

REVIEW AND
SYNTHESIS

A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants

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Abstract

Alien plant species can alter pollinator visitation and, in turn, the sexual reproduction of natives. Using a conventional and a phylogenetically controlled meta-analytical approach on a data set of 40 studies, we evaluated the effect of alien neighbour plant species (aliens) on visitation to and reproduction of native co-flowering focal species (focals), and compared such effect to that of native neighbours (natives). An overall significantly negative effect of aliens on visitation to and reproduction of focals was confirmed. Interestingly, aliens differed from natives in their effect on visitation, but not on reproductive success. The negative effect of aliens on visitation and reproductive success increased at high relative alien plant abundance, but this increase was proportionally lower than the increase in relative plant abundance. Likewise, effect of aliens on visitation and reproductive success was most detrimental when alien and focal species had similar flower symmetry or colour. The phylogenetic relatedness between alien neighbours and focals influenced the reproductive success effect size. Results of the phylogenetic meta-analysis were only partly consistent with those of the conventional meta-analysis, depending on the response variable and on whether we controlled for the phylogeny of neighbour or focal species, which calls for special attention to control for species relatedness in this type of review. This study demonstrates the predominant detrimental impact of alien plants on pollination and reproduction of natives, and highlights the importance of phenotypic similarity to the outcome of the interaction.

Keywords

Competition, exotic plants, facilitation, phenotypic similarity, phylogenetic meta-analysis, phylogenetic relatedness, plant abundance, plant–plant interactions, pollination.

Ecology Letters (2009) 12: 716–728

INTRODUCTION

Plant invasions are recognized as one of the major threats to biodiversity, as they may modify different processes which are important for ecosystem functioning (Sala *et al.* 2000; Brooks *et al.* 2004). Information is accumulating about how alien plants interfere with natives in the capture of resources – space, water or nutrients (Levine *et al.* 2003). Much less is known, however, about the ways in which aliens may hamper existing interactions in the communities they invade. Given the fact that alien plants are well integrated into local plant–pollinator webs (Memmot & Waser 2002; Olesen *et al.* 2002; Lopezaraiza-Mikel

et al. 2007; Aizen *et al.* 2008), they can alter the pollination of other plants through their shared pollinators (reviewed in Traveset & Richardson 2006; Bjerknes *et al.* 2007).

Sympatric co-flowering plant species experience interspecific interactions due to pollinator sharing (Armbruster & Herzig 1984; Campbell 1985). Such pollinator-mediated interactions may have negative (competitive), neutral or positive (facilitative) impacts on pollination and, in turn, in the reproductive success of one or both of the interacting species (Rathcke 1983), assuming that changes in pollinator visitation and pollination translate into changes in plant reproduction.

Competition for pollination occurs when a plant species suffers pollen limitation (i.e. produces fewer fruits and/or seeds than it would with adequate pollen receipt; Knight *et al.* 2005) as a result of pollinator sharing. Such competition may result from two processes: (i) competition for pollinator visits occurs when the pollinator visitation to one plant species is sufficiently reduced in the presence of other preferred species so that conspecific pollen deposition is diminished (Campbell & Motten 1985) and (ii) interspecific pollinator transfer occurs when pollinators switch between flowers of different species in floral mixtures, in the process increasing heterospecific pollen deposition and/or decreasing conspecific pollen deposition (reviewed in Morales & Traveset 2008).

Conversely, facilitation of pollination takes place when the presence of a plant species increases the rate of pollinator visitation to and, in turn, the reproductive success of a second species (Ghazoul 2006). Mechanisms by which pollination facilitation may occur include (i) mutually beneficial pollinator attraction strategy based on increased floral visitation to larger collective floral display, which is expected to benefit species occurring at low densities (Schemske 1981; but see Feldman 2008); (ii) increased pollinator visitation to rewardless species due to their proximity to a rewarding species that attracts pollinators acting as a 'magnet' species (Lavery 1992; Johnson *et al.* 2003; but see Lammi & Kuitunen 1995); (iii) increased pollinator numerical response across years in species mixtures (Moeller 2004); and (iv) increased pollinator attraction due to enhanced floral resource diversity (Ghazoul 2006).

Understanding the balance between competition and facilitation in pollination dynamics is relevant to the conservation of plant–pollinator communities (Ghazoul 2006). Recently, a growing number of studies have investigated the outcome of interactions between alien and native plants mediated by pollinators (reviewed in Bjerknes *et al.* 2007). Despite the increasing amount of literature examining the impact of alien flowering plants on native pollination, no quantitative synthesis has been attempted to date. Given the increasing rate of invasion of alien plants (Reid *et al.* 2005), it is important to evaluate the overall effect of invasive alien species on the pollinator visitation to and reproductive success of natives, as well as to examine the factors that modulate this effect. This is the main goal of our study.

Recent studies have highlighted the role of floral abundance and/or floral traits in determining the visitation frequency as well as the number and composition of pollinator visitors at the community level (Hegland & Totland 2005; Morales & Aizen 2006; Stang *et al.* 2006). Furthermore, population size and density, which influence floral abundance, as well as similarity in floral morphologies

with the natives, have been recently proposed as two of the most important properties making aliens strong interactors for pollinators (Bjerknes *et al.* 2007). Here, we explored the influence of these two factors on the outcome of alien–native plant interactions through pollination.

Alien species may occur, as invasive plants, in denser and larger populations than natives (Bjerknes *et al.* 2007). If competitive and facilitative interactions among plants for pollination service are opposite extremes of a continuum which is a function of relative floral density (Rathcke 1983; Feldman *et al.* 2004), the deleterious impact of some alien invasive species on natives' pollination might be simply explained by their propensity to numerically dominate the community (Bjerknes *et al.* 2007). The effect of controlled densities of neighbour and focal species on the pollination of focal plants has been experimentally tested for both alien and native neighbours. We took advantage of these experimental studies to test the influence of relative plant density on the overall effect of alien species on pollination performance of natives.

