

REVIEW AND SYNTHESIS

No consistent pollinator-mediated impacts of alien plants on natives

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Abstract

The introduction of an alien plant is widely assumed to have negative consequences for the pollinator-mediated fitness of nearby natives. Indeed, a number of studies, including a highly cited meta-analysis, have concluded that the trend for such interactions is competitive. Here we provide evidence that publication bias and study design have obscured our ability to assess the pollinator-mediated impacts of alien plants. In a meta-analysis of 76 studies, we demonstrate that alien/native status does not predict the outcome of pollinator-mediated interactions among plants. Moreover, we found no evidence that similarity in floral traits or phylogenetic distance between species pairs influences the outcome of pollinator-mediated interactions. Instead, we report that aspects of study design, such as distance between the control and nearest neighbour, and/or the arrangement of study plants better predict the impact of a neighbour than does alien/native status. Our study sheds new light on the role that publication bias and experimental design play in the evaluation of key patterns in ecology. We conclude that, due to the absence of clear, generalisable pollinator-mediated impacts of alien species, management schemes should base decisions on community-wide assessments of the impacts of individual alien plant species, and not solely on alien/native status itself.

Keywords

Competition, experimental design, facilitation, invasive species, phylogenetic meta-regression, pollinator-mediated interactions, publication bias, seed set, visitation.

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INTRODUCTION

One of the most studied changes to plant communities is the introduction of an alien species. Generally, studies have focused on identifying the impacts of aliens, but not necessarily on the mechanisms that underlie them (Levine *et al.* 2003). A recent shift towards more mechanistic studies has revealed that indirect interactions between alien and native plants, such as those mediated by herbivores (Bhattacharai *et al.* 2017), soil microbial communities (Hawkes *et al.* 2005; Mangla *et al.* 2008) and pollinators (Goodell & Parker 2017) can have significant ecological (Lau & Strauss 2005) and evolutionary (Lau 2006) consequences. Our ability to better understand the impacts of alien invasions requires more information about the mechanisms and processes involved (Levine *et al.* 2003).

The degree to which a plant receives adequate pollination to set seed is known to be influenced by the density, diversity and identity of other plants residing nearby (Ashman *et al.* 2004; Vamosi *et al.* 2006). Pollinator-mediated interactions therefore offer a potential mechanism by which aliens can impact native plant communities. Indeed, over the past decade, the invasion literature has increasingly focused on the pollinator-mediated impacts of aliens – more so than any other mechanism (Skurski *et al.* 2014). Furthermore, evidence is mounting that the density and composition of species in a plant community have the potential to influence the size and diversity of the pollinator community (Westphal *et al.* 2003; Moeller 2005), and vice versa (Biesmeijer *et al.* 2006),

suggesting that alien introductions could have widespread implications for pollination services (Traveset & Richardson 2014). Yet, whether any generalities can be drawn about how alien introductions influence pollination services to natives remains an open question. It is important that we better understand the pollinator-mediated impacts of aliens on native plant communities in order to: (1) gain a more complete picture of the overall impact of an alien introduction and (2) make better predictions about which aliens are expected to impose the most negative impacts, and where, enabling better management schemes.

Interspecific interactions, especially those involving alien species, have tended to be viewed through the lens of competition, and pollinator-mediated interactions are no exception. Alien plant species have been hypothesised to compete directly with native species for pollinators for a wide variety of reasons, including their propensity to grow in large, high-density populations (Bjorknes *et al.* 2007; Skurski *et al.* 2014; Goodell & Parker 2017), the potential for release from natural enemies to promote the evolution of greater investment in floral display (Blossey & Notzold 1995) and the fact that many are introduced as ornamental plants, which are typically specifically bred/selected for their floral display (e.g. Chittka & Schurkens 2001). Negative effects of alien plant species may also operate indirectly, through their influence on local pollinator populations, by, for example, outcompeting and driving to extinction the local plant species the pollinators rely on (Cox & Elmqvist 2000; Traveset & Richardson 2014). Finally,

even if visitation is not altered, invasive species can negatively impact post-pollination processes in natives through the introduction of heterospecific pollen, which can clog native stigmas (e.g. Lopezaraiza-Mikel *et al.* 2007; Arceo-Gomez & Ashman 2016), or through pollen loss from native pollen deposited on non-native stigmas (e.g. Campbell & Motten 1985).

On the other hand, as far as we can tell, there is no particular reason to expect that an alien plant might not facilitate pollination of nearby native species. Facilitation is well known among plants (Johnson *et al.* 2003; Moeller 2004). Data from flowering plant communities in the Andes suggest that pollinator-mediated facilitation can be even more common than competition in some ecosystems (Tur *et al.* 2016). Similarly, Hegland *et al.* (2009) reported mainly facilitative interactions via pollinator attraction among six plant species in a temperate grassland community. Indeed, for the same reasons described above to predict competition, alien species, growing in high-density populations, with conspicuous/showy floral displays, may facilitate pollination of natives through what has been termed the 'magnet species effect' (Thomson 1978; Da Silva *et al.* 2013). Furthermore, the introduction of an alien plant species may improve the near- and long-term prospects of pollination services to the local plant community by enhancing the population and/or year-to-year survival of its key pollinator populations – through processes such as complementarity (Waser & Real 1979). And yet, overall, the impact of alien species on the pollination of natives is frequently reported to be competitive (Bjerknes *et al.* 2007; Goodell & Parker 2017). In particular, a prominent meta-analysis, cited 141 times as of this writing, found evidence that these interactions tended to be competitive overall (Morales & Traveset 2009).

