

# Mutualistic Interactions and Biological Invasions

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Annu. Rev. Ecol. Evol. Syst. 2014. 45:89–113

First published online as a Review in Advance on  
September 22, 2014

The *Annual Review of Ecology, Evolution, and  
Systematics* is online at [ecolsys.annualreviews.org](http://ecolsys.annualreviews.org)

This article's doi:  
10.1146/annurev-ecolsys-120213-091857

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## Keywords

belowground mutualisms, invasion facilitation, invasion impacts, invasional  
meltdown, mutualistic networks, pollination, seed dispersal

## Abstract

Mutualisms structure ecosystems and mediate their functioning. They also enhance invasions of many alien species. Invasions disrupt native mutualisms, often leading to population declines, reduced biodiversity, and altered ecosystem functioning. Focusing on three main types of mutualisms (pollination, seed dispersal, and plant-microbial symbioses) and drawing on examples from different ecosystems and from species- and community-level studies, we review the key mechanisms whereby such positive interactions mediate invasions and are in turn influenced by invasions. High interaction generalization is “the norm” in most systems, allowing alien species to infiltrate recipient communities. We identify traits that influence invasiveness (e.g., selfing capacity in plants, animal behavioral traits) or invasibility (e.g., partner choice in mycorrhizas/rhizobia) through mutualistic interactions. Mutualistic disruptions due to invasions are pervasive, and subsequent cascading effects are also widespread. Ecological networks provide a useful framework for predicting tipping points for community collapse in response to invasions and other synergistic drivers of global change.

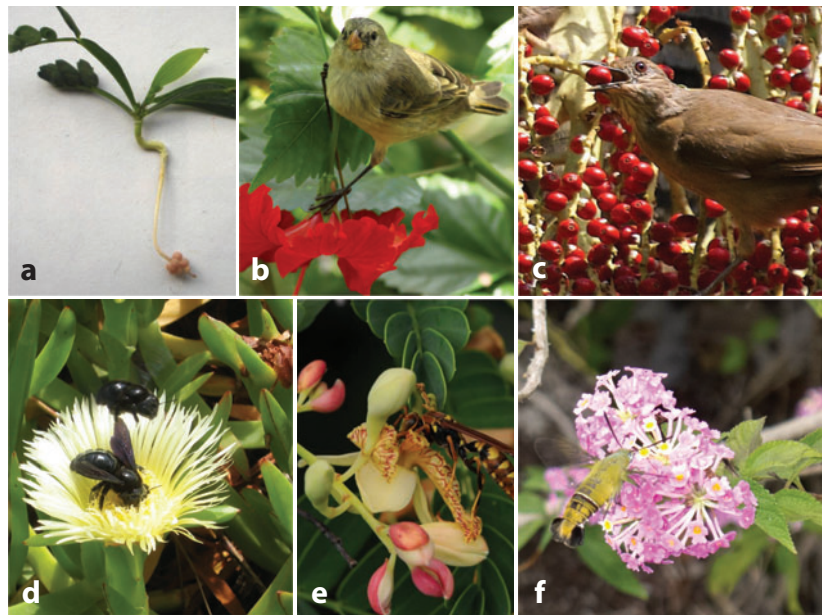
## 1. INTRODUCTION

### 1.1. Importance of Mutualisms in Nature

**Facilitation:** an interaction in which the presence of one species benefits the performance of a second, neighboring species

Every organism interacts with other organisms, and the nature of such interactions is hugely important for the structure and functioning of ecosystems. Among the different types of interactions (facilitative, neutral, antagonistic), mutualisms—i.e., those in which the two or more organisms involved benefit each other's fitness (Bronstein 2009)—are prevalent in all types of ecosystems and play essential roles in determining how communities are organized and how they perform (**Figure 1**). Most organisms are directly or indirectly associated with at least one mutualistic partner, and some are associated with hundreds of mutualists. Mutualistic interactions have driven the diversification of life and were crucial for the colonization of land by plants associated with fungal symbionts (Kiers et al. 2010). Many mutualisms have been shaped and persisted over millions of years of evolution, whereas others have undergone spectacular shifts in partner identities, in specificity over evolutionary time scales, and even in outcomes ranging from mutualism to antagonism (Sachs & Simms 2006).

Compared with other types of interactions, such as competition and predation, facilitation has been given surprisingly little attention by ecologists. However, an increasing number of studies show that positive interactions are at least as important as negative ones in mediating the structure and functioning of ecosystems (Bruno et al. 2003, Kiers et al. 2010). Essential services provided



**Figure 1**

Examples of different types of mutualisms considered in this review: (a) nodule of *Rhizobium* in the alien *Acacia longifolia* in Portugal, (b) *Camarhynchus parvulus* on the flowers of the alien *Hibiscus rosa-sinensis* in Galápagos, (c) *Turdus amaurochalinus* on fruits of the alien palm *Archontopoeonia cunninghamiana* in Brazil, (d) *Xylocopa violacea* on alien *Carpobrotus edulis* flowers in Mallorca island, (e) *Polistes versicolor* on flowers of *Tamarindus indica* in Galápagos (both alien species), and (f) *Cephonodes bylas* on flowers of the alien *Lantana camara* in Seychelles. Photo credits: (a) S. Rodríguez-Echeverría, (b) R. Heleno, (c) P. Jordano, (d,e) A. Traveset, and (f) C. Kaiser-Bunbury.

by mutualists include pollination, seed dispersal, and the constitution of critical components of global cycles of carbon and other nutrients. Other services, such as those between fungi and insects (Frago et al. 2012) or snails (Silliman & Newell 2003) and those between corals and dinoflagellates (Brading et al. 2013), are less known but also important.

Biotic pollination, in particular, is an essential service, because insects and/or other animals pollinate >90% of flowering plants (Ollerton et al. 2011). Approximately 75% of the world's main food crops depend on animals to set fruits (Klein et al. 2007). Biotic pollination is also a key driver of diversification of some major groups of plants and animals (Johnson 2010). Seed-dispersing animals also provide crucial services for plants worldwide. They disperse up to 90% and 60% of plant species in tropical and temperate regions, respectively (Farwig & Berens 2012). This mutualism provides a way of escaping from competing siblings and natural enemies around parent plants, facilitates the colonization of vacant recruitment sites, helps in maintaining genetic diversity, and drives adaptation of plants to changing environments (Traveset et al. 2013b). Moreover, rare long-distance seed dispersal by animals is crucial for population spread and maintenance of genetic connectivity (Trakhtenbrot et al. 2005).

