



Effects of Native and Non-Native Vertebrate Mutualists on Plants

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Abstract: *Extinctions can leave species without mutualist partners and thus potentially reduce their fitness. In cases where non-native species function as mutualists, mutualism disruption associated with species' extinction may be mitigated. To assess the effectiveness of mutualist species with different origins, we conducted a meta-analysis in which we compared the effectiveness of pollination and seed-dispersal functions of native and non-native vertebrates. We used data from 40 studies in which a total of 34 non-native vertebrate mutualists in 20 geographic locations were examined. For each plant species, opportunistic non-native vertebrate pollinators were generally less effective mutualists than native pollinators. When native mutualists had been extirpated, however, plant seed set and seedling performance appeared elevated in the presence of non-native mutualists, although non-native mutualists had a negative overall effect on seed germination. These results suggest native mutualists may not be easily replaced. In some systems researchers propose taxon substitution or the deliberate introduction of non-native vertebrate mutualists to reestablish mutualist functions such as pollination and seed dispersal and to rescue native species from extinction. Our results also suggest that in places where all native mutualists are extinct, careful taxon substitution may benefit native plants at some life stages.*

Keywords: islands, meta-analysis, mutualism, non-native species, restoration, taxon substitution

Efectos de Vertebrados Mutualistas Nativos y No Nativos sobre Plantas

Resumen: *Las extinciones pueden dejar a especies sin socios mutualistas y por lo tanto potencialmente reducen su adaptabilidad. En casos en los que especies no nativas funcionan como mutualistas, la disrupción del mutualismo asociada con la extinción de la especie puede ser mitigada. Para evaluar la efectividad de especies mutualistas de orígenes diferentes, realizamos un meta-análisis en el que comparamos la efectividad de las funciones de polinización y dispersión de semillas por vertebrados nativos y no nativos. Utilizamos datos de 40 estudios en los que se examinó un total de 34 especies de vertebrados mutualistas no nativos en 20 localidades geográficas. Para cada especie de planta, los polinizadores vertebrados no nativos oportunistas generalmente fueron mutualistas menos efectivos que los polinizadores nativos. Sin embargo, cuando los mutualistas nativos fueron extirpados el funcionamiento de las semillas y plántulas aumentaba en presencia de mutualistas no nativos, aunque los mutualistas no nativos tuvieron un efecto general negativo sobre la germinación de semillas. Estos resultados sugieren que los mutualistas nativos no pueden ser reemplazados fácilmente. En algunos sistemas, los investigadores proponen la sustitución de taxón o la introducción deliberada de vertebrados mutualistas no nativos para restablecer las funciones mutualistas como la polinización y la dispersión de semillas y para rescatar de la extinción a especies nativas. Nuestros resultados también sugieren que en sitios en los que están extintos todos los mutualistas nativos, la sustitución de taxón cuidadosa puede beneficiar a las plantas nativas en algunas etapas de su vida.*

Palabras Clave: especie no nativa, islas, meta-análisis, mutualismo, restauración, sustitución de taxón

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Introduction

In recent decades, widespread environmental changes have caused extinction rates to move well beyond normal background levels (Pimm et al. 1995; Brook et al. 2008; Barnosky et al. 2011). As species disappear, the ecological functions they provided may be lost as well, potentially affecting the taxa with which they interacted (Petchey & Gaston 2002; Srivastava & Bell 2009; Anderson et al. 2011). Loss of a critical function may increase the probability of extinction of other species in the community (Hobbs & Mooney 1998; Luck et al. 2003; Zavaleta et al. 2009). Such cascading effects may arise when lost functions include mutualistic services such as pollination or seed dispersal (Bond 1994; Rezende et al. 2007; Hansen et al. 2008).

Because mutualisms provide reciprocal fitness benefits (Foster & Wenseleers 2006) to the species involved in the relationship, their disruption can reduce the fitness of species (Kiers et al. 2010; Traveset & Richardson 2011). Reproductive declines following extirpation of mutualists have been observed, for example, for mammal-dispersed trees in Thailand and central Africa (Brodie et al. 2009; Vanthomme et al. 2010), bird-dispersed plants in Australia and Hawaii (Moran et al. 2009; Chimera & Drake 2010), and bat-pollinated plants in the South Pacific (Cox et al. 1991). In some systems, non-native species have been observed acting as pollinators and seed dispersers for native plants (e.g., Foster & Robinson 2007; Pattermore & Wilcove 2011). Non-native species have become integrated into many mutualistic networks (Richardson et al. 2000; Olesen et al. 2002; Traveset & Richardson 2006), but the degree to which species' origins affect their capacity to provide mutualistic functions is debated (Aizen et al. 2008; Davis et al. 2011; Traveset & Richardson 2011).