Notably, since Morales & Traveset (2009) was published, a number of new studies have reported neutral, or positive (facilitative) impacts of an alien neighbour on pollination of native species, leading to speculation that there may exist bias in the species selected for such studies (Harrison & Winfree 2015). There may also generally exist bias in which results tend to be published in ecology and evolution (Parker *et al.* 2016). Together, these factors cast doubt on the conclusion that alien species tend to impose competition on natives. Indeed, even within a single system, pollinator-mediated interactions have been shown to vary in direction. For example, Albrecht *et al.* (2016) found that invasive *Oxalis pes-caprae* reduced seed set of the native *Diplotaxis eruroides* when the invader was present only at the landscape scale, but improved seed set when it was present at both the local and landscape scales. Similarly, Bruckman & Campbell (2016) showed that either facilitation or competition can arise in interactions between the invasive *Brassica nigra* (L.) Andr. and the native *Phacelia parryi* Torr., depending on whether the invasive was present at the landscape or local scale. These effects also depended on invasive plant density. In yet another study, McKinney & Goodell (2011) discovered that the direction of the impact on the invasive shrub *Lonicera maackii* (Rupr.) Herder on a native herb, *Hydrophyllum macrophyllum* Nutt., switched from competitive to facilitative depending on the degree of synchrony in flowering phenology between the two species. Overall, these studies indicate that multiple factors,

many of which are not considered in any individual study, can impact the direction of pollinator-mediated interactions among aliens and natives.

In addition to alien/native status, species traits may influence the direction and intensity of pollinator-mediated impacts of a neighbour plant on a focal species. Theory predicts that plant species that share floral traits should compete more strongly for pollinators (Grant 1972; Fishman & Wyatt 1999; Fenster *et al.* 2004). On the other hand, trait similarity could promote facilitative interactions among plants (Moeller 2004; Sargent & Ackerly 2008). A number of studies have found that alien plants that share certain traits with a focal species (e.g. floral symmetry, floral colour) tend to impose more negative pollinator-mediated impacts than those that do not (Morales & Traveset 2009; Gibson *et al.* 2012; Goodell & Parker 2017), suggesting that a species' traits, rather than its alien/native status, may provide more power for predicting impact.

Here we address whether any generalisations can be made about the pollinator-mediated impacts of alien plant species on focal native plant species. Specifically, using a phylogenetic meta-regression approach, we test:

- (1) whether alien plants have an overall competitive effect on pollinator visitation to and reproductive success of natives,
- (2) whether there is evidence for publication bias in the set of existing studies and
- (3) whether trait overlap, the phylogenetic distance among species pairs or particular elements of study design (e.g. distance between control plants and the nearest neighbour plants, arrangement of study plants, species choice) influences the outcome of studies of pollinator-mediated interactions among plant species.

METHODS

Data collection

Our study expands on data collected for a meta-analysis published by Morales & Traveset (2009), which is composed of experimental and observational studies measuring the effect of the presence of a neighbouring species (alien or native) on the pollinator-mediated aspects of fitness (i.e. pollinator visitation and/or plant reproductive success) of a particular focal species. To expand the set of studies included, we searched the electronic databases Scopus, Web of Science and Google Scholar, using their same search terms: [pollinat* OR visit* OR reproduc*] AND [compet* OR facilita* OR 'interspecific interaction' OR 'plant-plant interaction']. Once studies were assessed for inclusion criteria (see below), we were able to add a total of 60 new outcomes for both native–native and alien–native pollinator interactions to the original set, 40 reporting visitation outcomes and 20 reporting reproductive success outcomes; we did not add any unpublished records.

For each new study, we recorded the mean, standard deviation and sample size for visitation and/or fruit or seed set, measured in the presence (treatment) or absence (control) of the neighbour species, and used this information to calculate effect size. When data were not available from tables or in the text, they were obtained from published figures using

DATATHIEF III software (Tummers 2006), which uses axis measurements to determine the precise values presented in figures. We also recorded data for several independent variables (see below). In cases where the necessary data could not be obtained, the study was excluded.

Criteria for study inclusion

Independent observations were selected based on the following criteria:

- (1) Studies of the same neighbour species, focal species or neighbour–focal pair were treated as independent observations if they were reported in different articles.
- (2) Eleven articles reported results for more than one species pair (e.g. Gibson *et al.* 2013); each species pair was treated as an independent observation.
- (3) For articles where results were reported using both observational and experimental approaches ($n = 4$ for visitation data, $n = 2$ for reproductive success data) for a single species pair, each approach was treated as a separate study (e.g. Baskett *et al.* 2011).
- (4) When a single article reported results for multiple sites (e.g. Gibson *et al.* 2013), years (e.g. Liao *et al.* 2011) treatment densities (e.g. Sun *et al.* 2013) or other factors (e.g. spatial scale, Albrecht *et al.* 2016) for a single species pair, one observation was randomly selected for inclusion.
- (5) In three studies, pollinator visitation to both the neighbour and the focal species were reported (i.e. with a control and treatment group for both); these were considered as different species pairs. Consequently, these studies supplied one observation for each species pair.
- (6) In Morales & Traveset (2009), summary analysis was used to obtain an overall effect size and mean study variance across data reported for multiple days for two studies (Jennersten & Kwak 1991; Bell *et al.* 2005). These observations were retained as reported by Morales & Traveset (2009).
- (7) Studies that separated control and treatment groups temporally rather than spatially were excluded from the data (e.g. Takakura *et al.* 2009), as we consider this type of design fundamentally different from one in which the control group is defined on the basis of distance from the nearest neighbour plants.
- (8) Observations from unpublished sources reported by Morales & Traveset (2009) were excluded from the present analysis because relevant information about the factors under investigation could not be obtained.
- (9) In the Morales & Traveset (2009) data set, conspecific pollen load was used as a proxy for visitation frequency for two studies (Caruso 2000; Larson *et al.* 2006). These data points were retained as reported by Morales & Traveset (2009).