Mycorrhizal or rhizobial symbioses (associations between plants and fungi or bacteria) occur in most terrestrial habitats. Nearly 95% of the world's plant species belong to families that are characteristically mycorrhizal (Pringle et al. 2009). Three types of mycorrhizas exist: arbuscular mycorrhizas, especially common in undisturbed terrestrial ecosystems and formed in approximately three-fourths of all plant species; ectomycorrhizas, more prevalent in woody plants from tropical, temperate, and boreal forests; and ericoid mycorrhizas, which predominate in heathland and boreal habitats (Pringle et al. 2009, Johnson et al. 2013). All three facilitate soil aggregation and carbon sequestration by plants (Wilson et al. 2009). By contrast, a large number of plants are associated with nitrogen-fixing bacteria: legumes with proteobacteria (e.g., *Rhizobium* and *Bradyrhizobium* spp.) and actinorhizal plants with actinomycetes (e.g., *Frankia* spp.). Rhizobial symbiosis occurs in ~80% of legumes (of which there are >19,400 species, including many key crops; e.g., peanuts, soybean). Such belowground associations have a major influence on aboveground processes, such as levels of herbivory and pollination (reviewed in Bardgett & Wardle 2010 and Bennett 2013).

## 1.2. Threats to Mutualisms

Human activities are influencing mutualistic interactions in many ways. The most influential drivers of changes to mutualisms include habitat fragmentation and alterations in land use; modern agricultural practices; the global movement of organisms (including many symbionts) that often translate into biological invasions; and climate change, which can cause temporal and spatial mismatches among mutualists. Interactions among these factors are also important. Mutualistic disruptions often result in declines in species populations, with potentially detrimental consequences for ecosystem functioning. Several good reviews have appeared recently on different aspects of threats to mutualisms. Kiers et al. (2010) identified three ways in which mutualisms can respond to global change: (a) Mutualistic interactions can shift to antagonistic ones under particular situations (e.g., mycorrhizal populations can become less beneficial or even antagonistic to hosts at nutrient-enriched sites); (b) species can switch partners, i.e., forming novel interactions, after species loss or strong alteration of the environment (e.g., they can become more generalized in their interactions); and (c) mutualistic interactions can also be abandoned completely in response to the degradation of entire mutualist guilds, even if the partners are not lost (e.g., insect-pollinated plants can become more dependent on abiotic factors, such as wind or water, or can even become self-pollinated, in response to pollinator declines). These authors stressed the need to consider

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**Anthropogenic**

**change:** modification of ecosystems in response to diverse human activities

**Invasibility:**

the properties of a community, habitat, or ecosystem that determine its inherent vulnerability to invasion

**Invasiveness:** features of an alien organism that define its capacity to invade, i.e., to overcome various barriers to invasion

**Novel mutualisms:**

mutualistic interactions established between an alien species and the species present in the recipient community

**Disrupted**

**mutualism:** changes to the interactions among species that benefit each other

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both ecological and evolutionary perspectives when seeking ways to preserve mutualisms, take into account the scale at which mutualisms need to be conserved and their evolutionary context, determine how changes in the abundance of mutualists influences network structure, and assess whether mutualists change strategies in the face of anthropogenic change. Focusing on seed dispersal mutualisms, Farwig & Berens (2012) reviewed direct (hunting, poisoning for pest control, etc.) and indirect (deforestation, fragmentation, invasions, etc.) threats to seed dispersers, and they identified the dispersers that suffer most (mainly, less mobile species, those with large body size, and those with narrow niche breadth). They proposed testable predictions of the consequences for plant regeneration (changes in the disperser community lead to altered spatial recruitment patterns of affected species), shifts in plant communities (changes in seed dispersal processes influence the genetic makeup of plant populations, potentially diminishing the adaptation potential and enhancing the impact of inbreeding and genetic drift), and declines in ecosystem function (loss of seed dispersers modifies plant diversity and community dynamics, potentially diminishing population sizes of valuable timber species and nontimber forest products). These authors also call for studies at the community level—using a network approach—that consider the role of functional traits (e.g., gape width) in disperser networks under changing environmental conditions. Aslan et al. (2013) summarized the evidence for threats posed by vertebrate extinctions to plants that rely on their services for pollination and/or dispersal. They identified Africa, Asia, the Caribbean, and global oceanic islands as the geographic regions with highest risk of disruption of these mutualisms and estimated that plants that have lost their mutualists are likely to experience high reproductive declines (40–58%). Finally, Johnson et al. (2013) studied the various mechanisms whereby mycorrhizas can respond to different anthropogenic environmental changes, such as CO<sub>2</sub> enrichment, N eutrophication, invasive species, and land-use changes. These authors categorized such responses on the basis of three principles: (a) optimal allocation (host and fungal symbionts optimize resource use through changes in allocation to biomass and associated enzyme systems depending on availability of soil-based resources); (b) biotic context (biotic interactions determine which plant and fungal phenotypes are most efficient at acquiring limiting resources and avoiding losses to antagonistic interactions); and (c) adaptability (the range of genetic variability within plant and fungal populations ultimately determines their potential responses to environmental changes).

### 1.3. Aims of This Review

Focusing on one of the most pervasive and influential anthropogenic changes—biological invasions—we aim to integrate issues relating to mutualistic interactions into considerations of habitat invasibility, species invasiveness, and impacts of invasive species. We first synthesize available information from terrestrial ecosystems to identify the key mechanisms whereby different types of mutualisms can mediate invasions. We then evaluate how invasive species potentially affect mutualistic interactions, combining information from different ecosystems and applying both species-centered and community-level approaches. Invasive alien species do not always have negative effects on mutualisms and can actually act as beneficial partners. We give some examples of invaders that somewhat replace functions lost owing to the extinction of native mutualists, thereby contributing to the maintenance of the other partner. An increasing number of studies have examined the impacts of alien species on mutualistic networks, and we identify the emerging patterns. By altering the composition and abundance of species in communities, invasions offer new insights regarding the strength, resilience, and robustness of mutualistic interactions. Our review, therefore, contributes to a general framework for improving the understanding of novel mutualisms and their implications for pressing conservation issues, such as the management of biological invasions and disrupted mutualisms. Most assessments of impacts of introduced species

have all but ignored the effects on such facilitative interactions (Ehrenfeld 2010, Vilà et al. 2010, Simberloff et al. 2013, Gutiérrez et al. 2014; but see Blackburn et al. 2014). We focus on the three main types of mutualisms involving plants: pollination, seed dispersal, and plant-microbial symbioses. We leave aside protection mutualisms and plant-plant mutualisms, as the links between these and biological invasions have been recently reviewed (Helms 2013 and Valiente-Banuet & Verdú 2013, respectively). This review builds on two previous review papers: Richardson et al. (2000), which discusses how mutualisms enhance invasions, and Traveset & Richardson (2006), which deals with the impact of invaders on mutualisms, and here we report on considerable work done in recent years. We also seek to merge our results with those from the recent reviews mentioned above on other threats to mutualisms.