Bjerknes *et al.* (2007) proposed that aliens with similar floral morphologies as the natives, and/or that are more attractive than the natives, have a competitive advantage in pollinator attraction. Corolla colour is one of the most important floral traits used by pollinators to discriminate among flowers (Menzel & Shmida 1993; Neal *et al.* 1998). In addition, flower symmetry (radial vs. bilateral, also known as actinomorphic and medial zygomorphic, respectively) is also a key trait influencing the perception, processing of information and activity patterns of pollinators (Neal *et al.* 1998). Thus, we evaluated how the phenotypic similarity in these floral traits between alien and native co-flowering species influences the effect of the alien on the pollination of native species.

Since phylogenetic constraints influence floral traits (Schemske 1981), phylogenetic relatedness between plant species is assumed to correlate with their phenotypic and ecological similarity, influencing in turn pollinator-mediated interactions between them. However, the assumption that phenotypic similarity resembles phylogenetic relatedness has been previously inferred (e.g. Memmot & Waser 2002) but rarely tested in the context of plant–pollinator interactions. Hence, we first asked whether phylogenetic relatedness correlates with phenotypic similarity, and subsequently whether phylogenetic relatedness influences the impact of alien species on natives' pollination.

The accumulated knowledge of the mechanisms of interspecific pollination interaction among native species and their consequences for plant reproduction may help us to understand pollination impacts of alien species on natives (Bjerknes *et al.* 2007). Despite the increasing amount of literature on plant–plant pollination interactions, we still know rather little on what kind of outcome prevails in

alien–native interactions through pollination, whether they differ from the better-studied native–native interactions, and what features might facilitate to predict such outcomes. Therefore, our approach in this study has been to compile and summarize all available studies where the pollinator visitation and reproductive success of a focal plant species were measured both in the presence and absence of a second neighbour (alien or native) plant species, and analyse these data by means of meta-analysis.

Phylogenetically related species might share life histories that lead them to have either similar impacts on pollination of co-flowering species, or similar susceptibility to the presence of neighbour species. Therefore, following Adams (2008), we confirmed the validity of some of our results by controlling for the phylogenetic relatedness of the neighbours, on one hand, and of the focal species on the other.

Specifically, our aims in this review were to:

- (1) Test whether there is an overall effect of the presence of alien neighbour plants on pollinator visitation and reproductive success of co-flowering native focal plants, and determine the direction (competition or facilitation) of the overall effect.
- (2) Determine whether the overall effect of alien plants differs from that of native neighbour plants.
- (3) Estimate to what extent plant relative abundance, phenotypic similarity in floral traits, and phylogenetic relatedness between neighbour and focal species, influence the overall effect of aliens, as well as the potential differences with natives.

MATERIAL AND METHODS

Data search

We searched observational and experimental studies that evaluated the effect of the presence of a given neighbour plant species (hereafter ‘neighbour’) on flower visitation frequency (hereafter ‘visitation’), and reproductive success (seed set per fruit or flower or fruit set per flower) of a target or focal plant species (hereafter ‘focal’). Searches were carried out in the electronic databases ISI Web of Science, Elsevier, Scopus, and Blackwell-synergy, using the following combinations of keywords (pollinat* OR visit* OR reproduc*) and (compet* OR facilita* OR interspecific interaction OR plant–plant interaction). We also obtained data from ongoing projects by contacting colleagues, and included our own unpublished records.

We recorded mean, standard deviation (SD) and sample size for each response variable measured on focals growing either in the presence (‘mixed’ treatment) or absence (‘pure’ treatment) of neighbours. Focals (i.e. the species in which response variables were measured) were always native,

whereas neighbours (i.e. the species whose presence and absence gave place to the ‘mixed’ and ‘pure’ treatments, respectively) were either alien or native. Means and SD from published figures were obtained using the DATATHIEF II software (B. Thumers; <http://www.datathief.org>). DATATHIEF is a program to reverse engineer a set of data from a given plot for which one does not have the data in table format. In some cases, authors provided the original data of their published work (See Acknowledgements). By comparing some data estimated with DATATHIEF from published graphs with original data obtained from the authors, we calculated the range of the estimation errors to 0.09–0.66%. Thus, we confidently included data obtained from graphic sources. If any of the required data (mostly information about sample size) were not reported in the published studies, it was obtained by contacting authors, or otherwise the study was excluded from the database.

For each study we also recorded whether it was observational or experimental, as well as the type of experimental approach. In addition, in experimental studies we recorded the plant abundance of focal and neighbour species, when available.

Effect size metrics and criteria for data selection

Because the first step was to obtain an effect size for each single observation, by comparing the response variable means from mixed (presence of neighbour) vs. pure (absence of neighbour) treatments, we selected Hedges’ d as the measure of effect size, which is an estimate of the standardized mean difference that is not biased by small sample sizes (Hedges & Olkin 1985). We chose Hedges’ d rather than the response ratio because some studies showed zero values for visitation frequency and for reproductive success. The individual effect size ‘ d ’ and its associated variance ‘Var (d)’ were calculated for each observation. The highest effect sizes are from those studies showing large differences between treatments and low variability. Positive d values imply facilitative effects of neighbours on focals’ visitation or reproductive success, whereas negative d values entail competitive effects. We adopted the following criteria for data inclusion:

- (1) When the same neighbour (e.g. *Taraxacum officinale*), or the same focal (e.g. *Ipomopsis aggregata*) was studied in different papers, we considered each study as an independent data record.
- (2) Three neighbour–focal pairs were studied by different research groups in different regions and years (*Impatiens glandulifera*–*Stachys palustris*; *Carpobrotus edulis*–*Lotus cytisoides* and *Carpobrotus acinaciformis*–*Cistus monspeliensis*). We included all studies in our data set, except when otherwise indicated.