In systems where cascading extinctions resulting from mutualism disruption appear likely, introduction of non-native species that are functional analogues of an extirpated species has been proposed as a way to restore mutualist processes (Griffiths & Harris 2010; Kaiser-Bunbury et al. 2010; Parker et al. 2010) and is known as "taxon substitution" (Atkinson 2001). Recent taxon substitutions have been implemented under controlled conditions in Mauritius and in the Galápagos (Griffiths & Harris 2010; Knafo et al. 2011). However, deliberately introducing non-native species to a new area has substantial risks. Invasive species in many regions were originally introduced to provide ecological functions such as erosion control (Underwood et al. 2007; Pearce & Smith 2008) and biological control (Howarth 1991; Simberloff & Stiling 1996). Before taxon substitution becomes common practice, we believe existing patterns of interspecific interactions in invasion biology and community ecology should be examined to determine under what circum-

stances non-native species become effective mutualists with natives.

We conducted a meta-analysis of the ability of non-native species to provide effective mutualistic services (pollination or seed dispersal) to native plants. We restricted our analyses to vertebrate-plant mutualists because in general vertebrates are introduced in taxon substitutions (Parker et al. 2010; Griffiths et al. 2011; Knafo et al. 2011) and because declines and extinctions of native vertebrate mutualists are better-documented than those of invertebrates (Dunn 2005; IUCN 2011). Vertebrates are estimated to pollinate 5.6% and disperse the seeds of well over half of all angiosperm genera (Howe & Smallwood 1982; Renner & Ricklefs 1995).

We examined seed dispersal and pollination by non-native vertebrates versus native vertebrates; plant reproductive success in the presence of non-native seed dispersers and pollinators and in the absence of seed dispersers and pollinators; and the number of species with which native and non-native mutualists interact.

The species we examined were in most cases introduced accidentally or for purposes other than taxon substitution. Their mutualistic roles resulted from opportunistic foraging. Thus, these species may be less well associated with local plant reproduction than would vertebrates introduced deliberately as seed dispersers or pollinators. Nevertheless, by synthesizing information on existing interactions and examining factors underlying effectiveness of non-native mutualists, our results provide a baseline that may help prioritize and guide efforts to restore mutualisms.

Methods

We searched ISI Web of Science and Google Scholar for publications (spanning the years 1899–2011) that reported non-native vertebrates as reproductive mutualists for native plants. We used 3 groups of search terms: (1) *non-native, exotic, alien, introduced, invasive, adventive, naturalized*; (2) *bird, mammal, bat, reptile, lizard, tortoise, fish*; and (3) *mutualism, pollination, seed dispersal*. Search strings included one word from each group and all possible strings were used. We used all strings with and without *native*. We searched the reference lists of all relevant papers for additional sources.

All papers included in our meta-analyses reported data on quantitative mutualism effectiveness, by non-native vertebrate species, for pollination or seed dispersal. Furthermore, all papers included quantitative information that allowed us to compare the effectiveness of non-native mutualists with native mutualists or with the absence of mutualism. In only 2 quantitative studies were the effects of non-native pollinators compared with

reproduction in the absence of all pollinators. Due to this small sample size, we did not attempt a meta-analysis of these studies; instead, we summarized the results of these studies.

Metrics of the effectiveness of plant mutualism vary considerably in the ecological literature (Herrera 1987; Schupp et al. 2010). Considering each metric in a separate meta-analysis would have resulted in a prohibitively small number of studies that used any given metric. However, all of the studies we used allowed us to examine the same metric for within-study comparisons (either the comparison between non-native and native mutualists or the comparison between non-native mutualists and mutualist absence). This ensured that our quantitative estimates of effect size were derived only from within-metric comparisons. On the basis of the results of within-study comparisons, we used a common effect metric that allowed us to consider various measures of effectiveness combined. We used the response ratio as a common measure of effect size (Hedges et al. 1999; Rosenberg et al. 2000). For the analyses of non-native disperser or pollinator effectiveness compared with that of natives, the response ratio R was calculated as

$$\ln R = \ln \left(\frac{\bar{X}^E}{\bar{X}^C} \right), \quad (1)$$

where \bar{X}^E is the weighted mean of a specific component of non-native mutualist effectiveness (e.g., average pollen load on captured pollinators) and \bar{X}^C is the weighted mean of the identical component of native mutualist effectiveness. In our comparison of the effectiveness of the presence and absence of non-native dispersers, the response ratio was the natural log of the ratio of the weighted mean of a given component of non-native mutualist effectiveness to the same component in the absence of mutualists.