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**Invasional meltdown:** community-level phenomenon whereby alien species enhance one another's establishment, spread, and impacts

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## 2. MUTUALISMS AS MEDIATORS OF BIOLOGICAL INVASIONS


Alien species must negotiate several biotic and abiotic barriers to colonize, survive, regenerate, and disperse (Richardson et al. 2000). They never arrive with their full suite of mutualists and antagonists; new interactions are thus established in the receiving habitat. Colonization, establishment, spread, and impact of alien species are promoted by resident species through a variety of mechanisms. This section details the mechanisms documented to date. Our main focus is on mutualisms that drive plant invasions, but we also deal with animal invasions that are enhanced by mutualistic interactions with plants. All symbiotic microbiota invasions are mediated by mutualistic interactions with their hosts, and we review only cases that provide evidence for the spread of such microbes. We also touch on the concept of invasional meltdown.

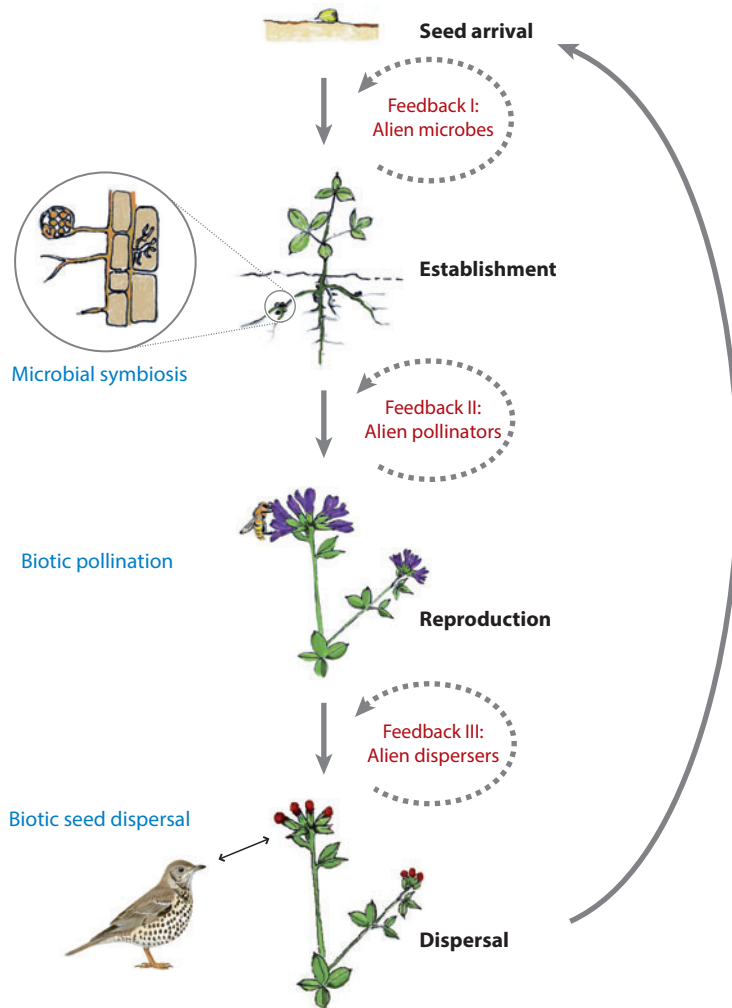
### 2.1. Mutualisms Enhancing Plant Invasions

Mutualisms can be important at all stages of the introduction-naturalization-invasion continuum for plants (Richardson & Pyšek 2012) and at all phases of a plant's life cycle (**Figure 2**). Their importance at each stage depends on the traits and requirements of the invader, mainly (*a*) its ability to establish without symbiotic microbiota, (*b*) its capacity to self, (*c*) its degree of specialized pollination, and (*d*) its capacity to propagate vegetatively and/or disperse abiotically.

**2.1.1. Incidence of symbiotic microbiota in invasive alien floras.** The mechanisms by which microorganisms facilitate plant invasion include the alteration of nutrient uptake, competitive dynamics, successional changes, and/or plant-herbivore interactions to the advantage of the alien species and the detriment of native species. Fewer studies have explored the role of microbial symbionts in invasiveness of alien species and invasibility of communities than have examined other mutualistic interactions. Nonetheless, some generalizations can be made (see also reviews by Pringle et al. 2009, Shah et al. 2009, Callaway & Rout 2011).

A large proportion of successful plant invaders form symbioses with mycorrhizal fungi (Pringle et al. 2009). Well-known examples are introduced conifers in the southern hemisphere, which coinvasioned with alien mycorrhizal fungi (Dickie et al. 2010). However, research seems to have a bias toward certain life forms, such as annual and perennial forbs in grassland ecosystems, as opposed to forests or wetlands (Shah et al. 2009). On some oceanic islands, the invasion of certain plant species was possible only because such mycorrhizas were already naturally present on the islands (Richardson et al. 2000). At least one-third of the world's most widespread invasive woody species (Rejmánek & Richardson 2013) form mycorrhizal symbioses (**Supplemental Table 1**; follow the **Supplemental Material link** from the Annual Reviews home page at <http://www.annualreviews.org>).

 **Supplemental Material**



**Figure 2**

Phases of a plant's life cycle that can be influenced by different types of mutualists. During the establishment phase, a plant can benefit from mutualistic interactions with the soil microbiota (bacteria or fungi). For plants that are biotically pollinated, animals enhance seed set, especially in nonautogamous plants. Later, plants that rely on animals for seed dispersal will benefit from fruit/seed consumption and/or attachment for dissemination (from a few centimeters to several kilometers or, perhaps, even long-distance dispersal events). Alien plant species establish positive interactions with both native and alien partners. In the latter case, three types of positive feedback can occur (potentially leading to invasional meltdown). Note also that a mutualism in a previous phase may influence the outcome of the mutualism in a subsequent phase (e.g., belowground species interactions may have positive/negative effects on those occurring aboveground). Illustration credit: C. Vignolo.

