

Invasive non-native plants have a greater effect on neighbouring natives than other non-natives

Sara E. Kuebbing^{1*} and Martin A. Nuñez²

Human activity is creating a global footprint by changing the climate, altering habitats and reshuffling the distribution of species. The movement of species around the globe has led to the naturalization and accumulation of multiple non-native species within ecosystems, which is frequently associated with habitat disturbance and changing environmental conditions. However, interactions among species will also influence community composition, but little is known about the full range of direct and indirect interactions among native and non-native species. Here, we show through a meta-analysis of 1,215 pairwise plant interactions between 274 vascular plant species in 21 major habitat types that interactions between non-native plants are asymmetrical with interactions between non-native and native plants. Non-native plants were always bad neighbours, but the negative effect of non-natives on natives was around two times greater than the effect of non-natives on other non-natives. In contrast, the performance of non-native plants was five times higher in the presence of a neighbouring native plant species than in the presence of a neighbouring non-native plant species. Together, these results demonstrate that invaded plant communities may accumulate additional non-native species even if direct interactions between non-natives species are negative. Put another way, invasions may be more likely to lead to more invasions, requiring more active management of ecosystems by promoting native species restoration to undermine invasive positive feedback and to assist native species recovery in invaded ecosystems.

Some non-native plant species are commonly found in many communities, and some communities harbour multiple non-native plants^{1,2}. Interactions between native and non-native species are commonly evoked as a primary explanation for why certain non-natives are able to naturalize, invade and become dominant in ecosystems (Fig. 1a,b)³. A primary hypothesis for explaining the accumulation of multiple non-native species is the invasional meltdown hypothesis^{4–6}, which occurs when two or more non-natives have strong positive relationships that facilitate and magnify their spread or their ecological impact (Fig. 1c)⁴. However, globally and locally, ecological communities are accumulating non-native species^{1,2,7} with little evidence of widespread invasional meltdown^{8,9}.

A second, underexplored possibility is that interactions between non-native species are asymmetrical with interactions between naturalized non-native and native species. That is, non-native plants need not necessarily have positive pairwise interactions with other non-natives—requisite in the traditional invasional meltdown definition—to promote the spread of other non-natives into a community^{10–12}. When non-native plants compete with co-occurring natives and non-natives, then the relative strength of positive and negative interactions should predict the abundance and presence of co-occurring neighbours^{11,13}. Empirical evidence shows that removal of a dominant non-native plant frequently leads to the competitive release of other non-native species^{14,15}, which suggests that competition among non-natives is common. Thus, we may expect to see ‘non-native biotic resistance’ in communities where negative interactions are stronger between two non-native species than between non-native and native species (Fig. 1d)¹⁶. Conversely, the strength of negative non-native–non-native interactions may be weak relative to non-native–native interactions, thus indirectly promoting the accumulation of non-native species into that community over the retention or accumulation of native

species (Fig. 1e)^{10,11}. Alternatively, non-native accumulation could arise when the presence of native species enhances the performance of non-native species^{17,18}, by ameliorating stressful abiotic conditions^{19–21} or reducing predation or herbivory (Fig. 1f)¹².

To date, there is little empirical or theoretical work suggesting when to expect ‘non-native biotic resistance’ or ‘non-native accumulation’ in invaded communities¹⁶. We examine 1,215 pairwise plant interactions in 21 major habitat types using a meta-analysis approach (see Methods) to examine the magnitude and strength of interactions between plant species that vary by origin (Supplementary Table 1). These observations included observational and experimental studies in the field and greenhouse that measured plant growth or fitness in response to the presence or absence of a heterospecific neighbouring plant. Studies represented 274 plant species that ranged in growth habit (tree, shrub, herbaceous, graminoid, liana), nitrogen-fixing ability, life span (annual, biennial, perennial), origin (native, non-native) and non-native species type (invasive, naturalized; Supplementary Table 2 and Supplementary Information).

Results

Non-native plants had a larger negative effect on both native and non-native plants than the effects of a native neighbour (Fig. 2a; $Q_B = 31.57$, d.f. = 3, $P < 0.0001$). The negative effect of non-natives on natives was approximately two times greater than the effect of non-natives on other non-natives across all studies (Fig. 2a). As expected, the effect varied depending on the type of experimental control used in the study (Fig. 2b,c; $Q_B = 89.89$, d.f. = 1, $P < 0.0001$). Following previous evidence⁹, this difference in effect of non-natives on natives relative to other non-natives was greatly magnified to 210 times greater in studies testing the relative strength of interspecific and intraspecific competition (Fig. 2b; relative competition effect, RCE). The effect was slightly mitigated to 1.2 times higher in

¹School of Forestry & Environmental Studies, Yale University, 195 Prospect Street, New Haven, Connecticut 06511, USA. ²Grupo de Ecología de Invasiones, INIBIOMA, CONICET, Universidad Nacional del Comahue, Quintral 1250, San Carlos de Bariloche CP 8400, Argentina. *e-mail: sara.kuebbing@yale.edu