To assess the relative contributions of each effectiveness metric to overall meta-analysis results, we used categorical analyses to generate separate meta-analysis results for each effectiveness metric with a sample size of ≥ 2 in our data (Rosenberg et al. 2000). Other variables for which we used categorical analyses to explore underlying structure in our data included non-native mutualist class (mammal vs. bird), land type (island vs. continental), and taxonomic match (i.e., whether the non-native mutualist was in the same taxonomic class as the extinct or extant native mutualist). All pollination records were for non-native species in the same taxonomic class as the natives they were compared with, so this categorical variable was examined only for dispersal records. When a study reported mutualism effectiveness for multiple native vertebrate species interacting with the same plant species, we used the mean, weighted by sample size, of those reports to generate the denominator of the response ratio.

For approximately one-fifth of the records in our data set, the only metric reported was the diversity of the species of fruiting or flowering plants visited by the non-native mutualist. Although this metric does not provide information relevant to the effectiveness of the mutualism between these animals and each plant species, it provides information on how broadly their effects as introduced mutualists may propagate across the ecosystem. In cases of deliberate mutualist introduction, this diffuseness of effect is a particularly important component of the decision to introduce such a species. Therefore, we included diffuseness in an additional meta-analysis in which we compared the number of plant species with which each non-native mutualist interacted with the diffuseness of native mutualists.

Because studies with larger sample sizes contribute more to overall effect-size estimates in meta-analyses, the reported variances and sample sizes of all included means are used to generate the overall effect size (Rosenberg et al. 2000). For a large number of the studies included in our meta-analyses, however, the variances in effectiveness were not included. This was particularly common when diffuseness or percentages (e.g., percentage of all visits recorded to a plant or percentage of seeds germinated) were reported. These values were generally provided as direct counts. To allow inclusion of the results of these studies in our analyses, we performed unweighted meta-analyses (after Johnson & Curtis 2001). This method assigns a common weight (1) to all studies and bases calculations on sample sizes and mean effect sizes. However, certain species of non-native vertebrate mutualists occurred in multiple records because they interacted with multiple native plant species within a given study or because they appeared in multiple studies. To control for this potential bias, we conducted the overall meta-analyses at both the record and the species levels (Roberts et al. 2004). For species-level analyses, we calculated a single effect size for each species as the weighted average of all effect sizes for that species in the data. This reduced the number of records per meta-analysis and hence the analyses' power, but enabled examination of overall trends without potential bias toward more common species.

We calculated effect sizes, total heterogeneity or underlying data structure (Q_T), and between-group heterogeneity (Q_B) with a random-effects model in MetaWin 2.0 (Rosenberg et al. 2000). We evaluated significance of heterogeneity and significant differences between mean effect sizes for explanatory variables by calculating Bonferroni corrected p values. We generated 95% bias-corrected bootstrap confidence intervals around mean effect sizes by resampling with 5000 data randomizations because data randomization provides robust results when data are not normally distributed and this method is recommended for meta-analyses (Rosenberg et al. 2000). For ease of interpretation, we back-transformed all means

and confidence intervals to ratios of non-native to native mutualist effectiveness. After back-transformation, effect-size means and confidence intervals <1 signified that the effect of non-native mutualists was significantly less than that of native mutualists or mutualist absence, whereas effect-size means and confidence intervals >1 signified that the effect of non-native mutualists was significantly greater than native mutualists or mutualist absence. Confidence intervals encompassing 1 indicated there was no significant difference between non-native mutualists and native mutualists or mutualist absence.

In addition, we used Rosenberg's (2005) fail-safe calculations to determine the number of additional studies with nonsignificant results that would be required to reduce the overall significance of each of our meta-analyses to $\alpha = 0.05$. The fail-safe calculation addresses the potential of a file-drawer problem in a meta-analysis (i.e., nonsignificant results unreported and therefore the effect size may be artificially inflated by considering only published studies) (Rosenberg et al. 2000). A Rosenthal fail-safe calculation result of at least $5n + 10$ (where n is the original number of records) is an indicator of reliable meta-analysis results, whereas smaller fail-safe numbers imply that meta-analyses results are less robust (Rosenberg 2005).

To consider the environmental effects associated with non-native mutualist introductions, we examined the literature for records of negative environmental effects associated with each of the most common non-native mutualists in our data set (those appearing in >3 studies). We conducted our literature search in Google Scholar and Web of Science (1899–2011) and used as search strings the full scientific names of each non-native mutualist species.