The carbon costs of supporting mycorrhizas are considerable; thus, nonmycorrhizal aliens may have some advantages over those requiring mycorrhizas. However, nonmycorrhizal aliens invade mainly in disturbed environments but are rapidly replaced by mycorrhizal-dependent plants during succession (Richardson et al. 2000). Exceptions of persistent invasions of nonmycorrhizal plants include *Atriplex* spp. in the South African karoo, *Hakea* spp. in South African fynbos, and



*Brassica* spp. in North America. New nutrient-acquisition systems in the form of ectomycorrhizas may also confer advantages to some aliens in these environments. Some ectomycorrhizal plants have in fact invaded certain southern hemisphere systems in which ectomycorrhizas were absent or very rare. In New Zealand, only a few genera (e.g., *Kunzea*, *Leptospermum*, *Nothofagus*) form ectomycorrhizas, and in South Africa, native ectomycorrhizas are absent from many vegetation types. Therefore, all alien plants arriving in these areas and needing this type of symbiosis for their establishment and spread will need introduced mycorrhizal fungi (via airborne spores or spores in soil) to become invasive. The initial establishment of ectomycorrhizas from spores is slow, but once dense plant populations are established, seedlings are very rapidly infected from the fungal network (Richardson et al. 2000). Some alien plants are facultatively arbuscular mycorrhizal; they establish as nonmycorrhizal plants when mycorrhizal inocula are low (for instance, after a major soil disturbance) but associate with mycorrhizas when inoculum levels recover, thus allowing them to outcompete native mycorrhizal species. A loss of mycorrhizal dependence can evolve during invasion, e.g., in *Hypericum perforatum* in North America (Seifert et al. 2009), but it is unknown how widespread this phenomenon is.

Interactions between an introduced plant and resident fungi may promote or inhibit plant spreading, depending on the genotype of both partners and on environmental factors (Richardson et al. 2000). Moreover, the phylogenetic distance between the alien plant and the coexisting natives mediates its integration into the community; aliens more closely related to natives, and with the same or similar adaptations to nutrient acquisition systems, face fewer barriers (Koske et al. 1992; but see Jones et al. 2013 and references therein). For instance, several members of the Ericales—obligately mutualistic with ericoid mycorrhizal fungi—from the northern hemisphere and South Africa are invasive in Australia and New Zealand, probably because this type of symbiosis is not specialized and occurs in the native floras of these areas (Richardson et al. 2000). The association of invasive hosts with generalized rather than specialized fungal taxa has also been predicted to enhance mutualistic responses (Moora et al. 2011). Recent studies have shown that phylogenetically distant mycorrhizal lineages provide plants with complementary resources, which may explain the success of some invasions (Pringle et al. 2009). However, when predicting invasions, we need to consider the net effects of mutualistic microbiota and antagonistic taxa (Callaway et al. 2011). Morrien & van der Putten (2013) suggested that successful establishment of some range-expanding plant species may be related to an accumulation of bacterial and fungal pathogens in the rhizosphere that is lower than what is found for phylogenetically related native species in the invaded range. Plants are frequently involved in complex multitrophic interactions that may differ between invasive and noninvasive alien species. However, Kempel et al. (2013) reported that alien plants use a variety of defense strategies, varying in their interactions with mycorrhizal fungi, but that such multitrophic interactions are not consistently related to plant invasiveness. In another recent study, Bennett & Strauss (2013) showed that alien species are less responsive to landscape variability in soil communities than are native species, suggesting that this may allow them to establish and dominate plant communities in multiple habitats.

Many legumes associated with nitrogen-fixing proteobacteria (e.g., *Rhizobium* and *Bradyrhizobium* spp.) are important invaders in different parts of the world (e.g., *Acacia*, *Cytisus*, *Leucaena*, *Mimosa*, *Prosopis*, *Robinia*, *Ulex*). Except for a few cases (Rodríguez-Echeverría et al. 2011), no barriers to establishment exist for most legumes in new areas (Birnbaum et al. 2012). Most show high levels of nodulation in invaded ranges, indicating either that effective rhizobia are widely distributed between continents and/or that many legumes can nodulate with a wide range of rhizobia strains (Rodríguez-Echeverría et al. 2011, Ndlovu et al. 2013). For some invasive legumes, however, novel mutualisms appear to be less effective in terms of nodulation, nitrogenase activity, and plant growth than the interactions of plants and bacteria of the same origin (Rodríguez-Echeverría

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**Phylogenetic distance:** time since divergence from the most recent common ancestor of two species

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et al. 2012). Other studies have shown that alien legumes may become invasive by using alien microsymbionts (Rodríguez-Echeverría 2010). The degree of specialization in the plant-rhizobial mutualism and the variation in the response to different potential symbionts are crucial factors for understanding the process of invasion by alien nodulating plants and the consequences for the native resident plants and bacteria (Rodríguez-Echeverría et al. 2012).


Regarding actinorhizal plants, some species (e.g., *Casuarina* spp.) need specific *Frankia* bacteria strains to establish and become invasive. By contrast, others (e.g., *Alnus* spp., *Elaeagnus* spp.) are not selective in their use of such symbionts (Richardson et al. 2000). Actinorhizal plants, much used in restoration, are typically early-successional species on nutrient-poor soils and are widely cultivated outside their native ranges.

Because of the tight interdependence of plant-bacteria mutualistic interactions, a microevolutionary shift in one partner, due to changing abiotic conditions, may cause a parallel shift in biotic selection on the other (Thrall et al. 2007). The heterogeneity in abiotic conditions across environments can generate mosaics in the outcome of the mutualism for either partner; for example, mutualisms may be more important in low-quality environments (Porter et al. 2011). The adaptive divergence across habitats in coinvasive partners colonizing heterogeneous landscapes is now beginning to receive attention, and interesting results are likely to emerge soon.

**2.1.2. Incidence of self-pollination in invasive alien floras.** Baker (1955) predicted that selfing and unspecialized pollination systems should promote invasiveness in introduced plants by assuring reproduction, mostly when mates and pollinators are limiting (also see Barrett 2011). An increasing number of studies are reporting positive associations between selfing ability and invasiveness (Burns et al. 2011, Pyšek et al. 2011, Rodger et al. 2013), although little quantitative information is available on the breeding system and pollination requirements of most alien plants, even for the most invasive species (Barrett 2011). Approximately 66% of Canadian weeds are facultatively selfers, whereas approximately 56% of the invasive alien woody plants in North America are apparently outcrossers (Richardson et al. 2000). A study of 17 invasive alien plant species in South Africa using controlled pollination experiments showed that all were either self-compatible or apomictic and that 72% were capable of autonomous selfing (Rambuda & Johnson 2004). A survey in Missouri, USA, found a similar pollination ecology and degree of autogamy between 10 closely related pairs of native and alien plant species, although of those that differed, the alien species were more autogamous than were their native congeners (Harmon-Threatt et al. 2009). Lastly, the frequency of self-pollination of the alien flora of Central Europe increases along the introduction-naturalization-invasion continuum, suggesting a pivotal role for breeding systems in successful invasions (Pyšek et al. 2011).