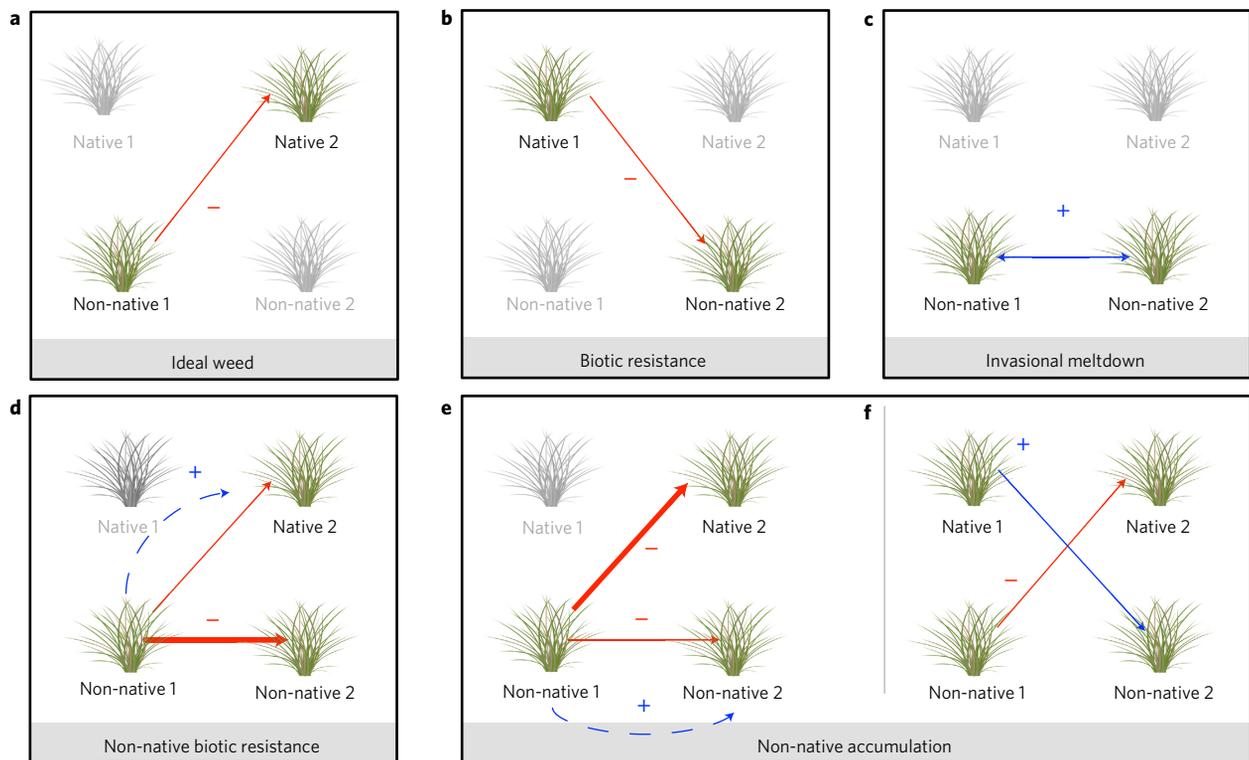


Figure 1 | Extension of non-native plant interaction theory. Plant communities are now likely to contain multiple native and non-native species and plant ecology theory must extend to consider the implications of these interactions. **a–c**, Contemporary theory has focused on how negative native–non-native interactions promote invasion (**a**, ideal weed hypothesis⁴³), prevent invasion (**b**, biotic resistance hypothesis^{43,44}) or how positive interactions between invaders might exacerbate spread or impacts (**c**, invasional meltdown hypothesis⁴). **d–f**, Extending this theory to include multiple non-native species might provide indications of when the presence of a non-native might prevent further invasion (**d**, non-native biotic resistance hypothesis¹⁶) or promote further invasion (**e, f**, non-native accumulation hypothesis) depending on the relative strength of other interactions in the community²⁵. Each solid arrow represents the sign (positive, blue, or negative, red) and strength (thicker lines represent stronger interactions) of the effect of neighbour species on a target species. Dashed arrows represent hypothetical indirect consequences of direct interactions. The plant graphic represents four distinct species and is courtesy of Tracey Saxby, IAN Image Library (ian.umces.edu/imagelibrary/).

studies testing the total competition intensity of a neighbouring plant (Fig. 2c; relative neighbour effect, RNE; please see Methods for full detail). Effect sizes of RNE experiments are frequently more negative than effect sizes in RCE experiments⁹ because control treatments in RNE experiments are the target plant grown in the absence of competition (that is, alone). Conversely, the performance of a non-native plant was roughly five times higher in the presence of a neighbouring native plant species than in the presence of a neighbouring non-native plant species. Again, this difference in the performance of a non-native plant in the presence of a neighbouring native plant relative to a neighbouring non-native plant was amplified to 240 times higher in studies testing for the RCE (Fig. 2b) and reduced to ~1.5 times higher in studies testing for the RNE (Fig. 2c).

The majority of observations that included non-native species used ‘invasive’ non-natives (non-natives that sustain self-replacing populations over several life cycles and have already spread or have the potential to spread long distances from the original site of introduction²²; $n = 444$, 79.1%). The remainder of observations considered ‘naturalized’ non-natives (non-natives that sustain self-replacing populations for several life cycles without direct intervention by people, but have not spread beyond original point of introduction²²; $n = 117$, 20.9%). The mean effect of a neighbouring non-native species did not differ whether the non-native was classified as invasive or naturalized (Hedges’ $d^+ = -0.65$, $CI = -0.78$ to -0.52 ; $Q_B = 0.59$, $d.f. = 1$, $P = 0.44$; Supplementary Fig. 1). Conversely, the effect of a neighbour plant on a naturalized non-native target plant was four times greater than the effect of a neighbour plant

on an invasive non-native target ($Q_B = 4.23$, $d.f. = 1$, $P = 0.04$; Supplementary Fig. 1). However, this may reflect the limited sample size of observations considering naturalized non-natives across experimental control types: 36% of the studies with invasive non-native targets and only 12% of studies with naturalized non-native targets tested for the RNE, which tended to be more negative than studies testing for the RCE.