- (3) When a single study reported results for more than one species pair (e.g. Larson *et al.* 2006), we considered each species pair as an independent data record (Aguilar *et al.* 2006), except when otherwise indicated.
- (4) When the same study or set of related studies reported results for the same species pair for different years, sites, habitat types, or experimental approaches, we randomly selected one observation per species pair, except when otherwise indicated.
- (5) Two studies reported results for different days separately (Jennersten & Kwak 1991; Bell *et al.* 2005). We performed a summary analysis to obtain a single overall effect size and mean study variance from individual effects sizes and study variances of all the daily observations, and used these values as the effect size d and variance $\text{Var}(d)$ for that species pair in further analyses, following Verdú & Traveset (2005).
- (6) In four native–native species' studies, response variables were measured in both species (Waser 1978; Armbruster & McGuire 1991; Jennersten & Kwak 1991; Kasagi & Kudo 2003). In those studies, each species was considered either focal or neighbour in a different observation, and both observations were included, except when otherwise indicated.
- (7) Some studies evaluated the effect of varying plant abundance (i.e. number of individuals) of either neighbours (e.g. Campbell 1985) or focals (e.g. Caruso 1999). We randomly selected one observation per species pair, except when otherwise indicated.
- (8) In two studies (Caruso 2000; Larson *et al.* 2006), conspecific pollen load was the response variable; in such cases, we used this measure as a proxy of visitation frequency (see Aguilar *et al.* 2006).

Predictor variables

For each data record, we first classified the neighbour species as either alien or native. In addition, we compiled information on floral traits that might influence pollinator visits, and can be easily gathered from the literature. We recorded the flower symmetry (zygomorphic or actinomorphic) and colour (yellow, white, blue, purple and pink-red) for each neighbour and focal. Next, we assigned each species pair for each trait separately (flower symmetry or colour) to one of two binary classes (similar or dissimilar), depending on whether or not the neighbour and focal species had a similar or dissimilar flower symmetry or colour respectively.

Our aim was to test the role of floral trait similarity between neighbour and focal on visitation and reproductive success, rather than the role of floral traits *per se* of either neighbour or focal. Therefore, other important floral traits, like the presence of nectar guides, and quantity or quality of

floral reward were not included, because species pairs could not be assigned to binary classes (similar or dissimilar) for these traits. In addition, the quantity and quality of floral reward is often highly context (environmentally) dependent, and also could not often be measured in the same study in which floral traits, pollination and plant reproduction are measured with respect to the observations/experiments.

Data analysis

Both conventional meta-analysis and phylogenetic meta-analysis were performed to assess the effect of neighbour species on visitation and reproductive success of focals. For the conventional meta-analysis, we fitted random-effect models after checking for the existence of heterogeneity of effect sizes among studies. These models assume that studies differ not only by sampling error, but also by a random component in effect sizes between studies called 'pooled study variance'. To test the assumption of normality, on which a meta-analytic procedure is based, normal quantile plots with confidence intervals (CI) were explored, where deviations from linearity indicate deviations from normality (Rosenberg *et al.* 2000). These conventional meta-analyses were run in the METAWIN 2.0 statistical program (Rosenberg *et al.* 2000). CI of effect sizes (d) were calculated using bootstrap re-sampling procedures (999 iterations), except for groups with small sample sizes ($n \leq 10$) in which case bootstrap procedures were not used because they are biased due to resampling from the same small set of values (Bancroft *et al.* 2007). A cumulative effect size was considered significant if the 95% bias-corrected bootstrapped CI of the effect size (d) did not overlap zero (Rosenberg *et al.* 2000). For categorical comparisons (e.g. alien vs. native), we examined the ' P_{random} ' values associated with ' Q_{between} ' statistic, which describe the variation in effect sizes that can be attributed to differences between categories; category membership was randomized for resampling tests (999 iterations).

A continuous analysis was carried out to test the influence of phylogenetic distance between focal and neighbour plant on visitation and reproductive success effect sizes. Phylogenetic distances were calculated using the PHYLOCOM v. 3.41 software (Webb *et al.* 2007), and were logarithmically (\ln) transformed prior to analyses.

We run a Spearman rank-correlation analysis between phylogenetic distance and mean phenotypic distance between the neighbour and focal species. Mean phenotypic distance was obtained averaging phenotypic distances in flower symmetry and flower colour for each species pair. Phenotypic distance in flower symmetry was scored 0 when neighbour and focal had similar flower symmetry and 1 when neighbour and focal had dissimilar flower symmetry. The same was performed for flower colour.

Categorical analyses are among-species comparisons, and species are not independent observations (Maddison 2000). Thus, a phylogenetic meta-analysis was also performed to account for the possible lack of independence resulting from shared evolutionary history. For this, we used the approach recently developed by Adams (2008), with the R software, which takes advantage of common aspects of linear statistical models used by both meta-analysis and the phylogenetic comparative method, thereby allowing them to be analytically combined. The correlation structure generated by phylogenetic history can thus be incorporated directly into the meta-analytic procedure. This approach is innovative as it incorporates for the first time the phylogenetic information directly into the calculations of the meta-analysis itself.

First, for each response variable, we randomly selected a single observation per neighbour species, to account for the phylogeny of neighbours. Next, by using PHYLOCOM v. 3.41 software (Webb *et al.* 2007), we obtained the phylogenetic tree for the neighbour species. We did the same for focal species. We controlled for the phylogenetic history among neighbours and among focals separately, as no software is available yet to incorporate two phylogenies simultaneously. As for the conventional meta-analyses, the status of the species (alien vs. native) was incorporated in each case as our predictor variable.

The phylogenetic covariance among taxa was taken into account and the phylogenetic cumulative effect size was determined. The significance of the phylogenetic cumulative effect size was evaluated through randomization (see Adams 2008). The species' effect sizes and their associated weights were thus randomly assigned to tips of the phylogeny, and the phylogenetic cumulative effect size was recalculated. This procedure was repeated for 9999 iterations, and the distribution of randomly generated cumulative effect sizes was used to evaluate the significance of the observed cumulative effect size. All phylogenetic meta-analyses were performed in R (R Development, Core Team 2006). Computer code for performing a phylogenetic meta-analysis in R, along with an example, is found in the online Supporting Information of Adams (2008).