Notable cases of highly successful aliens that are mostly selfers include *Alliaria petiolata*, *Bromus tectorum*, *Carpobrotus edulis*, *Hypericum perforatum*, and *Mesembryanthemum crystallinum* (Richardson et al. 2000). However, other notable invaders that are obligate outcrossers (e.g., owing to self-incompatibility or dioecy, or if self-compatible, not capable of autonomous self-pollination) are *Centaurea diffusa*, *Centaurea maculosa*, and *Lytbrum salicaria* in North America as well as *Trifolium pratense* in New Zealand. Almost all of the world's most invasive woody plants are visited by animals and are likely to be biotically pollinated (**Supplemental Table 1**). Whether outcrossing is facultative or obligate will remain unknown for most invasive species until experimental studies are carried out.

Self-pollination assures reproduction. However, it can also have negative consequences for plant fitness because it tends to promote inbreeding depression. This needs to be considered when assessing the demographical advantages of selfing for an invader. Unfortunately, there are very few investigations on this subject for alien species (but see Rodger et al. 2010, 2013; Ward

 Supplemental Material




et al. 2012; Mullarkey et al. 2013). Studies of plants in the native range have shown that selfing ability and inbreeding depression vary among life forms. Woody plants, and trees in particular, are predominantly self-incompatible but show high levels of inbreeding depression, whereas herbs are much more variable in both traits (Rodger et al. 2013; but see Robertson et al. 2011). This suggests that, even if trees are not limited in terms of seed production, seeds from inbred individuals will be of lower quality than those from outbreeding individuals. This may explain why trees generally have outcrossing rates higher than those of herbaceous plants. However, we also need to consider that, compared with selfers, plant outcrossers may actually be more vulnerable to inbreeding depression because the phenotypic effects of recessive maladaptive alleles are rarely exposed with outcrossing, whereas such alleles have been purged in frequent selfing populations (Dart & Eckert 2013).

**2.1.3. Incidence of specialized pollination in invasive alien floras.** The prevalence of highly generalized pollinators in most communities may partly explain why pollen limitation is not important for most plant invaders. Figs are the best-studied case of pollinator-mediated constraints on invasion: several alien *Ficus* species spread in new habitats only after their specific wasp pollinators have arrived. However, at least for some species, the dependency on wasps may not be as strong as previously thought (Richardson et al. 2000).

Because the assemblage of pollinators visiting an alien plant species is partly explained by the phylogenetic distance (affinity) of that species with the native flora (Memmott & Waser 2002), specialist alien species will likely be visited by those generalist natives with some taxonomic affinity to their original mutualists. For example, the European native *Cytisus scoparius*, with zygomorphic flowers specialized for bumblebee pollination, is almost exclusively visited by native and generalist bumblebees in the invaded range in South America (Morales & Aizen 2002). Alien plants pollinated by birds in their native ranges are also usually well served by birds in their invading areas (Richardson et al. 2000, Geerts & Pauw 2009). However, many alien plants thought to be highly specialized in their native range have acquired completely new types of pollinators. For example, *Fuchsia magellanica* and *Nicotiana glauca*, pollinated by birds in South America, are visited by generalist insects in Europe (A. Traveset, personal observations).

Although more experiments are needed to elucidate the role of pollen limitation in alien plants, most alien plants are readily integrated into pollination networks and are serviced by either native or alien pollinators (see Section 4.1). We also predict that plant invaders should be more pollen limited in the tropics than in temperate zones, because of the significant positive relationship between pollen limitation and plant species richness (Vamosi et al. 2006).

**2.1.4. Incidence of animal-mediated dispersal in invasive alien floras.** Many alien plants rely on animal dispersers (Richardson et al. 2000). Compared with abiotic dispersal, such dispersal vectors have the added advantage of often moving seeds to sites that are nutrient enriched, disturbed, or otherwise favorable for germination and seedling establishment. A preliminary survey by Cronk & Fuller (1995) of ~200 invasive species showed that 25% were dispersed by birds, 14% by mammals, and 1% by ants; 45% had no obvious adaptations for animal dispersal, whereas the dispersal mode of 25% of the species was unknown. Other studies have shown that fleshy-fruited alien plants in many parts of the world benefit from mutualisms involving a wide range of animals with no previous experience of dispersing their seeds, just as in the case of quickly emerged pollination mutualisms. At least two-thirds of the most widespread invasive woody plants have fleshy fruits or produce other structures to attract animal dispersers (**Supplemental Table 1**). However, the large majority (>90% of those for which information is available) of those plant invaders can propagate vegetatively and, thus, are not dependent exclusively on animals to spread.

 [Supplemental Material](#)

As with biotically pollinated plants, animal-dispersed alien plants are usually readily integrated into dispersal networks by generalized dispersers. Frugivorous vertebrates, specifically, are often highly generalized, with wide food niches even in insular ecosystems due to resource limitation. Much evidence now exists to show that alien fleshy-fruited species have no constraints in being dispersed by either native or alien dispersers (Padrón et al. 2010, Farwig & Berens 2012, Heleno et al. 2013a), although we have very little quantitative data on the effectiveness of such new dispersers. Invertebrate dispersers, mainly ants, can also play an important role in propagating the invasion of alien plants; despite moving seeds over short distances, such invertebrates can be crucial for plant survival (Richardson et al. 2000). Some species that are considered typical seed predators (e.g., seed-caching rodents, granivorous finches, cockatoos) can also be effective dispersers and facilitate the invasion of alien species (Richardson et al. 2000, Heleno et al. 2013a). Carnivorous predators, which often eat fruit, and even raptors can also facilitate invasions (Richardson et al. 2000, Traveset & Riera 2005, Padrón et al. 2010). Some plant invasions occur as a result of the long-distance dispersal of alien seeds transported by animal species, such as gulls, pigeons, or stranded migrating birds (Nogales et al. 2012). Excessive long-distance dispersal of elements alien to ecosystems is considered an important threat to global biodiversity (Trakhtenbrot et al. 2005). An illustrative example of how a plant-seed dispersal interaction may drive an invasion comes from an arid savanna in South Africa where alien fleshy-fruited plants readily infiltrate prevailing seed dispersal networks (Milton et al. 2007). The entire system is then disrupted when the invasive plants suppress native trees that act as crucial perch sites and foci for directed dispersal (Iponga et al. 2008).

## 2.2. Mutualisms Enhancing Animal Invasions

Although several types of mutualisms contribute to the success of animal invasions, this aspect has received relatively little attention, and almost nothing is known of the link between animal population densities and the availability of mutualist-derived resources. A good example of how mutualisms can drive an animal invasion is provided by the establishment and spread of the fire ant (*Solenopsis invicta*). This species benefits from its mutualistic interaction with honeydew-producing Hemiptera (and other carbohydrate-producer organisms), which raises its competitive performance (Wilder et al. 2011). Although we know of no reported cases of specific plant partners promoting the invasion of a pollinator or seed disperser, available evidence from several studies shows that some alien animals have spread in a region feeding on the same flower or fruit resources as closely related native animals. At least 15% of the alien insects reported from the Galápagos archipelago visit native flowers for pollen and nectar (Traveset et al. 2013a); their invasion success is probably dependent mainly on the generalized mutualistic interactions they establish with plants.