We explored two possible reasons for the observed success of non-natives: (1) natives enhance abiotic conditions through nitrogen fixation (Fig. 3)²¹, or (2) the presence of herbivores alters competitive interactions between natives and non-natives (Fig. 4)²³. To consider the former, we explored the effect of nitrogen-fixing neighbouring plants, which can increase available soil nitrogen levels and promote non-native performance^{4,9}. Because effect sizes differed between experiments using different experimental controls (that is, RCE vs. RNE) and the limited number of experiments testing for RNE with nitrogen-fixing neighbours ($n = 14$), we only considered observations testing for RCE (Fig. 3). Non-native performance was ~17 times greater with a neighbouring nitrogen-fixing native relative to a non-nitrogen-fixing native ($Q_B = 22.55$, $d.f. = 1$, $P < 0.0001$) and ~11 times greater with a neighbouring nitrogen-fixing non-native relative to a non-nitrogen-fixing non-native (Fig. 3; $Q_B = 14.25$, $d.f. = 1$, $P = 0.001$). Conversely, native performance was not significantly affected by the presence of nitrogen-fixing neighbours, regardless of whether this neighbour was a native ($Q_B = 0.66$, $d.f. = 1$, $P = 0.42$) or non-native ($Q_B = 3.06$, $d.f. = 1$, $P = 0.08$). To consider the latter, we assessed how the presence of herbivores affected plant–plant interactions (23 studies, 188 observations). The

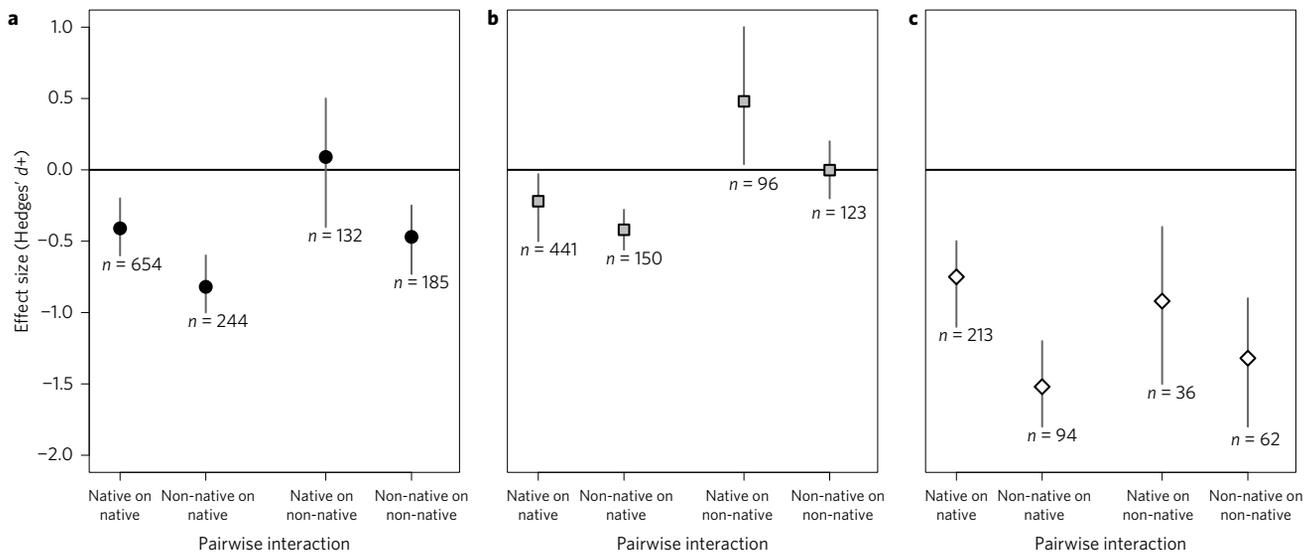


Figure 2 | Plant interactions by species origin. **a**, The origin of a species had a significant influence on the performance or fitness of a target plant species with a neighbouring species. Data taken from 118 studies involving 1,215 plant interaction observations (between study heterogeneity (Q_B) = 31.57, degrees of freedom (d.f.) = 3, $P < 0.0001$). **b,c**, This effect was significant whether an observation tested the relative strength of interspecific and intraspecific interactions (**b**; relative competitive experiments; $Q_B = 23.56$, d.f. = 3, $P < 0.0001$) or the total competition intensity between two species (**c**; relative neighbour experiments; $Q_B = 18.93$, d.f. = 3, $P = 0.0002$). Values are mean effect sizes (Hedges' d_+), and negative values indicate that target plant species have lower performance in the presence of a heterospecific neighbour relative to a conspecific neighbour (**b**) or no neighbour (**c**). Error bars represent 95% bias-corrected bootstrap confidence intervals of the mean, and effect size is significant when the confidence intervals do not cross zero. Sample sizes for each mean effect are found below the point. Statistical tests are described in detail in the Methods.

effect of a native plant on a non-native plant was higher in the presence of herbivores than in the absence of herbivores (Fig. 4; $Q_B = 4.58$, d.f. = 1, $P = 0.03$). This difference remained significant when considering observations testing for the RCE ($Q_B = 4.38$, d.f. = 1, $P = 0.04$; Supplementary Fig. 2), but there were not enough observations to test for the effects of herbivores on native–non-native interactions in RNE experiments (Supplementary Fig. 2). Although the origins of herbivores and plants are important for determining the outcome of native–non-native plant interactions²⁴, sample sizes for most plant interactions by plant species origin were too low to evaluate whether the origin of the herbivore was influential across pairwise interactions.

Interactions between plants also varied by habitat type (forest, savannah, shrubland, grassland, wetland, desert, marine intertidal, marine coastal, artificial terrestrial, artificial aquatic; $Q_B = 86.82$, d.f. = 9, $P < 0.0001$), experimental design (greenhouse, field experiment, field observation, common garden; $Q_B = 36.90$, d.f. = 3, $P < 0.0001$), target species life stage (seed, juvenile, adult; $Q_B = 11.12$, d.f. = 2, $P = 0.004$), life cycle of the neighbour plant (annual, biennial, perennial; $Q_B = 7.94$, d.f. = 2, $P = 0.02$) and growth habit of the neighbour (grass, herb, shrub, tree, vine; $Q_B = 64.88$, d.f. = 4, $P < 0.0001$) and the target plant ($Q_B = 36.66$, d.f. = 4, $P < 0.0001$; Supplementary Table 3). Although characteristics of the species and studies influenced the mean effect of a neighbour plant on a target plant, the differences between pairwise interactions among natives and non-natives were robust (Supplementary Table 3). For example, plant interactions measured in field observation experiments tended to be neutral (Hedges' $d_+ = 0.04$, CI = -0.5 to 0.7; Supplementary Table 3) whereas interactions measured within other experimental designs were strongly negative. However, over half of the field observations studied native–native pairs ($n = 19$, 58%) and no field observations recorded the effects of a native neighbour plant on a non-native plant, which suggests that differences in experimental design is not biasing the pattern we observed across species pairs. Likewise, although plant interactions measured in deserts were positive (Hedges' $d_+ = 3.44$, CI = 2.6 to 4.5), but