Effect size

A single effect size metric and its associated variance were calculated for each observation included in the analysis; because data compared responses in control vs. treatment conditions, we selected Hedge's d as our effect size metric (Hedge & Olkin

1985). Hedge's d is a popular estimate of the standardised mean difference between treatments that adjusts for differences in variance in the two groups and incorporates a correction term to remove bias from small sample sizes (Rosenberg *et al.* 2013).

$$d = \frac{\bar{Y}_1 - \bar{Y}_2}{\sqrt{\frac{(n_1-1)s_1^2 + (n_2-1)s_2^2}{n_1+n_2-2}}} J \text{ where } J = 1 - \frac{3}{4(n_1 + n_2 - 2) - 1}$$

Positive values of d indicate that the outcome (visitation or reproductive success) is higher in the treatment group (i.e. facilitation), while negative values indicate that the outcome is lower in the treatment group (i.e. competition). The larger the absolute value of d , the greater the difference. The estimate of variance on this metric was used to weight studies in the model:

$$w_i = \frac{1}{v_i + \hat{\tau}^2}$$

Consequently, studies with higher sample sizes and/or greater precision were more highly weighted than those with low sample sizes and/or precision.

Independent variables

Using phylogenetic meta-regression (described below), we explored whether the following independent variables impacted overall study outcome:

(1) Alien–native status of the neighbour species

We distinguished whether the neighbour species studied is native or alien to the community studied.

(2) Treatment arrangement

The arrangement of the neighbour species in the treatment plots was categorised into one of the following: natural, wherein plant arrangements were not manipulated or controlled by the researchers; clumped, wherein neighbour plants were present in a clump or cluster close together within or adjacent to the treatment; interspersed, where neighbour plants alternated with focal plants or were regularly spaced through the treatment; or random, where the spatial arrangement of neighbour plants was determined randomly (Fig. 1a).

(3) Distance between the control group and the neighbour species

For the purposes of this investigation, the minimum distance of the control to the nearest 'neighbour' plant was determined, as per the description in the Methods section of the study, as the distance between treatments in experimental studies using blocked designs or as the edge of the largest extent the researchers specifically verified or treated as the exclusion zone for the neighbour (e.g. the size of a clipping treatment that removed the competitor neighbour; Fig. 1b). Some studies provided maps of their sites, or GPS coordinates, which were used to determine the distance of the control groups to the nearest neighbour plant when this information could not be gleaned from the text; when maps with scale bars were provided, measurements were obtained using callipers and printed maps; when GPS coordinates were provided, measurements were obtained using online Google Maps.

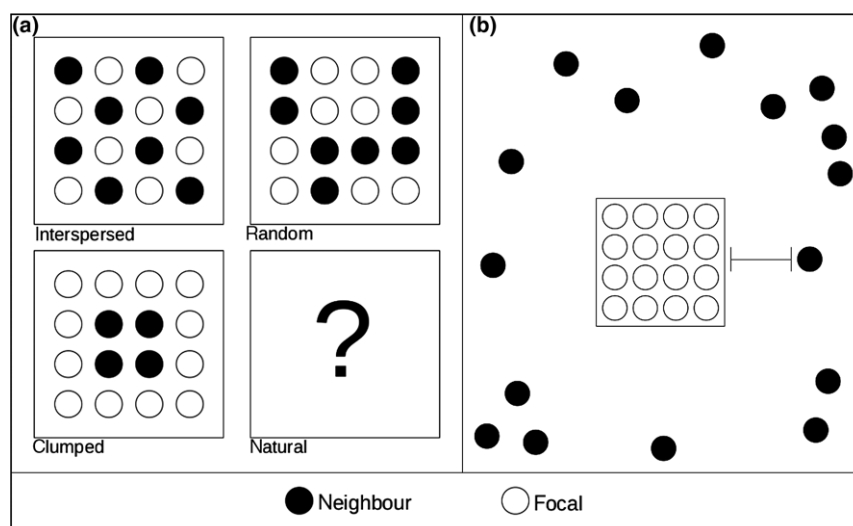


Figure 1 Graphical representation of different arrangements of neighbour and focal plants in treatment groups (A), and of the definition of the factor “distance of the control group to the nearest neighbour plant” (B).

(4) Study approach

We distinguished whether the study used an observational or experimental approach.

(5) Phylogenetic distance

A tree of study species was created by pruning a recent tree of angiosperms (Zanne *et al.* 2014). A phylogenetic distance matrix among species pairs, based on the branch lengths from the Zanne tree, was then created in R 3.2.3 (R Core Team, 2015) using tools from the package Ape (Paradis *et al.* 2004).

(6) Floral trait overlap

For each pair of species, we assessed similarity of (1) floral colour and (2) floral symmetry. Data on flower colour was obtained, by preference, directly from the descriptions in the article, or by searching for the species of interest in the USDA plants database (USDA 2017), and, if the floral colour was not listed, by searching for photographs of the species and manually coding their colour. Similarity in floral colour was determined as follows: like colours were treated as similar (e.g. red and red) and different colours were treated as dissimilar (e.g. red and white), following the conventions of previous work (e.g. Morales & Traveset 2009). In all cases, floral colour was coded based on human perception and so does not constitute a complete representation of the spectral properties of the species in question (i.e. UV reflectance data were not available for the vast majority of species, and were therefore not included). Data on floral symmetry was obtained using genus or family descriptions from Mabberley (1997) or Judd *et al.* (2002) or, less commonly, through searching the Internet for a reliable species description.

Publication bias

Finally, we explored the potential for systematic bias in the choice of alien–native species pairs and/or publication bias:

(1) Publication bias

As described in Supplement 1, we examined funnel plots to look for possible asymmetry in the distribution of effect sizes and

their variances around the population means according to the following: (a) alien–native neighbour distinction, (b) time of publication (pre-2009, post-2009) and, in the Morales & Traveset (2009) data set, (c) published and unpublished records.

(2) Bias in selection of species pairs

There are several ways by which the particular species chosen for study could bias our ability to meaningfully assess the overall impact of a neighbour species on a focal species through pollinators. For example, if researchers tend to select pairs of species that are close relatives, the overall outcome might differ compared to a sample of pairs selected randomly with respect to relatedness. In order to test for bias in the diversity or phylogenetic distance among species selected for study, we examined whether there was a relationship between the phylogenetic distance between species pairs and the reporting period (i.e. whether or not it was included in Morales & Traveset 2009, see S1).