RESULTS

The data set

Our final data set comprised 40 studies (35 published or *in press* papers, one Doctoral dissertation and four unpublished records; Appendix S1) that evaluated the effects of neighbour species on visitation and/or reproductive success of a total of 57 focal species (Appendix S2). The studies comprised a research period of 32 years, from 1978 to

2009. Since not all studies evaluated both response variables, sample size varies among analyses. Ten studies recorded only visitation, seven recorded only reproduction, and 18 recorded both response variables (Appendix S2). Two related studies recorded one response variable each for the same species pair (Campbell 1985; Campbell & Motten 1985). Additionally, two related studies recorded one response variable each for one species pair, and only visitation for the other species pair (Jennersten & Kwak 1991; Kwak & Jennersten 1991). Finally, a study recorded only visitation for one species pair, and both visitation and reproductive success for the remaining three species pairs (G. Carvalho, unpublished data).

Our data set contained 14 (35%, seven natives and seven aliens) observational studies, 23 (57.5%, 10 natives, 12 aliens and one both) experimental studies, and three studies (7.5%, one native and two aliens) combining both observational and experimental approaches. Fourteen (82.3%) observational studies compared focals growing in sites with contrasting natural abundance of neighbours, whereas only three (17.7%, two natives and one alien) compared focals flowering during seasonal or daily periods of overlap with neighbours vs. focals flowering during non-overlapping periods. Four basic types of experimental studies were represented: (i) in seven studies (27%, four natives and three aliens) potted plants or flowers of neighbour and focal species were arranged in plots; (ii) in five studies (19.2%, one native, three aliens and one both) potted neighbours were added to plots where the focal naturally occurred; (iii) in three studies (1.15%, all natives), potted focals were added to plots where the neighbour naturally occurred; and (iv) in eight studies (30.8%, two natives and six aliens), neighbour plants or flowers were removed from plots. Finally, three studies (1.15%, one native and two aliens) combined two different experimental types. The frequencies of alien and native studies were balanced between observational and experimental studies. Visitation and reproductive success effect sizes did not significantly differ between observational and experimental studies ($Q_{\text{between}} = 0.08$, $P_{\text{rand}} = 0.75$; $n = 58$; and $Q_{\text{between}} = 0.39$, $P = 0.65$, $n = 36$ for visitation and reproductive success, respectively).

Overall patterns of visitation and reproductive success

Visitation

The overall weighted mean effect size of alien neighbour plant species on focals' visitation was negative and significantly different from zero according to the 95% bias-corrected bootstrap CI (Fig. 1a). *P* values associated to the Q_{between} statistic showed that alien and native neighbours significantly differed in their effect ($Q_{\text{between}} = 3.40$, $P_{\text{rand}} = 0.04$), despite CI slightly overlapped (Fig. 1a).

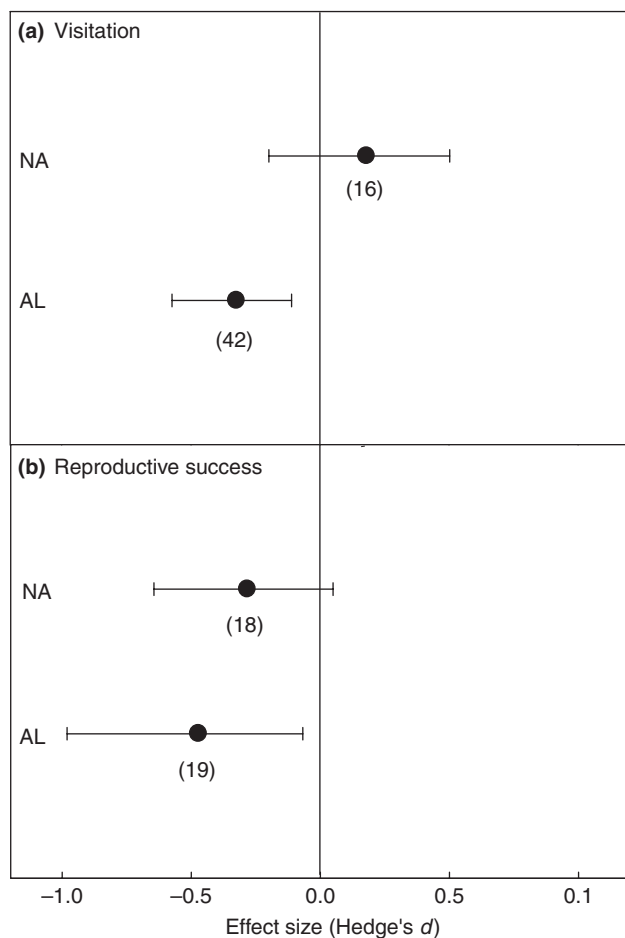


Figure 1 Mean effect size (Hedge's *d*) and 95% bias-corrected bootstrap intervals of the effect of alien (AL) or native (NA) neighbour plant species on visitation frequency (a) and reproductive success (b) of focal plant species. Sample sizes for each category are shown in parenthesis.

Each observation represents a single neighbour–focal species pair per study or set of related studies. Nevertheless, some observations were drawn from the same study, in multiple species studies (Appendix S2), or from the same research group, which might bias the result. Despite a *c.* 50% reduction in the sample size, the results did not qualitatively change when we randomly selected a unique observation per research group [$Q_{\text{between}} = 4.40$, $P_{\text{rand}} = 0.02$; mean effect size: $d = -0.69$; $(-1.15 \text{ to } -0.32)$, $n = 16$ and $d = 0.17$ $(-0.35 \text{ to } 0.56)$, $n = 12$, for aliens and natives, respectively].

In addition, some neighbours were present in more than one species pair (Appendix S2) but, again, results did not change when we randomly selected a single observation per neighbour species [$Q_{\text{between}} = 2.44$, $P_{\text{rand}} = 0.04$; mean effect size: $d = -0.42$; $(-0.90 \text{ to } -0.01)$, $n = 16$ and $d = 0.18$; $(-0.24 \text{ to } 0.49)$, $n = 16$, for alien and natives, respectively].

Reproductive success

The overall weighted mean effect size of aliens on focals' reproductive success was negative and significantly different from zero (Fig. 1b). In this case, however, there were no differences between aliens and natives in their effects ($Q_{\text{between}} = 0.71$, $P_{\text{rand}} = 0.53$). In addition, contrary to the trend found for visitation, mean effect size of natives on reproductive effect size was negative, albeit not significant.