were negative in forests (Hedges' $d_+ = -0.36$, CI = -0.5 to -0.2), grasslands (Hedges' $d_+ = -0.58$, CI = -0.8 to -0.4) and artificial terrestrial habitats (Hedges' $d_+ = -0.35$, CI = -0.7 to -0.1), the mean effect of a native neighbour on a non-native was neutral in forests (Hedges' $d_+ = 0.53$, CI = -0.2 to 1.2), grasslands (Hedges' $d_+ = -0.07$, CI = -0.5 to 0.2) and positive in artificial terrestrial habitats (Hedges' $d_+ = 0.90$, CI = 0.1 to 2.0; Supplementary Table 3).

Discussion

Our analysis shows a mechanism for the accumulation of non-native species in habitats that do not require direct positive interactions between non-native species. The role of indirect and asymmetrical interactions as a facilitative force in promoting invasion is just beginning to be recognized^{11,25}, but may be influential in understanding non-native invasion and the likelihood of finding multiple non-natives within a plant community. Non-native species decreased the performance of both native and non-native species, but the negative effects of a non-native on a native was nearly two times greater than its effects on a non-native (Fig. 2). Additionally, neighbouring native species had a neutral effect on non-native neighbours and a negative effect on native neighbours (Fig. 2), suggesting that native species may indirectly promote the performance of non-native species relative to other native species. Together, these results provide an explanation of how invaded plant communities may accumulate other non-native plants at the expense of co-occurring natives even if direct interactions between the two non-natives species are negative (Fig. 1e,f).

Interaction asymmetry between species pairs of different origins was found whether comparing the relative differences between intraspecific and interspecific competition (Fig. 2b) or the relative differences between total competition intensity (Fig. 2c). Non-native plants were more constrained by intraspecific than interspecific competition in the presence of native species (positive Hedges' d_+ , Fig. 2b), and native plants were more constrained by interspecific than intraspecific competition in the presence of non-native species (negative Hedges' d_+ , Fig. 2b). This imbalance between

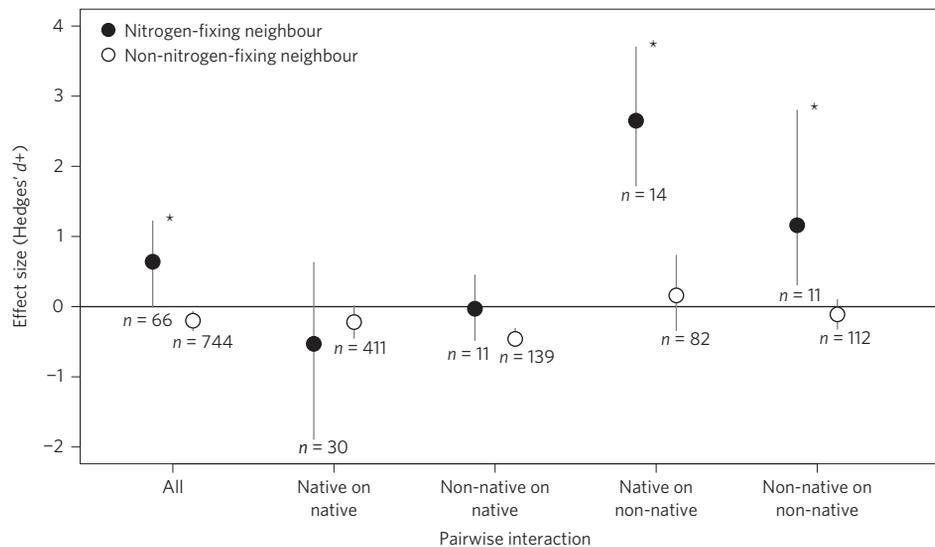


Figure 3 | Effects of nitrogen-fixing neighbours on plant interactions. Non-native plants are more likely to benefit (positive mean effect size, Hedges' d^+) from the presence of a nitrogen-fixing neighbour whereas native plant performance was equivalent with or without a nitrogen-fixing neighbour. These observations only include tests of the relative strength of interspecific and intraspecific competition. Positive mean effect sizes indicate that target plant species have higher performance in the presence of a heterospecific neighbour relative to a conspecific neighbour. Error bars represent 95% bias-corrected bootstrap confidence intervals of the mean, and effect size is significant when the confidence intervals do not cross zero. Sample sizes for each mean effect are found below the point. Asterisks (*) indicate that the between study heterogeneity (Q_B) was significant at $\alpha = 0.01$.

the relative strength of inter- and intraspecific competition for native and non-native species supports the frequent observation that non-natives become competitively dominant and natives subordinate in invaded communities³. Interestingly, intra- and interspecific competition intensity between two non-native species or two native species was neutral. This has been shown in previous syntheses on native plant competition and suggests that mechanisms other than resource partitioning—such as variation in competition in space or time or equivalence of competitive ability—are more important mechanisms for community stability^{26,27}. Taken together, the asymmetry in the relative strength of intra- and interspecific interactions suggests that environmental and species characteristics will be paramount in understanding competitive outcomes in invaded communities, and the balance of interactions among co-occurring native and non-native species may ultimately determine whether a community with a single dominant non-native or a community with multiple non-native species is more likely to persist. The total competition intensity varied among species pairs, but to a lesser degree than the relative strength of inter- and intraspecific competition (Fig. 2b,c). In light of the strong differences between relative strength of inter- and intraspecific competition, this suggests that the per capita effect of a neighbour plant on a target plant is more similar regardless of species origin, and that the important differences between pairwise interactions lie in the relative strength of intraspecific and interspecific competition.