Results

We found 40 publications with enough quantitative information to include in our meta-analyses (Supporting Information). These studies examined 34 unique non-native vertebrates acting as pollinators or seed dispersers (Supporting Information). Our data contained 74 unique records, and each non-native species in each study was a separate record. Pollination mutualisms were represented by 18 records from 9 studies, and 56 records from 31 studies concerned seed-dispersal mutualisms. Our data set included 1 non-native reptile, 15 non-native mammals, and 18 non-native birds (Supporting Information). Studies we included had been conducted in 20 geographic areas, 11 of which were islands (Fig. 1). In all, 13 different metrics of mutualism effectiveness were used, including 5 pretransport metrics (quantitative components of pollination and seed dispersal before propagule transport, for example, number of visits), 7 post-transport metrics

(quantitative components of pollination and seed dispersal following propagule transport, for example, number of seeds deposited), and number of plants interacting with pollinators or seed dispersers (Supporting Information). One study (Griffiths et al. 2011) reported results of a deliberate taxon substitution (giant tortoises [*Aldabrachelys gigantea*]).

Effectiveness of Non-Native Versus Native Mutualists

When the full data set was examined, the overall effectiveness of non-native dispersers was not significantly different from that of native dispersers (Fig. 2a). Heterogeneity of the data was low ($Q_T = 47.67$, $df = 56$, $p = 0.78$), which indicates little structure in the data set. After Bonferroni correction, non-native mutualists were significantly less effective than native mutualists when the taxonomic class of the mutualists differed (either bird or mammal) (Fig. 2a). However, native and non-native mutualists in the same taxonomic group did not differ significantly in effectiveness (Fig. 2a). Effect sizes did not differ significantly between non-native taxonomic groups ($Q_b = 0.07$; $df = 1$; between-group chi-square $p = 0.81$) or by land type after Bonferroni correction (island vs. continental) ($Q_b = 5.89$; $df = 1$; between-group chi-square $p = 0.03$). However, individual effectiveness metrics differed significantly in pattern ($Q_b = 58.98$; $df = 6$; between-group chi-square $p = 0.01$) (Table 1).

As a group, non-native pollinators were significantly less effective than native pollinators (Fig. 2b). Heterogeneity in this meta-analysis was significant ($Q_T = 43.11$, $df = 15$, $p < 0.001$). Fifteen of the records came from either Hawaii or New Zealand. These 2 geographic regions had different effectiveness trends. Non-native pollinators in Hawaii were more effective than native pollinators (Fig. 2b), whereas native pollinators in New Zealand were more effective than non-native pollinators (Fig. 2b). Effectiveness among individual metrics did not differ significantly ($Q_b = 10.26$; $df = 1$; between-group chi-square $p = 0.06$) (Table 1).

Non-native Mutualists in the Absence of Native Mutualists

When the full data set was examined, there was no significant difference in plant reproductive metrics between non-native dispersers and absence of dispersers (mean effectiveness ratio = 0.73; 95% bias-corrected CI 0.57 to 1.02, $n = 27$). However, heterogeneity was significant ($Q_T = 66.73$, $df = 26$, $p < 0.001$), which highlights the widely divergent patterns of effectiveness typical of studies in which measures of seed germination and seedling survival or growth rate are used to evaluate effects of mutualisms. In the absence of native seed dispersers, passage through the gut of non-native dispersers had a significant and negative effect on seed germination (Fig. 2c) compared with seeds that had not experienced gut passage. By contrast, although the sample size was



Location	Country or Island	No. Studies	Non-native Taxa
1	Argentina	2	5 mammals
2	Australia	1	1 bird
3	Azores	1	1 mammal
4	Balearic Islands	1	1 mammal
5	Bonin Islands	2	1 bird
6	Canary Islands	3	2 mammals
7	Chile	1	1 mammal
8	Connecticut	1	1 bird
9	Cook Islands	1	2 birds, 3 mammals
10	Costa Rica	2	2 mammals
11	England	1	1 mammal
12	French Polynesia	1	2 birds
13	Galápagos	1	1 mammal
14	Hawaii	6	6 birds
15	Illinois	1	1 bird
16	Mauritius	2	1 reptile
17	Mexico	2	2 mammals
18	New Zealand	9	8 birds, 2 mammals
19	Oregon	1	1 mammal
20	Spain	1	1 mammal

Figure 1. Geographic locations of published studies identifying non-native vertebrate mutualists of native plants. Numbers of non-native taxa indicate number of unique species examined in each location.

small, non-native seed dispersers had significant and positive effects on seedling survival and growth rate following dispersal (Table 1 & Fig. 2c). When the taxonomic group of the native mutualist and the non-native mutualist differed, seed germination was significantly lower than when mutualism was absent. When the native mutualist and the non-native mutualist belonged to the same taxonomic group, however, there was no significant difference between seed germination or seedling survival in the absence of mutualism and the same metrics in the presence of non-native mutualists (Fig. 2c). Effect sizes also differed by land type. On islands germination was significantly reduced in the presence of non-native seed dispersers (mean effectiveness ratio = 0.58; 95% bias-corrected CI 0.47 to 0.74, $n = 15$), whereas on continents germination was enhanced significantly by non-native seed dispersers (mean effectiveness ratio = 2.42; 95% bias-corrected CI 1.27 to 6.29, $n = 10$).