As in the case of visitation, results were consistent when we selected a random observation per research group [$Q_{\text{between}} = 0.65$, $P_{\text{rand}} = 0.52$; mean effect size: $d = -0.55$; $(-1.20 \text{ to } -0.12)$, $n = 14$ and $d = -0.34$; $(-0.78 \text{ to } 0.11)$, $n = 14$, for aliens and natives, respectively] or a random single observation per neighbour species [$Q_{\text{between}} = 1.99$, $P_{\text{rand}} = 0.23$; mean effect size: $d = -0.73$; $(-1.38 \text{ to } -0.17)$, $n = 12$ and $d = -0.34$; $(-0.72 \text{ to } 0.01)$, $n = 17$, for aliens and natives, respectively].

Relative plant abundance

Visitation

We selected the subset of experimental studies where either neighbour or both neighbour and focal species were added [i.e. experimental types (1) and (2)]. In all studies, plot size (area) was similar between treatments; therefore, any change in plant abundance implied also a change in plant density. In most studies, the number of focal plants in mixed and pure treatments was kept constant, and therefore, after addition of neighbour plants, total plant abundance per plot was higher in mixed than in pure plots. The only exceptions were three studies on which, in at least some of the neighbour–focal combinations, the number of focal plants was reduced in the mixed treatment to keep total plant abundance constant between treatments (Waser 1978; Ghazoul 2006; Kandori *et al.* 2009). Seven studies compared visitation and/or reproductive success of focal plants between 'pure' and more than one 'mixed' treatment. These different 'mixed' treatments varied in the number of neighbour or focal plants, resulting in different neighbour-to-focal relative plant abundance. The mean neighbour:focal plant ratio was 0.9 and 1.8 at low and high relative alien plant abundance, respectively. We performed the same alien–native categorical analyses described above. When we randomly selected one observation per species pair in the multiple relative abundance studies, the visitation effect size of aliens did not significantly differ from zero, and differences between categories (alien or native) were only marginally significant ($Q_{\text{between}} = 2.35$, $P_{\text{rand}} = 0.08$; Fig. S1a). When the lowest relative abundance of neighbours was selected, the effect size of aliens did not qualitatively change, and differences between aliens and natives were not significant ($Q_{\text{between}} = 1.42$, $P_{\text{rand}} = 0.13$; Fig. S1b). Lastly, when the highest relative abundance of neighbours was selected, visitation effect size of aliens was

significantly negative, and this effect size marginally differed from that of native neighbours ($Q_{\text{between}} = 3.04$, $P_{\text{rand}} = 0.06$). In this case, the magnitude of the effect of aliens was 1.5 times the magnitude of that obtained when the lowest relative abundance was selected (Fig. S1c). Overall, despite the influence of plant abundance, mean effect size of aliens was always negative whereas that of natives was almost zero.

Reproductive success

When we randomly selected one observation per species pair, only aliens showed a significant negative effect size on focals' reproductive success (Fig. S2a), despite the effect size did not differ from that of natives ($Q_{\text{between}} = 5.00$, $P_{\text{rand}} = 0.14$; Fig. S2a). Results were consistent regardless of whether the lowest or highest relative plant abundance was selected ($Q_{\text{between}} = 1.18$, $P_{\text{rand}} = 0.43$; Fig. S2b; and $Q_{\text{between}} = 4.58$, $P_{\text{rand}} = 0.15$; Fig. S2c respectively).

Phenotypic similarity between neighbour and focal species in floral traits

Visitation

We characterized neighbours by the combination of status (alien or native) and phenotypic similarity (similar or dissimilar) with the focal in flower symmetry or colour. Overall visitation effect size of aliens was significantly negative when flower symmetry was similar to that of focals, whereas such effect was not significant when flower symmetry was dissimilar (Fig. 2a). Categorical analyses showed no significant differences among different categories (alien similar, alien dissimilar, native similar and native dissimilar) ($Q_{\text{between}} = 4.56$, $P_{\text{rand}} = 0.12$, Fig. 2a). The same pattern was found for flower colour (Fig. 2b). However, a categorical analysis and pairwise comparisons (not shown) showed that alien similar to natives significantly differed from alien dissimilar to natives ($Q_{\text{between}} = 8.53$, $P_{\text{rand}} = 0.02$; Fig. 2b). Among aliens with a similar flower colour to natives, yellow flowers were most often represented.

Overall, although phenotypic similarity in floral traits between neighbour and focal species influenced the visitation effect size, the general trend was consistent. Mean effect sizes of aliens were always negative whereas mean effect sizes of natives were positive, albeit of low magnitude (Fig. 2a,b). Results of one-tailed Fisher Exact tests showed that flower symmetry and colour similarity and dissimilarity were equally represented among native and alien neighbours ($P = 0.38$ and 0.48 for symmetry and colour, respectively).

Reproductive success

The negative reproductive success effect size of aliens was significant only when flower symmetry was similar

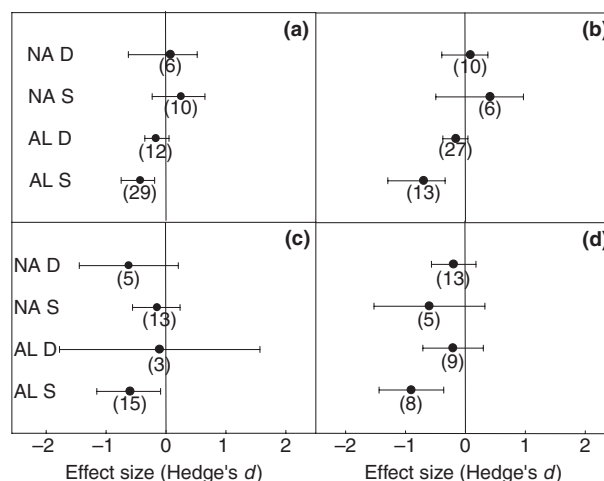


Figure 2 Mean effect size (Hedge's d) and 95% bias-corrected bootstrap intervals of the effect of alien or native neighbour plant species with similar (S) or dissimilar (D) flower symmetry (a, c) or flower colour (b, d) on visitation frequency (a, b) or reproductive success (c, d) of focal plant species. Abbreviations are as specified in Fig. 1. Sample sizes for each category are shown in parenthesis.

to that of focals (Fig. 2c). Nevertheless, categorical analyses showed no significant differences among the four status–symmetry similarity combinations ($Q_{\text{between}} = 4.10$, $P_{\text{rand}} = 0.46$; Fig. 2c). The same pattern was found for flower colour ($Q_{\text{between}} = 7.40$, $P_{\text{rand}} = 0.21$; Fig. 2d).