One possible explanation for the enhancement of non-native species with native neighbours is that natives may ameliorate the environment via increasing available soil nitrogen levels and promoting plant performance^{21,28}. Although no single study considered interactions between both native and non-native nitrogen-fixing neighbours, there was some overlap in the species or genera considered among studies (for example, *Acacia* spp.^{29,30}, *Medicago* spp.^{31,32} and *Trifolium pratense*^{33–35}), suggesting potential robustness of these findings. Interestingly, we did not find a response of target native plants to the presence of a nitrogen-fixing neighbour, which is counter to many studies that show nitrogen-fixation is a common mechanism of facilitation in plant communities^{20,28}. This may be because facilitation and competition

may occur in complex combinations that change depending on differences in the local environment (for example, higher shading under a tree canopy or an area where nitrogen is not a limiting resource) or life stage of the species involved in the interaction¹³. Our observations of plant performance with native and non-native nitrogen-fixing neighbours are based on a limited sample size (Fig. 3) and could be a function of the relative importance of other drivers in the ecosystem (for example, herbivory and water stress, respectively) or other study-specific differences. Although some propose management of soil nitrogen levels as an effective means for managing non-native species³⁶, others question whether this approach is effective in decreasing non-native abundance and increasing native abundance³⁷. The difference in response between natives and non-natives to nitrogen-fixing neighbours warrants further exploration, particularly in light of applying nitrogen manipulation as a tool for invasion management or native restoration.

A second possible explanation for the lowered inhibition of non-native species with native neighbours relative to non-native neighbours could hinge on the presence of herbivores²³. It is hypothesized that the performance of non-native plants may increase if herbivores have a greater impact on native plants than on non-native plants^{24,38}. We found that the effect of a native plant on a non-native plant was negative in the absence of herbivores but positive in the presence of herbivores. Because a sizeable number of the observations in this study took place in field conditions without herbivore exclusion ($n = 502$), these findings suggest that difference in herbivore preference may indirectly promote non-native plant performance in the presence of natives^{23,24,38}.

Our analysis has a few limitations that should be acknowledged. First, it is well recognized that a single measure of pairwise interaction outcomes may not predict the net effect of competitive and facilitative interactions in a multi-species community¹³. That is, it is possible that species may be facilitating one another, but the net effect of all species interactions leads to a competitive signal. Second, our study only considers non-native species that are naturalized or invasive within a community. Once a non-native species is introduced to a region, it may either naturalize (form

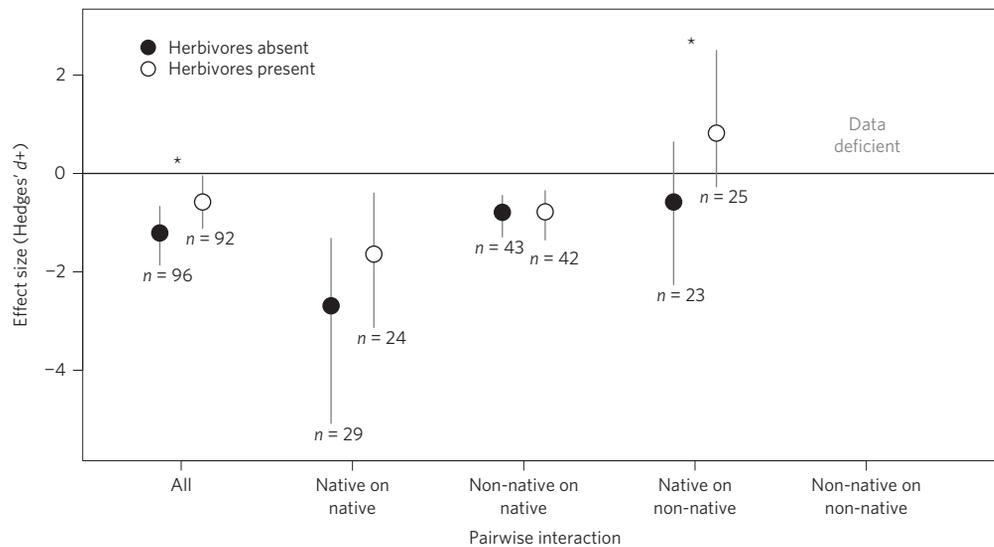


Figure 4 | Indirect effect of herbivores on plant interactions. The presence or absence of herbivores influenced the direction of the mean effect size (Hedges' $d+$) of neighbouring native plant species on the performance or fitness of a target non-native plant species. We do not present data on the effect of herbivory on non-native–non-native interactions because we only found a single study that compared non-native–non-native interactions in the presence and absence of herbivores. Positive mean effect sizes indicate that target plant species have higher performance in the presence of a heterospecific neighbour relative to a conspecific neighbour. Error bars represent 95% bias-corrected bootstrap confidence intervals of the mean, and effect size is significant when the confidence intervals do not cross zero. Sample sizes for each mean effect are found below the point. Asterisks (*) indicate that the between study heterogeneity (Q_b) was significant at $\alpha = 0.01$.

self-replacing populations) or remain 'casual' (not form self-replacing populations)²². The latter was not considered in this study owing to a lack of studies on the topic. By definition, casual non-natives cannot overcome barriers to naturalization, which may include a lack of compatibility with environmental conditions in the non-native range, absence of a facilitator (for example, pollinator, beneficial soil fungi or seed disperser) or competitive exclusion by other species²². It is possible that interactions including casual non-natives may demonstrate a very different pattern than the interactions between invasive and naturalized non-natives, and future research should explicitly consider how the relative strength of native and non-native plant interactions changes along the introduction–naturalization–invasion continuum²².

Our global survey of plant interactions suggests that the relative strength and sign of interactions among co-occurring native and non-native plants are important for predicting future composition of plant communities and the functions and services they provide in an ever-changing and increasingly connected world³⁹. Although traditional invasional meltdown scenarios are generally thought to require positive interactions among non-native species⁴, it may be appropriate to broaden the definition of meltdown to include indirect positive interactions as well (Fig. 1e). Although there is growing evidence that non-native plants are more likely to directly compete with, rather than facilitate, one another^{9,16}, this will not necessarily lead to a reduction in dominance by non-native species within ecosystems. Indeed, our results provide the mechanistic evidence for the common phenomena where the removal of a dominant non-native plant frequently leads to the competitive release of other non-native species^{14,15}. Natives may be more suppressed than other non-natives by a dominant non-native and thus more likely to have a greater response with the removal of the dominant non-native. However, if non-natives are generally more competitive than natives, the removal of a dominant non-native may still favour non-native recruitment over native recruitment into managed landscapes. Typical management strategies (for example reducing or eradicating a single dominant non-native species or introducing a biocontrol agent) may need to be amended to include more aggressive native revegetation

strategies¹⁵ if species interact in often increasingly connected webs of interactions among non-native and native species.

