**, 68–77.

Gómez-Aparicio L (2009) The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. *Journal of Ecology*, **97**, 1202–1214.

Grime J (1973) Competitive exclusion in herbaceous vegetation. *Nature*, **242**, 344–347.

Gurevitch J, Hedges LV (2001) Meta-analysis: combining results of independent experiments. In: *Design and Analysis of Ecological Experiments* (eds Scheiner SM, Gurevitch J), pp. 347–369. Oxford University Press, Oxford, England.

Hulme PE, Bremner ET (2006) Assessing the impact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal. *Journal of Applied Ecology*, **43**, 43–50.

Keane RM, Crawley MJ (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, **17**, 164–170.

Kettenring KM, Adams CR (2011) Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. *Journal of Applied Ecology*, **48**, 970–979.

Klironomos JN (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature*, **417**, 67–70.

Kuebbing SE, Nuñez MA, Simberloff D (2013) Current mismatch between research and conservation efforts: the need to study co-occurring invasive plant species. *Biological Conservation*, **160**, 121–129.

Lajeunesse MJ, Forbes MR (2003) Variable reporting and quantitative reviews: a comparison of three meta-analytical techniques. *Ecology Letters*, **6**, 448–454.

Lamarque LJ, Delzon S, Lortie CJ (2011) Tree invasions: a comparative test of the dominant hypotheses and functional traits. *Biological Invasions*, **13**, 1969–1989.

Levine JM, D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, **87**, 15–26.

MacDougall AS, Turkington R (2005) Are invasive species the drivers or passengers of change in degraded ecosystems? *Ecology*, **86**, 42–55.

Mangla S, Sheley RL, James JJ, Radosevich SR (2011) Intra and interspecific competition among invasive and native species during early stages of plant growth. *Plant Ecology*, **212**, 531–542.

Metlen KL, Aschehoug ET, Callaway RM (2013) Competitive outcomes between two exotic invaders are modified by direct and indirect effects of a native conifer. *Oikos*, **122**, 632–640.

Mitchell CE, Blumenthal D, Jarošík V, Puckett EE, Pyšek P (2010) Controls on pathogen species richness in plants' introduced and native ranges: roles of residence time, range size and host traits. *Ecology Letters*, **13**, 1525–1535.

Mony C, Koschnick TJ, Haller WT, Muller S (2007) Competition between two invasive Hydrocharitaceae (*Hydrilla verticillata* (L.f.) (Royle) and *Egeria densa* (Planch)) as influenced by sediment fertility and season. *Aquatic Botany*, **86**, 236–242.

Ogden JAE, Rejmánek M (2005) Recovery of native plant communities after the control of a dominant invasive plant species, *Foeniculum vulgare*: implications for management. *Biological Conservation*, **125**, 427–439.

Ortega YK, Pearson DE (2005) Weak vs. strong invaders of natural plant communities: assessing invasibility and impact. *Ecological Applications*, **15**, 651–661.

Ortega YK, Pearson DE (2010) Effects of picloram application on community dominants vary with initial levels of spotted knapweed (*Centaurea stoebe*) invasion. *Invasive Plant Science and Management*, **3**, 70–80.

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

Pearson D, Ortega Y, Columbus F (2009)Managing invasive plants in natural areas: moving beyond weed control. In: *Weeds: Management, Economic Impacts and Biology*. (ed. Kingley RV), pp. 1–21. Nova Science Publishers, Inc, Hauppague, New York, USA

Pfeifer-Meister L, Cole EM, Roy BA, Bridgham SD (2008) Abiotic constraints on the competitive ability of exotic and native grasses in a Pacific Northwest prairie. *Oecologia*, **155**, 357–366.

Pyšek P, Jarošík V, Hulme PE, Pergl J, Hejda M, Schaffner Vilà M (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.

Rauschert ESJ, Shea K (2012) Invasional interference due to similar inter-and intraspecific competition between invaders may affect management. *Ecological Applications*, **22**, 1413–1420.

Rees M (2013) Competition on productivity gradients–what do we expect? *Ecology Letters*, **16**, 291–298.