Overall, although phenotypic similarity in floral traits between neighbour and focal species influenced the reproductive success effect size, the general trend did not change: mean effect sizes of aliens and natives were always negative (Fig. 2c,d). Results of one-tailed Fisher Exact tests showed that flower symmetry and colour similarity and dissimilarity were represented with equal frequencies among native and alien neighbours ($P = 0.35$ and 0.20 for symmetry and colour, respectively).

Phylogenetic distance between neighbour and focal plant species

Visitation

Considering data on visitation, we found that phylogenetic distance between neighbour and focal was positively correlated with mean phenotypic distance ($r_s = 0.43$, $t = 3.51$, $P < 0.01$). However, such phylogenetic distance was not a good predictor on visitation frequency regardless of neighbour status ($Q_{\text{regression}} = 0.45$, $P_{\text{rand}} = 0.50$ and $Q_{\text{regression}} = 0.182$, $P_{\text{rand}} = 0.67$ for alien and native neighbours respectively). A test of homogeneity showed

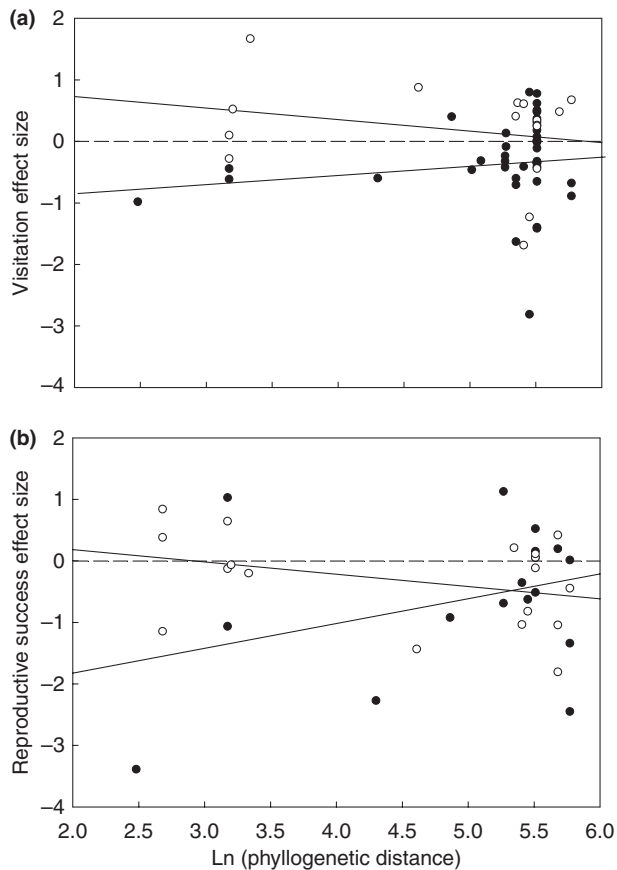


Figure 3 Visitation effect size (a), and reproductive success (b) vs. Ln (phylogenetic distance) for alien (black dots) and native (white dots) neighbour species. Dotted lines show Hedge's $d = 0$. Abbreviations are as specified in Fig. 1. Continuous analysis for visitation: alien slope = 0.16, $P = 0.18$ ($n = 40$); native slope = -0.08 , $P = 0.42$ ($n = 16$). Continuous analysis for reproductive success: alien slope = 0.41, $P = 0.05$ ($n = 17$); native slope = -0.18 , $P = 0.20$ ($n = 18$).

that slopes were similar between alien and natives ($F = 1.84$; $P = 0.18$; Fig. 3a).

Reproductive success

Phylogenetic distance between neighbour and focal species was again positively correlated with mean phenotypic distance considering this data set ($r_s = 0.34$, $t = 2.10$, $P = 0.04$). Interestingly, continuous analyses showed that such phylogenetic distance had a positive effect on reproductive success when neighbours were aliens ($Q_{\text{regression}} = 5.09$, $P = 0.02$), but not when neighbours were natives ($Q_{\text{regression}} = 1.64$, $P = 0.11$). Contrasting differences between alien and native neighbours were confirmed by differences in slopes when performing a test of homogeneity ($F = 4.09$; $P = 0.05$; Fig. 3b).

Phylogenetic meta-analysis

Visitation

Differences between alien and native neighbours on pollinator visits to natives became non-significant (or only marginally significant) when we controlled for the phylogeny of either neighbour or focal species ($P = 0.12$ and 0.08 , respectively). We must also consider that results might also differ slightly when considering both phylogenies simultaneously, something that cannot be performed yet as software is not available for this.

Reproductive success

Results of phylogenetic meta-analysis were consistent with conventional meta-analysis when controlling for the phylogeny of neighbour species, i.e. differences between alien and natives were not significant ($P_{\text{rand}} = 0.12$). On the contrary, these differences were significant when controlling for the phylogeny of focal species ($P_{\text{rand}} < 0.001$). These contrasting results indicate again the need to control for both the phylogenetic history of neighbours as well as of focal species simultaneously.

DISCUSSION

The results of this quantitative synthesis demonstrate for the first time that alien flowering plants overall compete with natives for pollination; thus, in the presence of alien competitors, pollinator visitation as well as reproductive success of native plants tend to decline. An important finding of this review was also to detect that alien and native neighbour plants species differ in their effect on visitation to natives, although these differences are not so apparent when looking at the effect on the reproductive success. The phylogenetic meta-analyses revealed that such effects might slightly differ depending on whether we controlled for neighbours' or focals' phylogenies.