Two studies examined non-native vertebrate pollinators in the absence of other pollinators. The only

pollinator bird species visiting the Hawaiian endemic *Freycinetia arborea*, whose known native pollinators are extinct, was the non-native Japanese White-eye (*Zosterops japonica*) (Cox 1983). Flowers exposed to birds set fruit, whereas those that were not exposed to birds did not, which suggests *Z. japonica* is the major pollinator of *F. arborea* (Cox 1983). On the basis of seed set and flower damage, Lord (1991) concluded that New Zealand’s kiekie (*Freycinetia baueriana*) is likely pollinated largely by the non-native brush-tailed possum (*Trichosurus vulpecula*) in the absence of its native pollinator, New Zealand lesser short-tailed bat (*Mystacina tuberculata*).

Diffuseness and Fail-Safe Analyses

Non-native mutualists visited significantly fewer native plants than native mutualists (mean effectiveness ratio = 0.35; 95% bias-corrected CI 0.25–0.49, $n = 27$). This pattern held for both pollinators and dispersers (95%

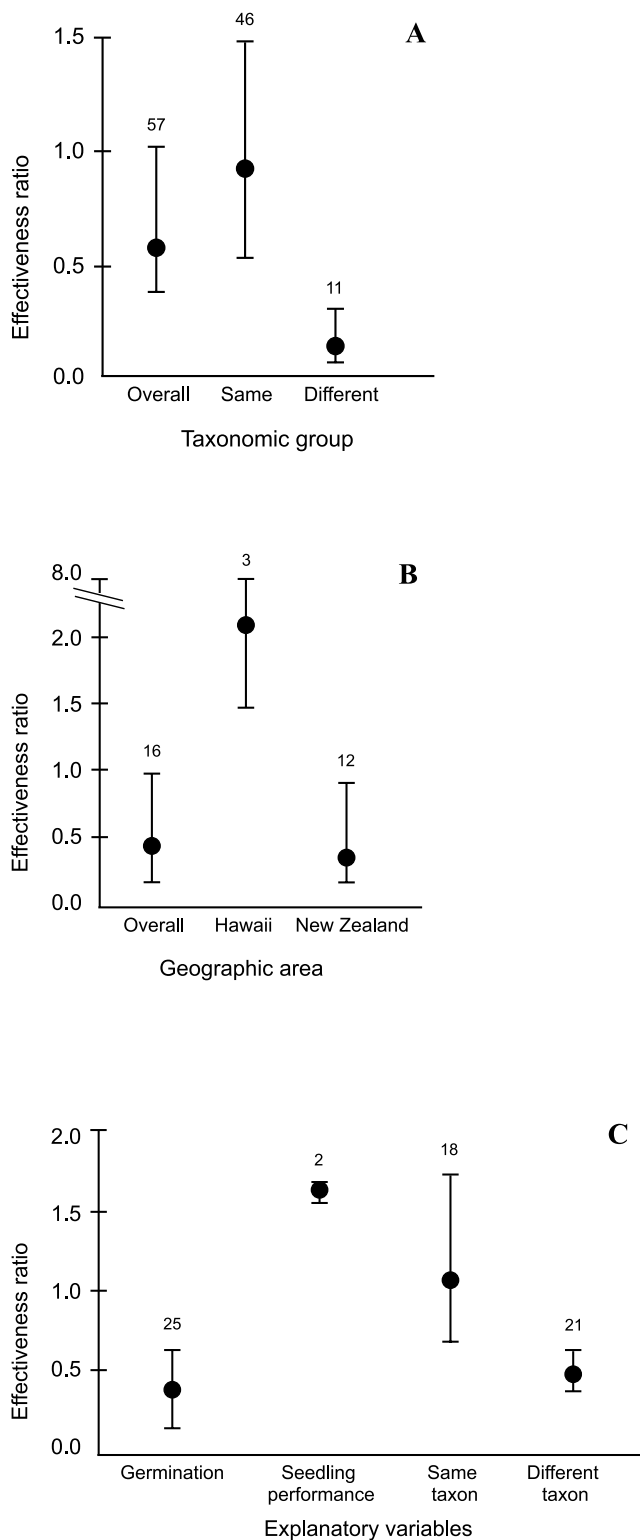


Figure 2. Mean effectiveness ratios (filled circles) and bias-corrected confidence intervals (vertical lines) for studies comparing (a) seed dispersal by non-native mutualists with seed dispersal by native mutualists (categorized by whether non-native and native mutualists were in the same or different taxonomic group), (b) pollination by non-native mutualists with

bias-corrected CI 0.15–0.26, $n = 5$ and 0.29–0.63 $n = 22$, respectively). All available records were for islands and birds.