Statistical analyses

To test the effects of the independent variables on d , we fitted a restricted maximum likelihood (Viechtbauer 2005) meta-regression model to (a) the visitation data and (b) the reproductive success data. Meta-regression tests the simultaneous effects of multiple explanatory variables against inter- and intrastudy variability (Mengersen *et al.* 2013).

Normality of the data was tested graphically and with Shapiro–Wilk tests (Shapiro & Wilk 1965). We examined plots of residuals against fitted values to test for heteroscedasticity and identify outliers in the fitted models (Viechtbauer 2010). We checked for publication bias in our data set using funnel plots (Sterne *et al.* 2005) (S1.1A and S1.1B).

Analyses were run in R 3.2.3 (R Core Team, 2015) using the Metafor 1.9-9 package (Viechtbauer 2010).

A restricted maximum likelihood meta-regression model was fitted to test for the effects of neighbour status (alien or native), control plot distance to the nearest neighbour,

study approach, treatment arrangement, phylogenetic distance and floral trait similarity between species pairs, as well as all first-order interactions among these explanatory variables, on the effect size, d . Because we fitted mixed-effects models, we used a Knapp and Hartung adjustment (Knapp & Hartung 2003) to account for uncertainty in the between-study variance estimate in random- and mixed-effects models; with this adjustment, residual variability is tested against a Q -distribution, overall model significance against an F -distribution and individual effects against t -distributions (Viechtbauer 2010); we report each of these statistics in the Results section. Variables that had no significant effect and no significant interactions were dropped from the model and the model was fitted again. The results of the full and reduced models were compared to confirm that the removal of the non-significant factors did not alter the predictions of the model.

Subsequent to the above-mentioned analysis, we fitted a follow-up maximum likelihood meta-regression model to test whether a change in visitation (d , visitation) could predict a change in reproductive success (d , reproductive success).

The articles from which our data were obtained are listed in Supplement 2.

RESULTS

Visitation

The results of a meta-regression testing the effect of our independent variables (alien or native status of the neighbour, study approach, phylogenetic distance, floral trait overlap, plant arrangement in the treatment group and distance from

the control group to the nearest neighbour) on the direction of the impact (i.e. facilitation, competition or neutral) of a neighbour species on visitation to a focal species (hereafter, 'visitation outcome') indicate that neighbour status (i.e. alien/native) does not explain a significant amount of the variation in visitation outcome (Fig. 2a; $t = 0.894$, $n = 76$, $P = 0.658$). This result does not change if we test the impact of neighbour status alone, without controlling for other effects ($F = 0.997$, $n = 76$, $P = 0.321$).

Similarly, we found no significant effect of study approach (i.e. observational vs. experimental: $t = -0.444$, $P = 0.658$, $n = 76$), or phylogenetic distance between species pairs ($t = 1.30$, $n = 76$, $P = 0.197$), or floral trait overlap (colour similarity: $t = 0.054$, $n = 76$, $P = 0.967$; symmetry similarity: $t = 0.481$, $n = 76$, $P = 0.632$) on visitation outcome. Plant arrangement in treatment plots (Fig. 1a) was found to significantly impact visitation outcome ($F = 2.81$, $n = 76$, $P = 0.056$), however, this result was not robust, as it disappeared when the single study that randomised plant arrangement in the treatment group (Brown *et al.* 2002) was excluded (Fig. 3: $F = 0.663$, $n = 75$, $P = 0.578$).

The distance between the control group and the nearest neighbour plant had a significant influence on visitation outcome, with competitive outcomes much more likely for greater distances among control and neighbour plants [d_{slope} : -0.0001 (-0.0001 to -0.0000), $t = -2.39$, $n = 76$, $P = 0.019$]. When this relationship was modelled while pooling across other factors, the intercept was positive, indicating facilitation is more commonly found at the closest distances, although we note high variability in study outcomes at the shortest distance [Fig. 4: $t = 2.01$, $n = 76$, $P = 0.049$, $d = 0.1890$ (0.001 to 0.377)].

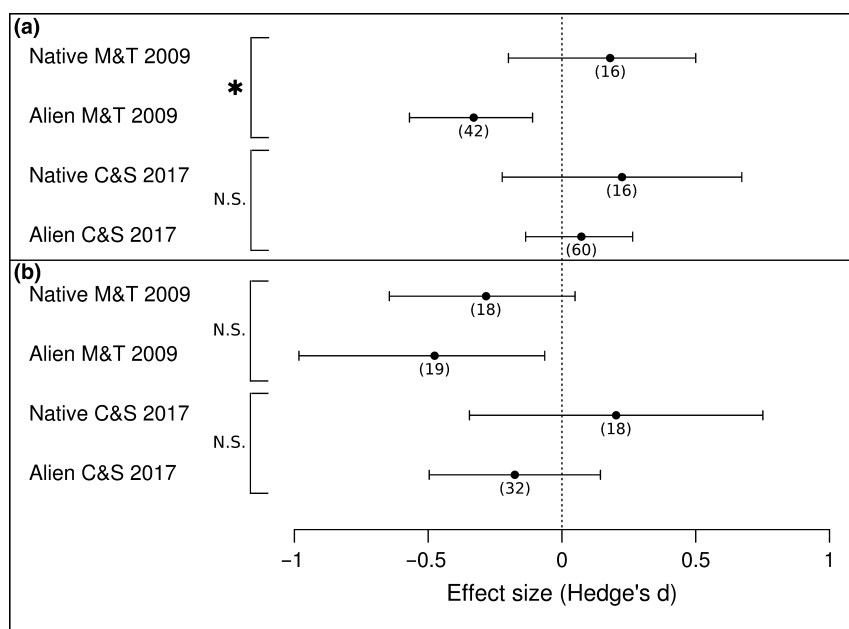


Figure 2 Forest plot of effect size and bootstrap-corrected 95% CIs in a prior meta-analysis MT (Morales and Traveset (2009)), and Knapp and Hartung-adjusted estimates and 95% CIs for the current data set (CS), examining the impact of alien or native neighbors on visitation (A) and reproductive success (B). Sample size for each estimate indicated in parentheses. Statistical results of pairwise comparisons between group estimates presented on the left, significant comparisons indicated with *, non-significant differences denoted N.S.