Available data on the diets of invasive alien dispersers also indicate that plant resources, such as fleshy pulp and seeds, are likely to be important for the establishment and invasion success of such dispersers in the new areas. The colonization and naturalization of alien birds in many oceanic islands, for instance, have balanced the large proportion of lost native frugivorous avifauna, causing regional avian species richness to remain fairly constant (Cheke & Hume 2008). Many alien birds depend on fruits for food and are effective dispersers of native plants. In Hawaii, the Bonin Islands, and New Zealand, alien birds feed on many native fruits and, to some extent, replace extinct native dispersers (Foster & Robinson 2007, Kawakami et al. 2009, García et al. 2014). In the Balearic Islands, the spread of some alien carnivorous mammals appears to have been enhanced by their capacity to consume fruits of many species, particularly when animal prey is scarce (Traveset et al. 2012).

### 2.3. Mutualisms Enhancing Microbe Invasions

Alien microbes are usually unintentionally cointroduced with forestry tree seedlings or potting medium; this introduction pathway seems to be more important than inoculation programs (Jairus et al. 2011). Alien microbes can face strong challenges to establishment in novel habitats, including abiotic stresses in the soil, competition with other soil biota, and the need to secure access to hosts at adequate densities to maintain viable soil populations (Porter et al. 2011). For instance, owing to their preferential allocation of photosynthate, host plants differentially promote certain arbuscular mycorrhizas (Pringle et al. 2009). An increasing number of studies document positive-feedback processes between soil microbiota and plant species that influence plant invasion success and resistance to invasion (Zhang et al. 2010). Moreover, the capacity of microorganisms to shift hosts in the introduced range and become invasive may also vary among regions. This has been demonstrated for ectomycorrhizal fungi associated with Australian eucalypts in south-central Africa; the Australian fungi do not show host shifts when cointroduced with the eucalypts, whereas the African fungi commonly do in mixed plantations where roots of different trees intermingle (Jairus et al. 2011). Thus, the introduced Australian fungi have naturalized but have not yet become invasive, although they may do so in the future after further adaptation to host trees and soil environment.

An emerging research field deals with the study of novel plant-microbe-insect interactions that are being established as new taxa in these groups are introduced to ecosystems (reviewed by Bennett 2013). Many novel plant-microbe-insect interactions are synergistic (nonadditive) and promote the invasion of several species (plants, insects, or microbes) with potentially dramatic consequences for native and agricultural systems. Mutualistic soil microbes, mostly arbuscular mycorrhizas, influence plant defense against herbivores in invasive plant species and may also affect their pollinating insects. Similarly, invasive insects can be subject to additive, synergistic, and antagonistic interactions with plants and microbes. Less evidence exists regarding cases in which insect interactions help invasive microbes to overcome the influence of negative plant interactions or cases in which positive plant interactions allow invasive microbes to overcome a negative interaction with insects. All these interactions merit further study.

### 2.4. Invasional Meltdown

Simberloff & von Holle (1999) coined the term “invasional meltdown” for the phenomenon whereby two or more introduced species facilitate the establishment and/or spread of each other (and potentially other species). This contributes to increased invasibility and accelerated invasion rates and to a synergistic amplification of the disruptive effects of invasive species. Positive interactions among invasive species are frequently documented, especially plant-pollinator and plant-seed disperser interactions. Even though the invasional meltdown hypothesis has been controversial (Simberloff 2006, Green et al. 2011), a growing number of studies have documented strong positive feedback between invaders that amplifies their impacts (Gaertner et al. 2014). Coinvasions of plants and their mutualist fungi (Dickie et al. 2010) or bacteria (Rodríguez-Echeverría 2010) represent clear cases of invasional meltdown.

Facilitation among invasives involving vertebrates (pollinators or dispersers) has been reported in different types of ecosystems, especially islands (Traveset & Richardson 2006). Invasion complexes are probably more common and influential on islands where ecosystems are simpler than they are on mainland, but more work is needed to test this hypothesis. Wild boar and deer on Isla Victoria (Argentina) enhance the invasion of alien pine trees by dispersing via their feces the ectomycorrhizal fungi needed for the establishment of the pines (Nuñez et al. 2013).

Specific plant traits, such as large floral displays and high nectar and/or pollen production, may promote more frequent interactions with invasive pollinators (usually social insects, mainly owing to their high energetic demand necessary to maintain their colonies) than with native pollinators. The honeybee and some bumblebee species, in particular, pollinate many invasive plants in areas where they have been introduced (Goulson 2003). Similarly, compared with native plants, invasive plants that produce large fruit crops and/or have long fruiting seasons usually attract more invasive alien animals; for instance, the invasive *Carpobrotus* spp. on many Mediterranean islands are mostly dispersed by introduced rats and rabbits that are very common in coastal habitats (Traveset & Richardson 2006).

The specificity of the interactions among invaders has been predicted to increase at more advanced stages of invasion (Aizen et al. 2008), because invasives tend to interact with generalist native species in the early stages of invasion (see below). Thus, in addition to coinvasions, processes of invasional meltdown are very likely to become more common in highly disturbed sites where mutualist invaders have a long residence time. However, more research is needed to confirm this hypothesis.