Further, despite the capacity of aliens to usurp pollinators increased with the alien relative abundance, their effect on natives' reproductive success was detrimental even when neighbour and focal plant abundances were similar. Alien species phenotypically similar to natives in floral symmetry and colour are especially unfavourable to natives' pollination and reproduction, and the more closely related the alien and native species are, the more negative is the effect of the alien on the native's reproduction. The diversity of species, habitat types and regions, and the variety of experimental approaches represented in this review suggest that these patterns can be generalized.

We found evidence that aliens draw pollinators away from natives, therefore reducing their reproductive success. The competitive effect of highly invasive alien plants (i.e. those alien species that recruit reproductive offspring in

large numbers, and spread at a considerable rate) has been commonly attributed to their dominance in the community and their associated high relative population size and density (Bjerknes *et al.* 2007). Two independent evidences challenged this view. First, the few studies that used non-invasive aliens, which were not established in the local communities, also found a negative effect of the presence of non-native species on visitation to (Totland *et al.* 2006) or reproduction (Lammi & Kuitunen 1995) of natives. Second, experimental studies at small spatial scales have shown that the overall negative effects of aliens on natives' reproduction occur even when alien and native plant abundances are similar (but see Muñoz & Cavieres 2008). Therefore, although we corroborated that numerical dominance exacerbates the competitive effect of aliens on natives, this attribute does not explain *per se* the consistent negative effects of aliens on visitation to and reproduction of native plants.

As an alternative view, we propose that aliens are superior and more attractive competitors than native co-flowering species on a *per capita* basis. Since visitation frequency has been identified to be strongly correlated with flower size and/or density (Hegland & Totland 2005), and most alien species had bigger flowers (Brown *et al.* 2002; Moragues & Traveset 2005) or inflorescences (Muñoz & Cavieres 2008; Kandori *et al.* 2009), or more flowers per plant (Brown *et al.* 2002; Kandori *et al.* 2009) than native plants with which they interacted, alien populations attract more pollinators than similar sized- native populations.

Despite this higher pollinator attraction, our results do not support the hypothesis of facilitation of pollination due to collective enhanced floral display size. It can be argued that facilitation mechanisms might be less difficult to detect in small scale experimental studies because such mechanisms are more likely to operate at larger spatial scales (Jakobsson *et al.* 2009). However, the significantly negative visitation effect size of aliens persisted when only observational studies at the landscape scale were considered (results not shown). A possible explanation is that aliens are not only more attractive but also more rewarding to pollinators than natives. In a large fraction of the reviewed studies, aliens offered more nectar or pollen per flower (Brown *et al.* 2002), or per capitulum (Kandori *et al.* 2009) than natives, and aliens' nectar tended to be richer (Chittka & Schürkens 2001; but see Kandori *et al.* 2009). Thus, from the viewpoint of the native plant, a potentially higher attraction of pollinators to mixed patches at a larger scale (Jakobsson *et al.* 2009) might not compensate for the usurpation of pollinators by a more rewarding alien neighbour at the smaller scale (e.g. Totland *et al.* 2006).

There are at least four potential explanations for the higher *per capita* attractiveness or reward offer of aliens compared with natives. First, some alien flowering plants are

superior competitors for abiotic resources (Bjerknes *et al.* 2007 and references therein; but see Daehler 2003) or are released from enemies in the invaded regions (Keane & Crawley 2002; but see Agrawal & Kotanen 2003) and, thus, can allocate more resources to floral display and rewards (Bjerknes *et al.* 2007). Second, if pollination is critical to successful establishment (Richardson *et al.* 2000), alien plants with greater floral display and higher reward quantity and quality might be more likely to establish. Third, many alien flowering plants were introduced as garden plants because of their big flowers or large floral displays (Stout & Morales 2009). Fourth, scientists might perceive alien plants with larger floral displays as more threatening to native biota than other aliens with smaller floral displays, resulting in a research bias toward studying alien plants with larger floral displays. A formal test of these hypotheses would be critical to understand which traits lead introduced species to become established and, in turn, potentially threaten the pollination of native plants.

Alien species with a flower symmetry or colour similar to that of co-flowering native species had a significantly negative effect on natives' visitation and reproduction, whereas this effect was not significant when species had a different symmetry or colour. These results indicate that beyond the role of alien plants floral traits *per se*, the phenotypic similarity with native species in floral traits influences the outcome of the interaction. Such pattern is indeed consistent with the predicted character divergence in morphology or colour in plants sharing pollinators, as a way to avoid competition for pollinator visits (Rathcke 1983).

Given that similarity in such floral traits increases the chance of interspecific pollinator transitions (Schemske 1981; Internicola *et al.* 2007), the negative impact of aliens on natives, in particular of those phenotypically similar, may result from a combination of the demonstrated competition for pollinator visits and interspecific pollen transfer (Brown *et al.* 2002; Larson *et al.* 2006; Cariveau & Norton 2009; Kandori *et al.* 2009). Furthermore, since the effect of heterospecific pollen is most deleterious when the donor and the receptor plant species are closely related, this mechanism may explain why the phylogenetic relatedness between alien neighbour and focal species significantly increased the negative impact of neighbours on focals' reproduction, but not on visitation. However, despite the lack of statistical significance, the competitive effect of aliens on visitation to natives tended to increase with phylogenetic relatedness. This relationship may simply reflect the fact that closely related species tend to be more similar in flower colour and/or symmetry, which in turn, greatly influenced visitation effect size.

Overall, our results suggest that alien species which are more similar and closely related to natives are expected to be stronger competitors for pollination. A practical corollary of

our finding is that either phenotypic similarity or phylogenetic relatedness between alien and native flora might actually be a valuable criterion for managers when predicting, and potentially preventing, the impact of invasive alien flowering species. Strauss *et al.* (2006) demonstrated that, among grasses, exotic taxa less related to native species are more invasive, which seems to contradict our finding, and therefore the message to managers might be confusing. Since the impact of exotics on native grasses are mostly expected to be mediated by vegetative interactions, it remains to be tested whether these vegetative interactions are also widespread between alien and native animal-pollinated flowering plants, and, in turn, to evaluate the relative importance of vegetative vs. pollinator-mediated interactions on the fitness of native plants.