Methods

Literature search. We searched the database Web of Science (v. 5.2 Thomson Reuters 2011) in November 2014 using the following 'Topic' search terms: facilitate* OR compet* OR positive interact* OR negative interact* OR interfere* OR mutualis* AND plant* AND interact* with no date restrictions for the search. We refined this initial search by selecting those articles indexed as 'plant sciences', which left us with 6,427 citations. For each citation, we reviewed titles and abstracts to select those articles that met the following criteria: (1) experimental or observational studies that measured direct interactions between two species. This excluded studies where multiple competitor plants were removed around a single target plant or studies that assessed the effect of a single neighbour plant on multiple target plants; (2) studies that measured the growth (for example, biomass production, tiller length, leaf length, and so on) or fitness (for example, the number of flowers or seeds produced) of at least one species; and (3) studies that provided the sample size, mean value and measure of variation around the mean value (for example, standard deviation or error) for growth of a plant species with and without a neighbouring plant species. When necessary, we extracted data from manuscript figures using Image J software (version 1.48, <http://imagej.nih.gov/ij>).

Using these criteria, we refined the original list of citations to 83 studies and 1,157 individual observations of plant–plant interactions (Supplementary Table 1). This initial search was not sufficient in capturing a large enough sample of two study types: first, this initial search only located seven studies and 59 observations that compared non-native–non-native interactions. Because we were interested in understanding how pairwise interactions differed by species origin, we included data from a previous meta-analysis that focused exclusively on interactions between non-native plant species⁹. This search took place 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 12,488 citations. These citations were culled according to the criteria listed above, and represented an additional 22 studies and 124 observations of non-native–non-native plant interactions. Second, the initial search showed a positive mean effect of native neighbours on non-native targets, and that the presence of herbivores provided a potential explanation for this pattern. However, this included very few studies that measured non-native interactions in the presence or absence of herbivores (native–non-native interactions, two studies and 20 observations; non-native–non-native interactions, no studies). To provide a more robust assessment of the influence of herbivory on pairwise interactions including non-native species, we conducted a more detailed search in March 2015, using the following 'Topic' search terms: *plant interact** AND *facilitate** OR *compet** AND *herbiv** AND *non-native* OR *exotic* OR *invasive** OR *alien*) with no date restrictions or other reductions. This produced 279 citations, which were culled to

13 additional studies and 112 observations. There were no differences in the overall effect sizes across pairwise interactions between the initial dataset and the additional searches, and so we present data from the entire combined dataset of 118 studies and 1,215 observations.

Data collection. Most studies contained multiple experiments or observations, either considering multiple plant species, comparing interactions in different environments (for example soil nutrient availability or herbivore manipulation) or measuring different plant responses (for example, growth or fitness) to these treatments. We considered an observation to be the outcome of a single plant–plant interaction, or the effect of species A (neighbour species) on species B (target species) in a particular environment for a particular response. For each observation, we extracted the following information: study location, target species, neighbour species and the measured response variable. If a study reported multiple response variables, we collected information on all response variables. If a study reported multiple observations through time (plant growth across seasons), we used only data from the last collection period to avoid temporal pseudoreplication of data. We also recorded the experiment design (greenhouse, field experiment, common garden or field observation) and the type of experimental manipulation (if applicable). Field observation experiments measured the response of individual plants found growing next to or far from a neighbouring species. Although field observations did not experimentally manipulate the presence/absence of species, they are a common method for assessing species interactions in plant ecology studies⁴⁰. Because a species' origin is relative to the habitat where it is found, we only include greenhouse studies that used soils and/or plant seeds that were local to the habitat under question, which maintains the distinction of 'native' or 'non-native' even in a controlled greenhouse study. We classified the primary and secondary habitat type following the International Union for Conservation of Nature Classification Scheme, which is a hierarchical system of 18 primary and 105 secondary global habitat types⁴¹. Studies in this analysis included the following habitat types: forest (subarctic, temperate, subtropical/tropical dry and subtropical/tropical moist montane), savannah (dry), shrubland (subarctic, temperate, subtropical/tropical dry, subtropical/tropical high altitude, Mediterranean-type shrubby vegetation), grassland (subarctic/alpine, temperate, subtropical/tropical dry lowland), wetland (permanent rivers/streams/creeks, seasonal/intermittent/irregular rivers/streams/creeks), desert (temperate), marine intertidal (salt marsh), marine coastal/supratidal (coastal sand dune), artificial terrestrial (pastureland/old-field, urban, subtropical/tropical heavily degraded former forest) and artificial aquatic (canals/drainage channels/ditches). Finally, we recorded the competition treatment employed in each study as either RCE or RNE. Studies measuring the RCE are designed to test the relative intensity of interspecific and intraspecific competition by comparing the performance of a target plant in competition with an individual of a different species to the performance of a target plant in competition with an individual of the same species. Studies measuring the RNE are designed to test the overall competition intensity of a pairwise interaction by comparing the performance of a target plant in competition with a neighbouring species to the performance of a plant species grown alone²⁷.