Fail-safe analyses indicated there was a potential for some of our results to be biased by a tendency to not report nonsignificant results. For pollinators only 48 additional, nonsignificant studies would be necessary to shift the results to a nonsignificant difference between native and non-native pollinators. In the diffuseness meta-analysis, 894 additional nonsignificant studies would be necessary to shift the results to a nonsignificant difference between non-native and absent dispersers.

Repeated Occurrences of Non-Native Species

When we used mean effect sizes for each species so that no species appeared more than once in each meta-analysis, results differed qualitatively from the results of the original meta-analyses. The overall comparison of non-native pollinators with native pollinators, adjusted for multiple records per species, showed no significant difference between the 2 groups (mean effectiveness ratio = 0.42; 95% bias-corrected CI 0.22 to 1.11, $n = 6$). Overall, plant dispersal facilitated by non-native species and native species, adjusted for multiple records per species, did not differ significantly (mean effectiveness ratio = 0.50; 95% bias-corrected CI 0.30 to 1.03, $n = 26$). Overall, seed germination and seedling survival and growth, adjusted for multiple records per species, were significantly lower when non-native species dispersed seeds than when dispersers were absent (mean effectiveness ratio = 0.69; 95% bias-corrected CI 0.53 to 0.99, $n = 16$). Overall comparisons of diffuseness, adjusted for multiple records per species, showed that non-native species visited significantly more plant partners than native mutualists (mean effectiveness ratio = 1.12; 95% bias-corrected CI 1.08 to 1.33, $n = 13$).

Ecological Effects of Non-Native Seed Dispersers and Pollinators

Six non-native mutualists appeared more than 3 times each in our data set (Table 2). Negative ecological effects were reported in the peer-reviewed literature for 5 of

pollination by native mutualists (categorized by geographic area), and (c) seed germination after ingestion by non-native mutualists with germination in the absence of mutualists (categorized by mutualist taxonomic group). Effect sizes are significant if their confidence intervals do not include one. Significant effect sizes <1 indicate non-native mutualists are significantly less effective than native mutualists. Numbers above each confidence interval are sample sizes.

Table 1. Mean effectiveness ratios and bias-corrected confidence intervals for individual metrics of effectiveness of pollination and seed dispersal in meta-analyses of the effectiveness of native versus non-native mutualists.

Meta-analysis comparison	Effectiveness metric (n)	Effectiveness ratio	Bias-corrected CI
Non-native and native dispersers	percent seed germination (16)	0.45	0.31–0.78
	no. seeds dispersed/weight of feces (16)	0.41	0.12–1.33
	time to germination (3)	1.82	1.11–2.33
	no. seeds/individual/day (8)	2.23	0.77–5.39
	percent samples with seeds (4)	4.21	1.18–10.30
	survival of defecated seeds (2)	1.94	1.25–2.95
Non-native and native pollinators	percent plants visited (7)	0.13	0.07–0.26
	visits/plant/hour (10)	0.84	0.27–2.03
	percent plants visited (5)	0.18	0.10–0.35
No dispersal and non-native dispersers	percent seed germination (25)	0.65	0.52–0.85
	seedling performance (2)	1.62	1.58–1.63

these 6 generalist species (Table 2). The only exception was the Chaffinch (*Fringilla coelebs*), which acts as a seed disperser and pollinator of native plants in New Zealand (Kelly et al. 2006).

Discussion

Negative effects of introduced species are well-known (e.g., Traveset & Richardson 2006; Richardson & Pyšek 2008). In recent years, a few articles have highlighted the positive effects of non-native species on native species (e.g., Goodenough 2010; Griffiths et al. 2011; Schlaepfer et al. 2011). The results of these studies underline a growing awareness of the multifaceted nature of species re-assembly driven by species introductions. Overall, we found that non-native vertebrate pollinators already interacting with native plants were generally less effective pollinators than are native vertebrates, although non-native

vertebrate seed dispersers, as a group, did not appear to differ in effectiveness from native seed dispersers. These results strongly support prioritizing the conservation of native vertebrate pollinators because their functions are unlikely to be replaced by non-native species (Traveset & Richardson 2011).

Although it is difficult to derive firm conclusions from our categorical analyses of individual metrics of effectiveness because the sample sizes of each metric were small, differences in mutualist performance were apparent. With native seed dispersers, seed germination was greater and faster than with non-native dispersers, whereas non-native dispersers defecated more seeds and these seeds demonstrated higher survival. Among both seed dispersers and pollinators, native mutualists were associated with higher proportions of visits to individual native plants, which suggests they may be prone to greater partner fidelity or to specialize more closely on individual native plants.

Table 2. Negative effects associated with generalist non-native mutualists.