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

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

Skaer MJ, Graydon DJ, Cushman JH (2013) Community-level consequences of cattle grazing for an invaded grassland: variable responses of native and exotic vegetation. *Journal of Vegetation Science*, **24**, 332–343.

Stephens AEA, Krannitz PG, Myers JH (2009) Plant community changes after the reduction of an invasive rangeland weed, diffuse knapweed, *Centaurea diffusa*. *Biological Control*, **51**, 140–146.

Stewart G (2010) Meta-analysis in applied ecology. *Biology Letters*, **6**, 78–81.

Story JM, Callan NW, Corn JG, White LJ (2006) Decline of spotted knapweed density at two sites in western Montana with large populations of the introduced root weevil, *Cyphocleonus achates* (Fahraeus). *Biological Control*, **38**, 227–232.

Tecco PA, Díaz S, Gurvich DE, Pérez-Harguindeguy N, Cabido M, Bertone GA (2007) Facilitation and interference underlying the association between the woody invaders *Pyracantha angustifolia* and *Ligustrum lucidum*. *Applied Vegetation Science*, **10**, 211–218.

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

Thomsen MA, Corbin JD, D'Antonio CM (2006) The effect of soil nitrogen on competition between native and exotic perennial grasses from northern coastal California. *Plant Ecology*, **186**, 23–35.

Truscott AM, Palmer SC, Soulsby C, Westaway S, Hulme PE (2008) Consequences of invasion by the alien plant *Mimulus guttatus* on the-species composition and soil properties of riparian plant communities in Scotland. *Perspectives in Plant Ecology, Evolution and Systematics*, **10**, 231–240.

Tylianakis JM, Didham RK, Bascompte J, Wardle DA (2008) Global change and species interactions in terrestrial ecosystems. *Ecology Letters*, **11**, 1351–1363.

Vilà M, Weiner J (2004) Are invasive plant species better competitors than native plant species?–evidence from pair-wise experiments. *Oikos*, **105**, 229–238.

Vilà M, Espinar JL, Hejda M *et al.* (2011) Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, **14**, 702–708.

Vitousek PM, Howarth RW (1991) Nitrogen limitation on land and in the sea: how can it occur? *Biogeochemistry*, **13**, 87–115.

Vitousek PM, Porder S, Houlton BZ, Chadwick OA (2010) Terrestrial phosphorus limitation: mechanisms, implications, and nitrogen-phosphorus interactions. *Ecological Applications*, **20**, 5–15.

Wardle D, Barker G, Bonner K, Nicholson K (1998) Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? *Journal of Ecology*, **86**, 405–420.

Weigelt A, Jolliffe P (2003) Indices of plant competition. *Journal of Ecology*, **91**, 707–720.

Wilson SD, Keddy PA (1986a) Measuring diffuse competition along an environmental gradient: results from a shoreline plant community. *The American Naturalist*, **127**, 862–869.

Wilson SD, Keddy PA (1986b) Species competitive ability and position along a natural stress/disturbance gradient. *Ecology*, **67**, 1236–1242.

Wright A, Schnitzer SA, Reich PB (2014) Living close to you neighbors: the importance of both competition and facilitation in plant communities. *Ecology*, **95**, 2213–2223.

Yang S, Ferrari MJ, Shea K (2011) Pollinator behavior mediates negative interactions between two congeneric invasive plant species. *The American Naturalist*, **177**, 110–118.

Zarnetske PL, Gouhier TC, Hacker SD, Seabloom EW, Bokil VA (2013) Indirect effects and facilitation among native and non-native species promote invasion success along an environmental stress gradient. *Journal of Ecology*, **101**, 905–915.

Zenni RD, Nuñez MA (2013) The elephant in the room: the role of failed invasions in understanding invasion biology. *Oikos*, **122**, 801–815.

Supporting Information

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

Appendix S1. List of references included in the review and meta-analysis of nonnative plant interaction studies.
Data S1. References.
Figure S1. Funnel plot of effect sizes (Hedges' *d*) of the raw data against the average sample size of the competition treatment.
Table S1. Full results from a meta-analysis of 22 published manuscripts entailing 124 observations of nonnative plant interactions.