For each target and neighbour species, we collected the following additional biological characteristics: origin (native or non-native), type of non-native (invasive or naturalized), life stage of the target species (seed, juvenile (non-reproductive) or adult (reproductive)), taxonomic family, growth habit (herb, grass, shrub, tree, vine) and life cycle (annual, biennial, perennial). We used the following widely used definitions to classify species based on the information provided by each study: a 'native' plant is one that has evolved in a region or that has arrived there by natural means without intentional or accidental intervention of humans. A 'non-native' plant is one whose presence in a region is attributable to human actions that enabled them to overcome fundamental biogeographical barriers. Non-native plants can be further divided into the following classifications: 'naturalized' non-natives are those that sustain self-replacing populations for several life cycles without direct intervention by people; and 'invasive' non-natives are those that sustain self-replacing populations over several life cycles and have already spread of have the potential to spread over long distances from the original site of introduction²². Species-specific information can be found in Supplementary Table 2.

Statistical analysis. We estimated the mean effect sizes using Hedges' $d+$, which corrects for small sample size bias and avoids overestimating effect sizes when study sample size is low^{27,42}. We calculated the grand mean effect size and biased-corrected 95% bootstrapped CI across observations of pairwise interactions of species of different origins (native on native, native on non-native, non-native on native and non-native on non-native). We also assessed how the characteristics of the species (origin, life stage, growth habit, life cycle) and study (experimental design, competition treatment, habitat type) influenced mean effect sizes (Supplementary Table 3). We consider a mean effect size to be significant when its 95% CI does not overlap zero, and in this review a positive mean effect size indicates that target plant performance increases in the presence of a neighbouring plant species. We calculated the total heterogeneity (Q_T) of all effect sizes and tested whether effect sizes are equal using a chi-squared test. A significant Q_T statistic indicates that the variance across effect sizes is greater than expected from sampling error alone, and indicates that other factors should be investigated. Overall, the mean effect of a

neighbour plant on a target plant was negative ($d+ = -0.40$, 95% bias-corrected bootstrapped CI = -0.52 to -0.29), and the total heterogeneity across all observations was significant ($Q_T = 3,353.11$, d.f. = 1239, $P < 0.0001$) indicating that variation among effect sizes is due to factors other than sampling error (Supplementary Table 3). Because we found a significant Q_T value, we evaluated potential factors (for example, origin of species pairs, presence of herbivores) using the total heterogeneity between groups (Q_B) statistic. These values were also compared against a chi-squared distribution. All models were constructed as random-effect models⁴².

To test the robustness of our results, we performed three additional tests. First, because some studies reported multiple performance measures for a plant species, we tested for potential pseudoreplication in our analyses by examining a reduced dataset of 754 observations that included only single performance measurements for a plant. For this reduced dataset, if a study reported multiple responses for a single plant, we selected the response metric that was most commonly reported across all studies (Supplementary Table 3). We found no evidence of pseudoreplication as the mean effect size and the total heterogeneity for observations within the reduced dataset was similar to those obtained across all studies, and the bias-corrected 95% bootstrapped confidence intervals overlapped between observations in both datasets (Hedges $d+ = -0.35$, CI = -0.50 to -0.18 ; $Q_B = 2135.40$, d.f. = 753, $P < 0.0001$). Thus, we report results from all observations, which allowed us to have the highest information content for the analysis. Second, we tested for publication bias of the studies by comparing the standardized effect size of the raw data and the sample size. We found a slightly negative but significant association (Pearson's $r = -0.11$, $P = 0.00007$) between effect size and sample size, which might suggest that studies with small sample sizes are slightly more likely to be published when they found a bigger difference in plant performance with and without a neighbouring plant species. We also examined a plot of the raw effect sizes against the sample size and found a funnel-shaped distribution of the data points, which is expected in the absence of a publication bias (for example funnel plot analysis⁴²; Supplementary Figs 3a and 3b). Finally, we assessed the number of studies that would have to be added to change the results of the meta-analysis (for example, fail-safe number⁴²). We found that 235,294 studies would have to be added, which is larger than 6,210 ($5N + 10$, $N = 1,240$ (number of observations)), and indicates that these results are a reliable estimate of the true effect⁴². We used MetaWin (v. 2.1) statistical software to calculate Hedges' $d+$ effect sizes, 95% CI (999 iterations), random-effect models, funnel plots and fail-safe number⁴². More information on the statistical equations can be found in the Supplementary Equation (1).

The list of studies included in the manuscript are available online (Supplementary Table 1) and the data extracted (including Hedges' $d+$ values) from each study as a Source Data File.

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References

- Chytrý, M. *et al.* Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. *J. Appl. Ecol.* **45**, 448–458 (2008).
- van Kleunen, M. *et al.* Global exchange and accumulation of non-native plants. *Nature* **525**, 100–103 (2015).
- Vilá, M. & Weiner, J. Are invasive plant species better competitors than native plant species? – evidence from pair-wise experiments. *Oikos* **105**, 229–238 (2004).
- Simberloff, D. & Von Holle, B. Positive interactions of nonindigenous species: invasional meltdown? *Biol. Invasions* **1**, 21–32 (1999).
- Catford, J. A., Jansson, R. & Nilsson, C. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Divers. Distrib.* **15**, 22–40 (2009).
- Jeschke, J. M. *et al.* Support for major hypotheses in invasion biology is uneven and declining. *NeoBiota* **14**, 1–20 (2012).
- Kuebbing, S. E., Simberloff, D. & Nuñez, M. A. Current mismatch between research and conservation efforts: The need to study co-occurring invasive plant species. *Biol. Conserv.* **160**, 121–129 (2013).
- Simberloff, D. Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? *Ecol. Lett.* **9**, 912–919 (2006).
- Kuebbing, S. E. & Nuñez, M. A. Negative, neutral, and positive interactions among nonnative plants: patterns, processes, and management implications. *Glob. Change Biol.* **21**, 926–934 (2015).
- Flory, S. L. & Bauer, J. T. Experimental evidence for indirect facilitation among invasive plants. *J. Ecol.* **102**, 12–18 (2014).
- Zarnetske, P. L., Gouhier, T. C., Hacker, S. D., Seabloom, E. W. & Bokil, V. A. Indirect effects and facilitation among native and non-native species promote invasion success along an environmental stress gradient. *J. Ecol.* **101**, 905–915 (2013).
- Cushman, J. H., Lortie, C. J. & Christian, C. E. Native herbivores and plant facilitation mediate the performance and distribution of an invasive exotic grass. *J. Ecol.* **99**, 524–531 (2011).