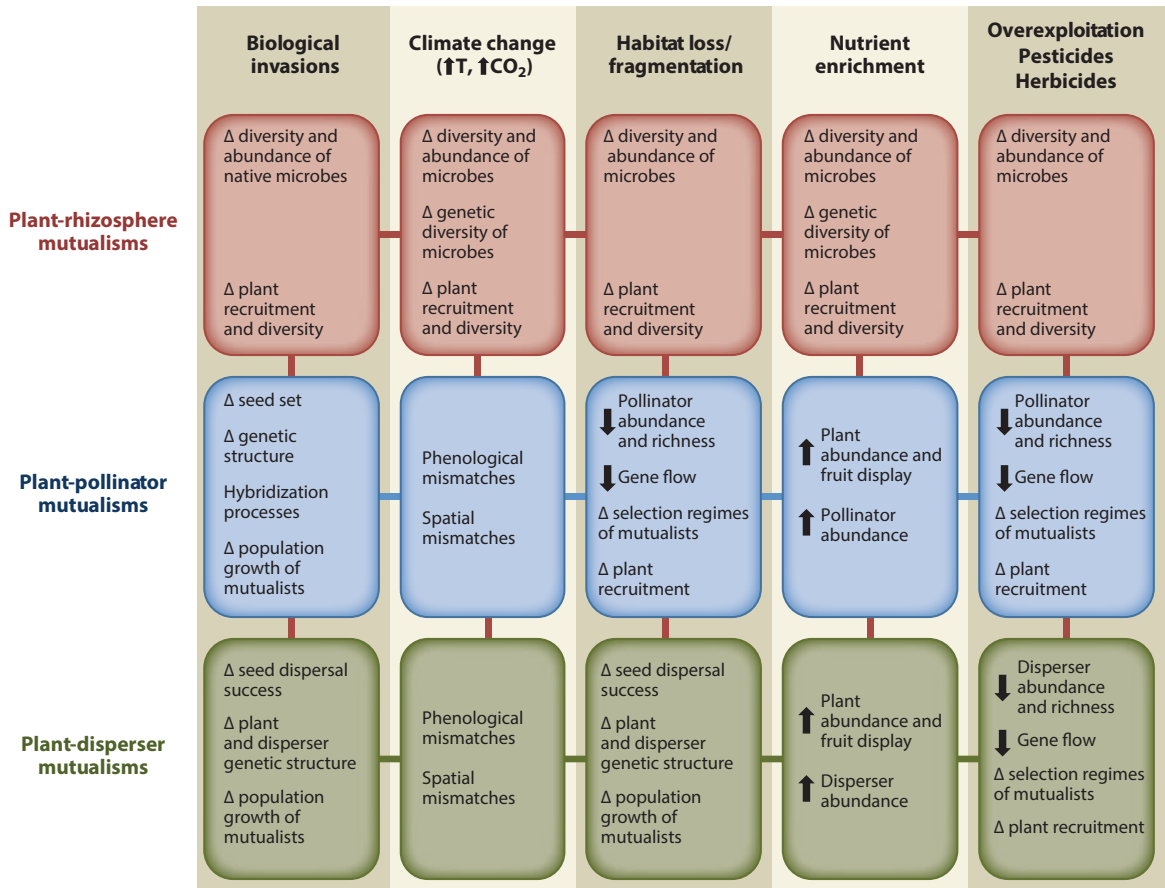
### 3. COLLATERAL EFFECTS OF INVASIONS ON NATIVE MUTUALISMS

Here we review evidence for different types of mutualistic disruptions caused by alien species. The ecological and evolutionary implications of these disruptions are also discussed. Most of the information is on pairwise interactions, although the community-level impacts of these disruptions are being increasingly studied. **Figure 3** summarizes the reported possible disruptive effects due to biological invasions.

#### 3.1. Pollination Disruptions

Disruptions caused by alien invasions that affect pollination and reproductive success of native plant species have been increasingly documented (Traveset & Richardson 2011). In the presence of more attractive alien plant species (e.g., with higher nectar rewards), natives can receive fewer pollinator visits and/or a reduction in the quality of visits as a result of changes in pollinator abundance or behavior (Lopezaraiza-Mikel et al. 2007, Gibson et al. 2013, LeVan et al. 2014). In either case, pollination levels and seed production of native plants may decrease, yielding potential population-level consequences. Alternatively, the presence of attractive invasive plant species may facilitate visits to less attractive natives either through an “overall attraction” of pollinators (Moeller 2005) or by promoting the population growth of some pollinators that then visit natives more often (but see Jakobsson & Padrón 2014), although the latter has been reported much less frequently. Both the spatial scale of investigation (Jakobsson et al. 2009) and the density of the invader (Muñoz & Cavieres 2008) affect the estimated strength of competition for pollinators between invasive and native plants; thus, researchers must account for both effects when planning experiments. Additionally, although an invasive alien species may have a negative (disruptive) impact on particular mutualistic interactions, its effect on the overall community may be neutral or even positive; its overall impact is influenced by many different interacting factors (e.g., floral abundance, pollinator abundance, community species richness), making the outcome highly context dependent.

A meta-analysis to evaluate changes in pollination and reproductive success of natives in response to alien plants showed an overall significantly negative effect (Morales & Traveset 2009), which increased at high relative alien densities and was most detrimental when alien and native plants had similar floral traits (specifically, flower symmetry and color). Besides floral abundance, floral “trait matching” has been proposed as an important property, making aliens strong interactors with pollinators (Bjerknes et al. 2007). Recently, Gibson et al. (2012) showed that similarity



**Figure 3**

Potential effects of biological invasions on different types of mutualisms compared with those caused by other drivers of global change (for further references, see Kiers et al. 2010, Johnson et al. 2013). Symbols:  $\Delta$ , changes in;  $\uparrow$ , increases in;  $\downarrow$ , decreases in.

in floral traits (clustering, color, shape, average number of floral displays, average area per floral display, and floral unit density) could be used to predict novel plant-plant interactions in an invasion context. Although not yet analyzed as far as we know, the phylogenetic relatedness of an invader to the native community should also be useful for predicting the pollination interactions it will establish in such a community.

Invasive animals may disrupt native plant-pollinator interactions by competitively displacing or directly preying on native pollinators; a meta-analysis showed that invasive animals have a more consistently negative effect on visitation rates than do invasive plants (Montero-Castaño & Vilà 2012). As many studies have demonstrated, introduced bees cause competitive displacement of native pollinators (reviewed in Stout & Morales 2009 and Dohzono & Yokoyama 2010; see also Morales et al. 2013). This promotes processes leading to inbreeding depression (by enhancing selfing) or hybridization (by moving pollen across closely related alien and native plants) and ultimately reducing plant fitness (Morales & Traveset 2008). So far, changes in the frequency of visits and interspecific pollen transfer induced by alien pollinators or plants have been evaluated separately, which has precluded an assessment of the relative importance of the two mechanisms and

their interactions. The invasion impact on the native plants will be higher if the plants are pollen limited (Dohzono & Yokoyama 2010). However, alien pollinators may also alter the outcome of competition among native plants, thereby disrupting plant community structure (Pauw 2012). Although flying alien insects have received the most attention, alien ants from several genera have also significantly reduced the abundance of important pollinators (other insects, birds, lizards) in different parts of the world, with potentially severe negative effects on many native plant species (LeVan et al. 2014). The disruptive effect can sometimes have multiple dimensions in the same system. For example, the invasive ant *Technomyrmex albipes* disrupts the unique pollination and seed dispersal interaction between an endemic gecko and a plant species in Mauritius (Hansen & Müller 2009). In the Bonin Islands, an alien predatory lizard (*Anolis carolinensis*) has disrupted pollination networks by reducing the endemic insect fauna, thus leading to high levels of pollen limitation in native plants (Abe et al. 2011).