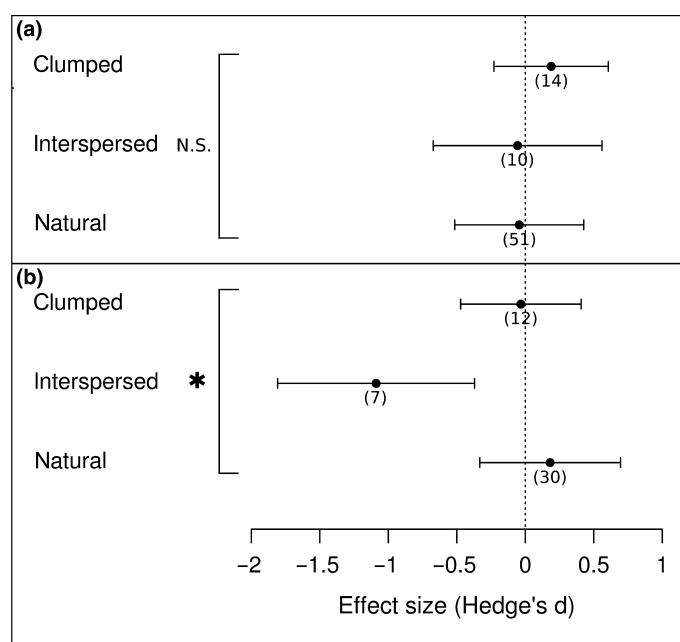


Figure 3 Forest plot of Knapp and Hartung-adjusted 95% CIs of the effect of arrangement of neighbour and focal plants in the treatment group on (A) visitation and (B) reproductive success; sample sizes contributing to each group estimate indicated in parentheses. Brackets indicate differences in estimates depending on category membership (N.S. = not significant, * = significant).

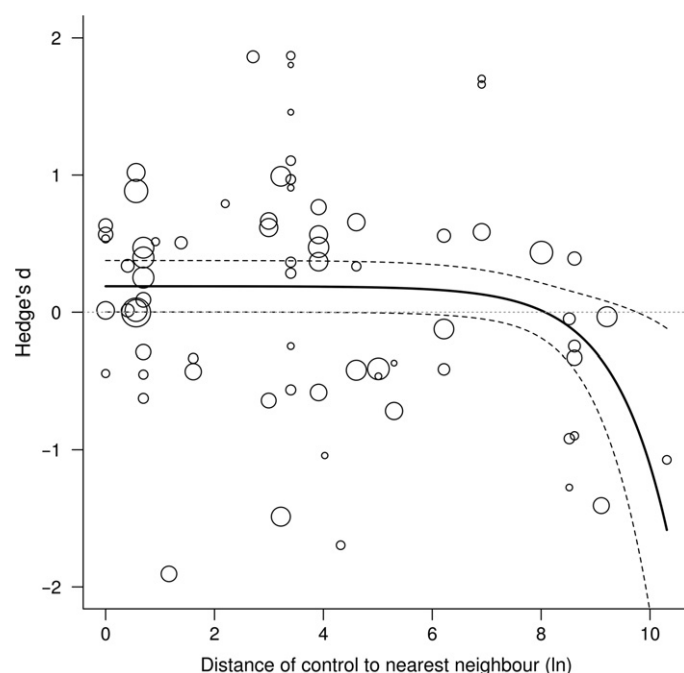


Figure 4 Standardized mean difference in visitation to native plants in [presence - absence] of a potential competitor. Point size reflects study weighting in the model, by inverse of variance. Solid line displays model regression ($y = -0.0001x + 0.198$) (dslope: -0.001 (-0.0001 to -0.0000); dinterscept: 0.189 (0.001 to 0.377)), converted to a natural log scale to encompass the entire range of x values (1m : $30,000\text{m}$); dotted lines show 95% CI.

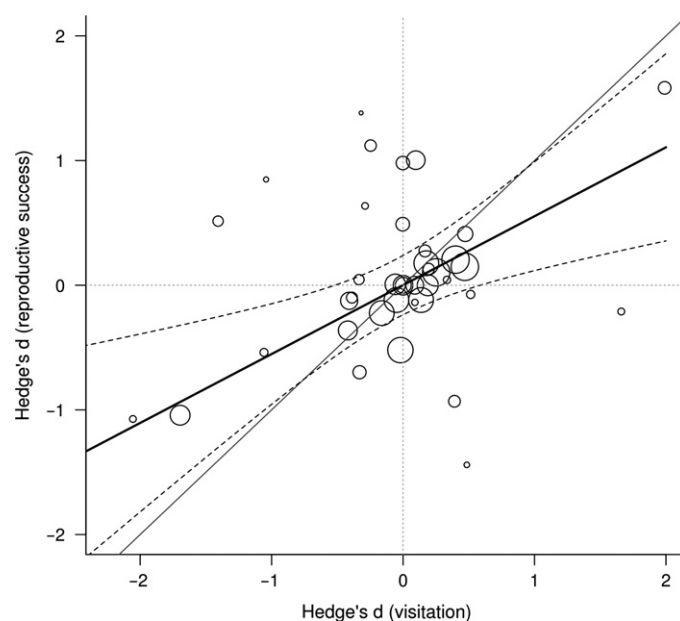


Figure 5 Relationship between change in visitation and change in reproductive success. The solid black line shows the predicted relationship between change in visitation and change in reproductive success ($y = 0.5528x + 0.0007$; dslope = 0.552 (0.026 , 0.899); dinterscept = 0.0007 (-0.237 to 0.239)); the black dotted lines show the 95% CI on the estimated relationship; the solid grey line shows the expected slope of a perfect relationship between change in visitation and change in seed set; the grey dotted lines show the zero line of each axis.