Species*	Effect	Reference
Chaffinch (<i>Fringilla coelebs</i>)	none reported in peer-reviewed literature	
Common Mynah (<i>Acridotheres tristis</i>)	competition with native fauna predation of native species dispersal of invasive non-native plants wildlife disease or parasite transmission	Peacock et al. 2007
European Blackbird (<i>Turdus merula</i>)	dispersal of invasive plants wildlife disease transmission	Williams 2006; Tompkins & Gleeson 2010
European rabbit (<i>Oryctolagus cuniculus</i>)	herbivory on native plants competition with native fauna increase in abundance of regional predators resulting in hyperpredation of native prey	Jaksic 1998; Lees & Bell 2008
European Starling (<i>Sturnus vulgaris</i>)	dispersal of non-native plants possible competition with natives disease transmission to wild animals	Aslan 2011; Koenig 2003; Linz et al. 2007
Japanese White-eye (<i>Zosterops japonica</i>)	dispersal of non-native plants	Vitousek & Walker 1989

*Each of these species occurred more than 3 times in our data set and interacted with a variety of native plants in a variety of geographic regions.

Specialization and generalization may explain several trends in our results. Overall, non-native mutualist species tend not to have specialized geographic distributions, behaviors, or physical features, such as curved bills (McKinney & Lockwood 1999; Traveset & Richardson 2011; Westcott & Fletcher 2011). For example, our data included livestock and introduced wild species strongly associated with humans (e.g., black rats [*Rattus rattus*] and House Sparrows [*Passer domesticus*]). Such species have been introduced in many regions and have been successful. They also have highly diverse diets and can thrive in a variety of land-cover types (Ehrlich 1989). Mutualisms between these species and native plants are opportunistic and transitory (Richardson et al. 2000; Aslan & Rejmánek 2010). This lack of specialization is likely responsible for reduced effectiveness demonstrated by non-native pollinators relative to native mutualists. Specialization in mutualisms enhances the efficiency of these relations while diminishing the total number of species involved (Schemske & Horvitz 1984). It seems highly possible that ecologically specialized species that are carefully selected for taxon substitution may be more effective pollinators and seed dispersers than generalists.

Careful selection of species for introduction and their deliberate introduction is most likely when all native mutualists are extinct. However, the relation between reproductive success of plants in the presence of known non-native mutualists and in the absence of mutualisms is unclear. The large majority of studies that could be used to compare reproduction in the absence of mutualisms with reproduction via non-native mutualists focused on percent seed germination, which is strongly and significantly lower after passage through the gut of non-native mutualists. Results of another meta-analysis showed that after a seed passes through the gut of an animal seed germination of half of all plant species is affected by endozoochory (gut passage), and germination is reduced for one-third of the species affected by endozoochory (Traveset 1998). In our study, because native mutualists in the relevant studies were extinct, it was impossible to know whether seeds that passed through the gut of native mutualists would also have reduced germination. Furthermore, in most studies that we could use in our analyses, seeds passing through non-native dispersers were compared with seeds from which the flesh was removed by hand. This action confounds the effects of pericarp removal and gut passage. Assessment of germination of whole fruits is necessary to fully understand the effect of non-native dispersers on germination rates (Samuels & Levey 2005).

Most non-native dispersers in our analyses (21 out of 25 records) were mammals. The digestive tracts of nonflying mammals may be more likely to damage seeds than the digestive tracts of birds (Traveset 1998; but see Verdú & Traveset 2004). Because seeds represent unusable ballast with the potential to interfere with flight, it is advantageous for birds to defecate seeds rapidly (Sorensen 1984;

Levey & Grajal 1991) and thus disperse largely undamaged seeds over a more limited distance. Many mammals can, by contrast, disperse a very large number of seeds over very long distances (Willson 1993). Dispersal that removes seeds from their parental neighborhood enhances their ability to escape natural enemies (Janzen 1970; Connell 1971) and on average generates elevated seedling survival (Harms et al. 2000; Wotton & Kelly 2011). With their contrasting dispersal distances and effects on germination, birds and mammals as seed dispersers may have different effects on fitness of plants (Howe 1990).

The results of the few studies we found in which mutualism effectiveness in the absence of native mutualists was examined with metrics other than percent seed germination (seedling survival, seedling growth, and seed set) showed that reproductive success for plants partnering with non-native species was significantly greater than when mutualists were absent, but it is not yet possible to examine global patterns. Germination may have little to do with mature plant populations, especially because many long-lived plants are insensitive to variations in seed survival (Silvertown et al. 1993; but see Brodie et al. 2009). If our results apply across more systems than we examined, native plants partnering with non-natives may have relatively higher seed set and seedling performance but relatively lower percent germination. The contribution of these demographic components to the overall population trajectory of a given plant species depends on species-specific demography (Morris & Doak 2002).