13. Callaway, R. M. & Walker, L. R. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* **78**, 1958–1965 (1997).
14. Kettenring, K. M. & Adams, C. R. Lessons learned from invasive plant control experiments: a systematic review and meta-analysis. *J. Appl. Ecol.* **48**, 970–979 (2011).
15. Pearson, D. E., Ortega, Y. K., Runyon, J. B. & Butler, J. L. Secondary invasion: the bane of weed management. *Biol. Conserv.* **197**, 8–17 (2016).
16. Henriksson, A., Wardle, D. A., Trygg, J., Diehl, S. & Englund, G. Strong invaders are strong defenders – implications for the resistance of invaded communities. *Ecol. Lett.* 1–12 (2016).
17. Bulleri, F., Bruno, J. F. & Benedetti-Cecchi, L. Beyond competition: Incorporating positive interactions between species to predict ecosystem invasibility. *PLoS Biol.* **6**, 1136–1140 (2008).
18. Bruno, J. F., Stachowicz, J. J. & Bertness, M. D. Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* **18**, 119–125 (2003).
19. Caviries, L. A., Quiroz, C. L., Molina-Montenegro, M. A., Muñoz, A. A. & Pauchard, A. Nurse effect of the native cushion plant *Azorella monantha* on the invasive non-native *Taraxacum officinale* in the high-Andes of central Chile. *Perspect. Plant. Ecol. Evol. Syst.* **7**, 217–226 (2005).
20. Bonanomi, G., Incerti, G. & Mazzoleni, S. Assessing occurrence, specificity, and mechanisms of plant facilitation in terrestrial ecosystems. *Plant Ecol.* **212**, 1777–1790 (2011).
21. Maron, J. L. & Connors, P. G. A native nitrogen-fixing shrub facilitates weed invasion. *Oecologia* **105**, 302–312 (1996).
22. Richardson, D. M. & Pyšek, P. Naturalization of introduced plants: ecological drivers of biogeographical patterns. *New Phytol.* **196**, 383–396 (2012).
23. Louda, S. M., Keeler, K. H. & Holt, R. D. in *Perspectives on Plant Competition* 413–444 (Academic Press, Inc., 1990).
24. Parker, J. D., Burkepile, D. E. & Hay, M. E. Opposing effects of native and exotic herbivores on plant invasions. *Science* **311**, 1459–1461 (2006).
25. Mitchell, C. E. *et al.* Biotic interactions and plant invasions. *Ecol. Lett.* **9**, 726–740 (2006).
26. Goldberg, D. E. & Barton, A. M. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. *Am. Nat.* **139**, 771–801 (1992).
27. Gurevitch, J., Morrow, L. L., Wallace, A. & Walsh, J. S. A meta-analysis of field experiments on competition. **4**, 539–572 (1992).
28. Brooker, R. W. *et al.* Facilitation in plant communities: the past, the present, and the future. *J. Ecol.* **96**, 18–34 (2008).
29. Iponga, D. M., Milton, S. J. & Richardson, D. M. Soil type, microsite, and herbivory influence growth and survival of *Schinus molle* (Peruvian pepper tree) invading semi-arid African savanna. *Biol. Invasions* **11**, 159–169 (2009).
30. Werner, C., Zumkier, U., Beyschlag, W. & Máguas, C. High competitiveness of a resource demanding invasive acacia under low resource supply. *Plant Ecol.* **206**, 83–96 (2010).
31. Lau, J. A. & Strauss, S. Y. Insect herbivores drive important indirect effects of exotic plants on native communities. *Ecology* **86**, 2990–2997 (2005).
32. Baude, M. *et al.* Litter inputs and plant interactions affect nectar sugar content. *J. Ecol.* **99**, 828–837 (2011).
33. Engel, E. C. & Weltzin, J. F. Can community composition be predicted from pairwise species interactions? *Plant Ecol.* **195**, 77–85 (2008).
34. Fortner, A. M. & Weltzin, J. F. Competitive hierarchy for four common old-field plant species depends on resource identity and availability. *J. Torrey Bot. S.* **134**, 166–176 (2007).
35. Mariotte, P., Buttler, A., Johnson, D., Thébault, A. & Vandenberghe, C. Exclusion of root competition increases competitive abilities of subordinate plant species through root-shoot interactions. *J. Veg. Sci.* **23**, 1148–1158 (2012).
36. Vasquez, E., Sheley, R. L. & Svejcar, T. Creating invasion resistant soils via nitrogen management. *Invas. Plant Sci. Manag.* **1**, 304–314 (2008).
37. James, J. J., Drenovsky, R. E., Monaco, T. A. & Rinella, M. J. Managing soil nitrogen to restore annual grass-infested plant communities: effective strategy or incomplete framework? *Ecol. Appl.* **21**, 490–502 (2011).
38. Keane, R. M. & Crawley, M. J. Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* **17**, 164–170 (2002).
39. Brooker, R. W. Plant-plant interactions and environmental change. *New Phytol.* **171**, 271–284 (2006).
40. Keddy, P. A. *Competition*. 1–565 (Springer Science+Business Media, 2001).
41. IUCN. *Habitats Classification Scheme*. 1–14 (International Union for the Conservation of Nature, 2012).
42. Rosenberg, M. S., Adams, D. C. & Gurevitch, J. *Metawin: Statistical software for meta-analysis* (Sinauer Associates, 2000).
43. Elton, C. S. *The Ecology of Invasions by Animals and Plants* (Methuen, 1958).
44. Levine, J. M., Adler, P. B. & Yelenik, S. G. A meta-analysis of biotic resistance to exotic plant invasions. *Ecol. Lett.* **7**, 975–989 (2004).

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Author contributions

S.E.K. and M.A.N. developed the approach and initial idea for the research. S.E.K. extracted and analysed the data, and led the writing of the manuscript. M.A.N. contributed substantially to the interpretation of the results and to the final version of the manuscript.

Additional information

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Competing interests

The authors declare no competing financial interests.