Reproductive success

As with the visitation data, we found no evidence that alien or native status of a neighbour had a significant effect on the reproductive success of a focal plant (Fig. 2b: $t = 1.28$, $n = 50$, $P = 0.208$). This result did not change if we tested the impact of status alone, without controlling for other effects ($F = 0.551$, $n = 50$, $P = 0.462$).

We found no significant effect of study approach ($t = -0.560$, $n = 50$, $P = 0.552$), distance from the control group to the nearest neighbour plant ($t = -0.113$, $n = 50$, $P = 0.911$), floral trait overlap (colour similarity: $t = -1.250$, $n = 50$, $P = 0.218$; symmetry similarity: $t = 0.248$, $n = 50$, $P = 0.806$) or phylogenetic distance between species pairs ($t = 0.0238$, $n = 50$, $P = 0.981$) on reproductive success outcome.

However, the arrangement of neighbour and focal plants within the treatment group significantly affected reproductive success outcomes, with competition more likely to be reported for studies that interspersed neighbour and focal plants ($n = 7$), as well as in the single study that arranged plants randomly in treatment plots (Brown *et al.* 2002) (Fig. 3: $F = 8.05$, $n = 50$, $P = 0.0002$). The effect of plant arrangement remained significant when the single study with a random plant arrangement was excluded ($F = 8.313$, $n = 49$, $P = 0.0008$).

Publication bias

The current data set shows no evidence of publication bias either for visitation or reproductive success outcomes

(Fig. S1.1a,b). However, results published prior to 2009 tended to report more competitive outcomes, while results published since 2009 reported more facilitative outcomes; overall effect size for visitation outcomes in alien–native studies in the pre-2009 and post-2009 data are significantly different (Supplement 1). Funnel plots describing the distribution of study effect sizes according to their variance, when divided according to their origin (i.e. the data collected by Morales & Traveset vs. the results we added), reveal differences in their degree of asymmetry. In particular, there is asymmetry with greater representation of competitive outcomes in the older data set, and a symmetrical representation of outcomes in the more recently published results (Fig. S1.2). In addition, for the pre-2009 data, the published effect sizes are significantly more extreme than unpublished ones (S1).

Relationship between visitation and reproductive success

For studies that looked at both factors, there was an overall significant effect of visitation outcome on reproductive success outcome (i.e. seed or fruit set: $F = 10.4$, $n = 41$, $P = 0.0025$), although the intercept of the relationship between visitation and seed/fruit set was not significantly different from zero [Fig. 5: $d = 0.0007$ (-0.237 , 0.239), $t = 0.006$, $n = 41$, $P = 0.996$], the slope was [Fig. 5: $d = 0.553$ (0.206 , 0.899), $t = 3.23$, $n = 41$, $P = 0.003$].

Outliers

All outcomes reported in the Results section above are robust to outlier effects unless otherwise specified; conclusions remain statistically and qualitatively unchanged when models are fitted without influential data points identified using the suite of diagnostic statistics available in Metafor (Viechtbauer 2010). Consequently, we report model estimates and outcomes with influential data points included.

DISCUSSION

Understanding the mechanisms that underlie the impacts of alien plant species on native communities is considered essential for successful invasive species management (Levine *et al.* 2003). In the case of pollinator-mediated impacts, a common conclusion is that aliens tend to depress the fitness of their neighbours through competition for shared pollinators (Bjerknes *et al.* 2007; Morales & Traveset 2009; Skurski *et al.* 2014). Our results, a meta-analysis of 76 studies, directly contradict this assertion. Specifically, we found that neither the rate of pollinator visitation, nor the seed/fruit set of a focal plant species, could be predicted on the basis of the alien or native status of a neighbouring plant. In fact, we found that alien neighbours appear to facilitate the pollination of natives as often as they reduce it. Further, we discovered that experimental design appears to have an outsized impact on the results of this type of study. For example, facilitation for visitation was more likely to be found when control plants were located closer to the nearest alien/native neighbour species, while competition was more likely to be reported as control plants were located farther from the nearest neighbour (Fig. 5). Moreover, a reduction in focal plant seed/fruit set

(competition) was more likely to be found when treatment plants were arranged in an ‘interspersed’ pattern with a neighbour, relative to natural or clumped arrangements (Figs 1 and 3). Overall, factors relating to experimental design were better able to predict study outcome (i.e. existence and/or direction of the impact) than were neighbour status (i.e. alien or native), or similarity in species traits, raising serious concerns about the ability of certain experimental designs to meaningfully assess the impact of an alien or native neighbour on pollinator-mediated interactions with a native.

Visitation was the most commonly collected response variable for studies included in our analyses: of the comparisons we considered, 58 reported visitation alone, 19 reported fruit or set alone and 41 reported both visitation and seed/fruit set. Visitation has been criticised as a misleading proxy for pollination because visitation rates do not distinguish between mutualist and antagonist visitors (King *et al.* 2013), because visitation is not consistently associated with pollen transport (King *et al.* 2013; Popic *et al.* 2013) and because visitor effectiveness can change from year to year (Fishbein & Venable 1996). Despite these criticisms, we found that a change in visitation rate was significantly associated with a change in seed/fruit set (Fig. 5). Nevertheless, considerable variability in reproductive success outcomes remains unexplained by variation in visitation outcomes, indicating that visitation is a useful but imperfect proxy for reproductive success.

Although less commonly reported, lifetime reproductive success is arguably the most defensible way to measure the ecological or evolutionary impacts of neighbour interactions on a focal plant. Several prior studies, including a meta-analysis, have reported an overall negative impact of an alien neighbour on the seed/fruit set of a focal species (Morales & Traveset 2009). Once again, our results contradict: we found that, similar to visitation, there was no overall impact of a neighbouring plant on a focal plant’s seed/fruit set, with no difference between alien and native neighbours. Our results strongly suggest that the impact of a neighbour cannot be predicted on the basis of the alien or native status of the neighbour plant.