When non-native seed dispersers were from a different taxonomic group than extinct or extant native seed dispersers, their mutualist effectiveness was significantly less than that of native seed dispersers. However, there was no significant effectiveness difference when non-native seed dispersers were from the same taxonomic group as extinct or extant native seed dispersers. These results suggest that taxonomic matching may be important when evaluating non-native species as potential seed dispersal mutualists.

The Role of Islands

Non-native seed dispersers exerted a positive effect on seed germination in continental ecosystems. In contrast, compared with absence of dispersers, non-native seed dispersers had a negative effect on seed germination on islands, where many species are specialists. It is unsurprising that introduced, generalist species are unable to match the mutualism effectiveness of remnant or extinct specialists. All native species we considered specialists (narrow dietary range, curved or large bills, and, among frugivorous birds, large body size) are island species (e.g., Hawaiian honeycreepers [*Drepanidinae*], New Zealand kereru [*Hemiphaga novaeseelandiae*], and Yellow-crowned Parakeet [*Cyanoramphus auriceps*]).

By contrast, both island and continental records contained generalist species (e.g., Japanese White-eye, guanaco [*Lama guanicoe*], and Baird's tapir [*Tapirus bairdii*]). In our data, then, random losses of native vertebrate species from islands may remove specialists, whereas losses on continents may not. Among pollination records, introduced pollinators in New Zealand were less effective than native pollinators, whereas non-native species in Hawaii were more effective pollinators than natives. This again likely reflects the difference between generalist and specialist species. Remnant native birds in Hawaii do not include many of the highly specialized pollinators that once visited Hawaiian flowers (Cox 1983). Both native and non-native birds in Hawaii today have less specialized morphology and behavior than was likely the case in the past (Freed et al. 1987).

Analysis Power

Results of our fail-safe calculation suggested that diffuseness analysis results were robust, but that the significant difference in effectiveness between native and non-native pollinators may be biased by a potential tendency not to report nonsignificant results. The overall effectiveness difference we found may be an artifact of this publishing bias. This would imply that non-native pollinators may be better substitutes than our results show.

Meta-analysis at the species (rather than study) level removed the significant difference between native and non-native pollinators. However, it introduced a significant difference between presence of non-native dispersers and absence of dispersers that increased the importance of reduced percent seed germination to the effectiveness of seed dispersal. Furthermore, the species-level meta-analysis reversed the results of the diffuseness meta-analysis (which indicated non-native species visited significantly more plant species). This suggests that results with the full set of records, in which native species visited significantly more plant species than did non-native species, were driven by a few non-native species that visited a particularly small number of native plants (e.g., Common Mynah [*Acridotheres tristis*], European Starling [*Sturnus vulgaris*], and House Sparrow [*Passer domesticus*]). These tests highlight the context dependence of these mutualisms and emphasize the need for careful study of effectiveness of novel mutualists before taxon substitution.

Taxon Substitution

Non-native species can displace or predate native species, transmit disease, and alter ecological communities (Traveset 1998; Clavero & García-Berthou 2005; Traveset & Richardson 2006). Negative effects on native species populations or diversity have been attributed to all but one of the most generalist non-natives in our study.

When all native pollinators or seed dispersers have become extinct, non-native vertebrates may enhance some native-plant fitness components, such as seed set and seedling survival. Their current rarity makes effective restoration management challenging.

As conservation practitioners seek new and innovative ways to conserve biological diversity, introduction of non-native mutualists to augment functional diversity may become a common conservation strategy, much like biological control (Hansen et al. 2010; Parker et al. 2010; Seddon 2010). We believe the risks of such introductions need to be minimized. Invasion biology is sufficiently well-developed to allow development and rigorous examination of a catalogue of likely risks before introduction of mutualist species. We suggest that deliberate introductions of mutualists be considered only where all native mutualists have been extirpated. Under these conditions, a carefully selected ecological analogue species might be able to provide the mutualistic functions that have been lost (Parker et al. 2010) if thorough screening and rigorous monitoring are applied and demographic studies of plants suggest that the analogue can facilitate ecosystem restoration and conservation of biological diversity. Our results pinpoint factors, such as taxonomic group, taxonomic matching, and specialization, that may influence the effectiveness of mutualist introductions and that may be considered when managers are determining whether to employ taxon substitution.

Control and eradication of non-native species are overwhelmingly beneficial to global biological diversity (Rejmánek & Pitcairn 2002; Howald et al. 2007), and novel mutualisms could complicate such conservation measures. As non-native species form mutualistic relations with native species, the non-native species may in some instances enhance site-specific species diversity. In such cases, eradication of the non-natives could threaten native species that depend on them.

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Supporting Information

The full lists of studies included in our meta-analyses (Appendix S1), non-native species appearing in our database (Appendix S2), and effectiveness metrics (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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