This study illustrates the challenge of accounting for phylogenetic relationships among species in meta-analyses. Regarding pollinator visitation, differences in effect sizes between alien and native species vanished when phylogeny of neighbours was taken into account, suggesting a phylogenetic signal for visitation effect sizes. A possible explanation for this finding is that more closely related neighbour species share attributes that make them more prone to usurp pollinators from co-flowering plant species. To predict potentially threatening alien species, we still need to identify which taxonomic groups of plants are stronger competitors for pollinator visits. By contrast, differences in effect sizes between alien and native neighbours persisted when phylogeny of focals was considered, suggesting that the general pattern is robust to the taxonomical identity of focal species and the phylogenetic relationships among them.

Regarding reproduction of focal species, we found no evidence that alien and native neighbours differ in their effect, and this was consistent when accounting for phylogeny of the neighbours. However, this pattern was not robust, as results differed when controlling for the phylogenetic relatedness of focal species, which suggests also a phylogenetic signal in this case. Thus, it would be necessary to account for both phylogenies simultaneously before making a generalization.

In relation to the comparison between alien and native species, our results showed that differences in visitation effect sizes between alien and native's neighbours cannot be attributed to a disproportional representation of aliens with symmetry and colour similar to focals. In addition, results of experimental studies suggest that difference in dominance or plant abundance cannot account for such differences in effect sizes. We propose that the same higher *per capita* attractiveness that may explain the competitive effect of aliens on co-flowering natives also underlies their comparative higher competitive effect in relation to other native neighbour species. Alternatively, the consistent lack of

significant effect of natives on visitation or reproduction of other co-flowering species may also reflect a better balance between facilitation and competition, or, in the case of visitation, a lower statistical power.

Future directions

Despite an overall negative effect size of aliens on native's visitation and reproductive success, there was a high variability not only in the magnitude, but also in the direction (positive or negative) of effect sizes within individual studies. For instance, some studies found no consistent trends among years (e.g. Moragues & Traveset 2005), among target species (e.g. Larson *et al.* 2006) and even between response variables (e.g. Aigner 2004). This highlights the importance of performing long-term and cross-scaled studies to capture this variability. More importantly, both observational and experimental studies should evaluate both visitation and reproduction simultaneously before concluding a facilitative or competitive effect on native plant reproduction solely based on observed changes in visitation.

Moreover, future studies aimed at unraveling the underlying mechanisms governing plant–plant interactions via pollination, in particular the role of competition for pollinator visits and interspecific pollen transfer, should consider changes not only in visitation and reproduction, but also on conspecific and heterospecific pollen deposition (Morales & Traveset 2008).

Small-scale experiments showed that pollinator usurpation by aliens increased at high relative alien plant abundance and density. Both abundance (number of individuals) and density (inter individual spacing) are correlated in this kind of experiments, but they represent different aspects of local abundance with sometimes contrasting effects on plant pollination (Mustajärvi *et al.* 2001). Therefore, studies that can separate the effect of number, distance, and area will help to build a conceptual framework that can integrate studies performed at different spatial scales, or that combine different relative abundances of focal and neighbour species.

Finally, pollinator-mediated interactions do not occur in isolation. Alien plants have been shown to compete for light, other resources, as well as for space with native species. Therefore, studies that test the relative importance of these different factors will provide the best ecological insights.

Concluding remarks

Our finding that phenotypic matching and phylogenetic relatedness between aliens and natives influence the competitive effect of the former on the latter contributes

towards increasing our ability to predict which native plant species in a given plant community might be more prone to suffer reduced pollination in the presence of an alien plant, on a case-by-case basis. In addition, our results suggest some potential consequences of recent findings showing that after integrating in plant–pollinator webs, invasive alien species usurp ‘links’ between native mutualists that previously interacted through pollination (Aizen *et al.* 2008). This study shows that this usurpation of interactions is happening at the expense of the pollinator visitation to native plants, which has detrimental consequences for their reproduction.

ACKNOWLEDGEMENTS

We specially thank to C. Caruso, D. Campbell, D. Cariveau, C. Kaiser, D. Moeller, R. Mitchell, P. Aigner, D. Larson, M. Lopezaraiza-Mikel, T. Feldman, L. Cavieres and L. Chittka for providing details about their published studies, and to G. Carvallo, B. Padrón, C. Suehs, and L. Navarro for generously sharing their unpublished records. We are very grateful to M. Verdú and A. Ruggiero for statistical help, and we specially thank D. Adams for his advice and checking the R code for our phylogenetic meta-analyses. We thank to M.A. Aizen, J.M. Olesen, M. Verdú, R. Aguilar, O. Totland, R. Irwin and three anonymous referees for providing many valuable comments to an earlier version of this manuscript, and to A.P. Morales for proofreading the text. This study was partially funded by a travel fund of CYTED, and a post-doctoral fellowship of CONICET (Argentina) to CLM and is framed within project CGL2007-61165BOS financed by the Spanish Ministry of Science and Education to AT.

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SUPPORTING INFORMATION

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

Figure S1 Mean effect size (Hedge's d) and 95% bias-corrected bootstrap intervals of the effect of alien (AL) or native (NA) neighbour plant species on visitation frequency of focal plant species at (a) random, (b) lowest and (c) highest relative neighbour plant abundance. Sample sizes for alien and native categories are $n = 9$ and 7 respectively.

Figure S2 Mean effect size (Hedge's d) and 95% bias-corrected bootstrap intervals of the effect of alien (AL) or native (NA) neighbour plant species on reproductive success of focal plant species at (a) random, (b) lowest and (c) highest relative neighbour plant abundance. Sample sizes for alien and native categories are $n = 9$ and 8 respectively.

Appendix S1 List of studies on data set.

Appendix S2 Plant species, characterization of study system and Hedges' d effect size for visitation and reproductive

success per observation. Authorities, when not provided in the articles, were obtained from Flora Europaea (for Europe), United States Department of Agriculture (for North America), Sistema de Información de Biodiversidad, and Administración de Parques Nacionales Argentina (for South America).

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Editor, Rebecca Irwin

Manuscript received 1 December 2008

First decision made 8 January 2009

Second decision made 3 March 2009

Manuscript accepted 27 March 2009