Trait overlap

The high variability in interaction outcomes suggests that other factors (e.g. trait overlap, density effects; e.g. Bjerknes *et al.* 2007; Muñoz & Cavieres 2008), or interference competition through heterospecific pollen deposition (e.g. Brown & Mitchell 2001; Matsumoto *et al.* 2010; Da Silva & Sargent 2011) could explain some of the remaining variation in study outcome. However, contrary to our expectation, neither phylogenetic distance among species pairs (as a proxy for trait overlap; Harvey & Pagel 1991), nor similarity in specific floral traits (i.e. colour and symmetry), were significant factors in our meta-regression, directly contradicting the findings of earlier studies.

Although floral trait overlap has been described as a predictor of the direction and severity of the impacts of alien plants on pollinator-mediated interactions with natives, the actual findings are mixed. In their meta-analysis, Morales & Traveset (2009) reported that similarity in floral traits (measured, as we

report here, as the phylogenetic distance, similarity in floral symmetry and similarity in flower colour among species pairs) was associated with more negative outcomes of pollinator-mediated interactions among aliens and natives. On the other hand, in a study of pollinator-mediated interactions between the showy invasive *Lythrum salicaria* L. and 36 native co-flowering plants, species with more dissimilar floral symmetry experienced a *more detrimental* impact of the invasive, while overlap in colour and inflorescence traits had no significant effect on impact (Goodell & Parker 2017). Meanwhile, Gibson *et al.* (2012) reported that, while trait overlap did predict the sharing of pollinator species among invasives and natives, there was no subsequent impact on visitation. These findings are consistent with our analysis: it would appear that the association between trait similarity among species pairs and study outcome is highly variable, with no differences associated with alien or native status of the neighbour.

Publication bias

There are several ways by which the literature on the ecological impacts of invasive species could suffer from publication bias. First, studies reporting significant results may be more likely to get published (Levine *et al.* 2003). Second, alien/invasive species are widely considered harmful, and thus, studies that suggest positive impacts (even if they are not really positive, see below) could face additional scrutiny by reviewers, making them less likely to be published. Finally, data that refute the commonly held idea that alien species impose ecological harm may face stronger scrutiny by authors themselves – if authors of such studies anticipate a difficult reviewer process, they may delay submitting the data for publication for longer, leading to a ‘file drawer effect’. We believe there is good evidence to support one or more of these mechanisms as an explanation for the differences in our findings in comparison to those reported in an earlier meta-analysis (Morales & Traveset 2009). Especially for visitation, there is an unexplained gap in studies showing mild facilitative effects and also low sample size in the earlier data (Fig. S2a), while no such gap exists for studies published since 2009 (Fig. S2b); we also found a significant difference in study outcomes depending on whether the data were published before or after 2009 (Supplement 1), and that the competitive effect of alien neighbours on native plant visitation and reproductive success disappears with the addition of the more recent data (Fig. 2). Together, these findings suggest that the expectation that alien plants impose pollinator-mediated competition on native plants is subject to the decline effect (Schooler 2011), in which support for a given hypothesis diminishes over time.

The decline effect has been previously demonstrated in ecology and evolution: Jeschke *et al.* (2012) showed that decline effects are the norm for six major hypotheses in invasion biology, and Jennions & Moller (2002) found that support for many hypotheses across various fields in ecology and evolution declined with time. The decline effect is usually attributed to publication bias, wherein positive effects with high statistical significance are most likely to be published first, while subsequent work shows moderate or no effects (Jeschke *et al.* 2012). The results presented here, with respect to the change

in conclusion since the publication of Morales & Traveset (2009), appear to be consistent with such a pattern.

Study design

Spatial arrangement of plants

Only one factor in our model was significantly associated with a directional impact of a neighbour species on a focal plant's reproductive success: the spatial arrangement of the plants in the treatment group. Specifically, when focal and ‘neighbour’ plants are arranged in a clumped or natural design (Fig. 1a), the impact of the neighbour on the seed/fruit set of the focal species is mixed (i.e. neutral, competitive or facilitative). In contrast, when focal and neighbour plants are arranged in an ‘interspersed’ design (Fig. 1a), the impact on seed/fruit set of the neighbour tends to be competitive, although there is no overall impact on visitation.

Theory suggests that the spatial arrangement of plants in a community influences pollinator behaviour in a manner that can impact the direction of the effect on a focal plant's visitation and reproductive success (Hanoteaux *et al.* 2013). In an experimental test, Seifan *et al.* (2014) demonstrated that the density and spatial arrangement of an introduced, conspicuous neighbour plant species influences whether it tends to facilitate or compete for pollinators with other species in a community. Although Seifan *et al.* (2014) were unable to identify a consistent effect of spatial arrangement on reproductive success outcomes for the focal species, their study was performed by introducing a conspicuous species to plants co-flowering in a single meadow community. Conversely, de Waal *et al.* (2015) varied the spatial arrangements of their focal species and found no consistent effects of plant arrangement on visitation rates, but plants that were clumped together had higher reproductive success at low densities.

It is notable that while some spatial arrangements influenced seed/fruit set, none had a detectable effect on visitation, suggesting that spatial arrangement might impact visit quality rather than visit quantity, through changes in heterospecific pollen transport. It has previously been found that the spatial arrangement of plants can influence pollinator behaviour in a manner that could impact heterospecific pollen deposition (Thomson 1983; Lopezaraiza-Mikel *et al.* 2007).

Distance to nearest neighbour

There was little agreement about the appropriate distance for the placement of the control group in the studies included in our analysis. Indeed, the distance between the control and the nearest neighbour varied widely across studies, from 1 to 30 000 m, with the majority of studies placing their control group within the first 50 m of the nearest neighbour. The preponderance of neutral and facilitative effects in these latter studies raises the concern that there may be interactions between the control group and the neighbour species when they are not sufficiently distant from each other (i.e. < 50 m). It is possible that it is better to be very close to an attractive neighbour (i.e. treatment condition, *c.* 1 m) than only somewhat removed from it (i.e. control condition, *c.* 20–50 m). Such scale-dependent effects have recently been identified in a variety of systems (Cariveau & Norton 2009; Albrecht *et al.*

2016; Bruckman & Campbell 2016). Consequently, control groups may be inappropriately defined in many studies.

Species selection

Although there has been no formal analysis, there is speculation that studies of pollinator-mediated interactions among alien and native species have tended to focus on showy alien species (e.g. Bjerknes *et al.* 2007; Chrobok *et al.* 2013; Harrison & Winfree 2015). In a broad review of the invasion literature, Levine *et al.* (2003) reported that nearly all studies were performed in systems where the alien exhibited larger than average potential to impose impacts. Recently, more studies that compare the impacts of one or more alien species on a multitude of natives have emerged (e.g. Williams *et al.* 2011; Chrobok *et al.* 2013; Garbuzov & Ratnieks 2014; Goodell & Parker 2017). By considering an entire community of interacting aliens and natives, such studies are less likely to focus on pairs that may simply reinforce the widely held assumption that aliens tend to impose pollinator-mediated competition on natives.

Implications

Several major reviews have reached the conclusion that, in terms of the description of hypotheses and study conclusions, the scientific literature on invasion biology is imbued with the language of competition (Levine *et al.* 2003; Vila *et al.* 2011; Skurski *et al.* 2014). This is as true of studies focused on community structure as those concerned with ecosystem processes (Levine *et al.* 2003). The impact of plant invasions on mutualisms, in particular, has received the lion's share of attention; with most studies reporting that alien plants tend to negatively interfere with interactions between native plants and their mutualists, including seed dispersers, beneficial microbes and pollinators (Traveset & Richardson 2006, 2014). Our results suggest that facilitation, at least in the context of pollinator-mediated interactions, may be much more common than previously thought. However, we put forth that there is no *a priori* reason to suspect that facilitation is any less deleterious than competition. For example, in the case of pollinator-mediated facilitation, increased visitation to a newly introduced species implies the movement of pollinators *away* from one set of plants to another (Bjerknes *et al.* 2007). In other words, as denoted by the few studies that have looked at pollinator-mediated interactions across multiple spatial scales, facilitation at one scale may well be connected to competition at another scale, either within or across a regional pool of species (Hegland 2014). Finally, as discussed earlier, what appears to be facilitation at the level of visitation may belie competition at another if increased visitation is accompanied by increased heterospecific pollen transfer (Lopezaraiza-Mikel *et al.* 2007).

In addition to its implications for invasion biology, our study has implications for the study of ecological patterns in general. Our results underscore the concern that publication bias is hampering our ability to draw accurate conclusions in the field of ecology, and indeed, in science as a whole (Mueck 2013; Parker *et al.* 2016). Across scientific disciplines, the proportion of published studies reporting negative or neutral

results is in the order of 10–15%, suggesting the literature is strongly biased towards positive results (Mueck 2013). This obviously puts disconcerting limits on our ability to reach general conclusions, even using quantitative methods such as meta-analysis. It seems likely that in particularly controversial fields, such as invasion biology (Davis *et al.* 2011), it would be even more difficult to make accurate generalisations, because the probability of missing data is higher. We echo the recent concerns and proposed solutions raised by our colleagues about this real and worrying issue (Parker *et al.* 2016).

CONCLUSIONS

We conclude that, through publication bias, and perhaps because of an early, undue focus on unusually 'showy' alien species as study subjects, the literature has conflated the pollinator-mediated impacts of (certain) neighbouring alien species with the impact of alien/native status itself. We provide compelling evidence that publication bias is likely part of the explanation for the difference between our findings and those of earlier reviews of this topic. We demonstrate that, when developing studies to predict the outcome of pollinator-mediated interactions among neighbouring plant species, one needs to pay careful attention to the potential effects of experimental design and species choice on outcome. Our results highlight the inherent limitations of trying to draw general conclusions from studies that examine interactions between a single pair of plant species: flowering plant communities rarely consist of just two interacting species, and yet this is where the vast majority of studies focus. Finally, our results suggest that our ability to draw general conclusions about ecological patterns could often be hampered by the availability of data, especially in fields where certain types of results are likely to face additional scrutiny in the publication process.

FUTURE DIRECTIONS

Several key questions about the pollinator-mediated impacts of alien neighbours remain unanswered: (1) Is the impact of an alien plant species on native visitation/reproductive success *disproportionate to its attractiveness/density*? (2) Is competition for pollination one of the avenues by which alien plant species become invasive? (3) What long-term effects do we expect from the disruption of plant-pollinator interactions (either facilitation or competition) through invasion? To address the first question, more studies are required in which the effect of an alien plant on native plant visitation and reproduction is compared to the effect of a similarly attractive native plant (e.g. Cariveau & Norton 2009). To address the second question, investigations would be better directed at comparing the competitive abilities (for attraction of pollinators) of invasive and naturalised alien plants. More work focusing on the direct impacts of alien introductions on pollinator communities (e.g. Stout & Tiedeken 2017), and the effects of targeted ecosystem restoration (e.g. Kaiser-Bunbury *et al.* 2017), would help address the third question. Overall, more studies that focus on the impact of an alien on multiple native species across a variety of community contexts (e.g. Goodell & Parker 2017), are badly needed.

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AUTHORSHIP

JAC conceived the idea for the study, searched the literature for suitable studies, collected the effect size and associated variance, study design and flower colour data, performed the phylogenetic meta-regressions and contributed to the writing. RDS contributed to data collection, advised on analyses, generated the phylogenetic distance data, obtained the floral symmetry data and contributed to the writing.

DATA ACCESSIBILITY STATEMENT

The data for this study has been made available on the Dryad Digital Repository (doi:10.5061/dryad.s1432).

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SUPPORTING INFORMATION

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