Little is known about whether alien species act as functional surrogates of, and occupy the same niches as, extinct native species. Several studies have shown that introduced pollinators are not as effective as the natives they have replaced (Traveset & Richardson 2006, Aslan et al. 2012). Even if certain alien pollinators, e.g., honeybees, can increase the reproductive success of some plant species, such increases may be at the cost of transmitting pathogens and parasites to the native pollinators (Kaiser-Bunbury et al. 2010). Moreover, little is yet known about the evolutionary consequences of novel interactions involving alien and native mutualists, but they could potentially counteract the pollination and dispersal selection of floral and fruit traits, such as the quantity or quality of rewards (Rowles & O'Dowd 2009). Functionally disparate mutualists (e.g., pollinators that have a long proboscis) are likely to be more difficult to replace with alien species. Thus, the loss of such native partners may alter the evolutionary trajectory of the mutualism more significantly than would the loss of other partner species (Kiers et al. 2010). Likewise, we expect that less specific mutualistic interactions will also be more susceptible to replacement and thus less susceptible to coextinction.

### 3.2. Seed Dispersal Disruptions

Many invasive alien plants have fleshy fruits and interfere with interactions between native plants and their frugivores (Traveset & Richardson 2006, Farwig & Berens 2012, Heleno et al. 2013b). Alien species with fruits that are more abundant or more nutritious to frugivores than those of natives cause frugivores to decrease their visits to the latter, which reduces their dispersal success (Mokotjomela et al. 2013). Greater variation in the fruit quality of invasive species may also cause frugivores to shift their foraging preferences away from native plants (Kueffer et al. 2009). As with disrupted pollination networks, reduced fruit/seed removal may result in lowered seed dispersal success and reduced recruitment (Hansen & Müller 2009, Rowles & O'Dowd 2009, Traveset et al. 2012).

Seed dispersal disruptions are also frequently documented when the invader is a frugivorous animal, usually a bird or mammal, although invasive ants have disrupted native dispersal mutualisms in several systems and may even drive shifts in community diversity as well as parallel changes in ecosystem functioning (Rodríguez-Cabal et al. 2009, Rowles & O'Dowd 2009, Davis et al. 2010, LeVan et al. 2014). Many introduced vertebrates have had detrimental effects on native floras and faunas, more notably on islands. The negative impact of, for example, introduced goats, cats, rats, opossums, and parrots on plant fitness and dispersal can be multifaceted, including the direct consumption of native plants and/or, more indirectly, the reduction of populations of legitimate seed dispersers (Traveset & Richardson 2011). Different novel mutualistic relationships with alien species compensate at least partly for the extinctions of native mutualists (Cheke & Hume 2008,



Kawakami et al. 2009, Traveset et al. 2012), perhaps because species abundances rather than trait-matching constraints ultimately determine the interaction patterns between birds and plants, as suggested by García et al. (2014). The demographic consequences of dispersal disruptions have been little studied but must be important because the quality of the seed dispersal service (e.g., dispersal distances, sites of seed deposition) can differ dramatically among frugivore species. Moreover, small differences in such dispersal services may have profound evolutionary consequences over multiple generations, for instance, by modifying the genetic structure of plant populations (Kiers et al. 2010) or promoting changes in fruit/seed traits. Almost nothing is known about the level of functional redundancy in disperser assemblages, making it difficult to predict evolutionary trajectories of mutualisms after the loss of particular dispersers. As in the case of pollination discussed above, however, we can expect that the loss of functionally disparate partners (e.g., dispersers that move seeds longer distances than the rest) is likely to alter evolutionary trajectories more than the loss of a disperser with a more “normal” function. Intuitively, generalized plants should be less vulnerable to mutualistic disruptions than specialized plants are, but this assumption may not hold if the diverse assemblage of dispersers of the former has little redundancy. More studies are needed to gain the level of understanding needed to make robust predictions, given widespread vertebrate frugivore losses, especially on oceanic islands. Also, as noted by Kiers et al. (2010), a key question is whether mutualists will evolve specialized traits as they interact with a narrower range of partners—after losing others—which would make them less flexible to interact with other species in future scenarios.

The invasion of alien species that act as enemies of any mutualist can drive losses of mutualistic keystone species, leading to a cascade of linked coextinctions and a disassembly of entire communities. For example, in Patagonia, introduced ungulates and wasps have directly and indirectly disrupted the pollination and seed dispersal interactions of a parasitic fleshy-fruited plant (Rodríguez-Cabal et al. 2013). Both direct and indirect species interactions can be important in maintaining community structure and need to be considered when assessing the consequences of invasions.

Finally, it is important to note that not only plants and animals are responsible for seed dispersal disruptions. Work by McKinney et al. (2009) in the Rocky Mountains showed how an invasive alien fungus has disrupted the obligate seed dispersal mutualism involving *Pinus albicaulis*, a keystone subalpine tree species, and the only bird (*Nucifraga columbiana*) capable of dispersing its large wingless seeds. The fungus kills tree branches and reduces cone production, thereby depleting a key food source for nutcrackers as well as their occurrence and seed dispersal success.

### 3.3. Plant-Microorganism Disruptions

Relatively little is known about the effects of plant invasions on belowground microbial communities. They may reduce densities of native fungal symbionts, causing subsequent losses of native host plants, but they may also increase the abundance and diversity of mycorrhizas (Johnson et al. 2013). Even if not mycorrhizal, an invader could facilitate the invasion of other nonmycorrhizal plants, thus creating long-term legacy effects (Johnson et al. 2013). This outcome (the “degraded mutualism hypothesis”) is possible when native plants are more dependent than invasive species on mycorrhizal symbiosis (Shah et al. 2009) and when invasive species directly degrade microbial targets (Cipollini et al. 2012). Increasing evidence is emerging that, by changing soil communities, invasive plants can generate positive feedback that enhances both its own competitiveness and subsequent interactions with its native neighbors (De la Peña et al. 2010, Zhang et al. 2010, Callaway & Rout 2011). Some alien plants release allelopathic compounds in the soil that directly affect not

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**Generalization level:**  
the number of interactions (links) that a particular species has with others in the community

**Phylogenetic signal:**  
the tendency of closely related species to resemble each other morphologically and/or ecologically

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only microbial mutualisms, but also pollination and seed dispersal mutualisms (Hale & Kalisz 2012). The effects of allelopathy seem dependent on ecosystem type and microbe identity, as a recent study has found that pine forests are more sensitive than oak forests and that soil bacteria are more sensitive than soil fungi (Lorenzo et al. 2013).

The invasion of nonmycorrhizal plants that causes a reduction in arbuscular mycorrhizal fungal abundance and diversity in soils may lead to selection for plant traits in native species that promote colonization by diverse fungal species to counteract such reduction. Such plant traits responsible for symbiotic preferences may evolve rapidly, as Lankau & Nodurft (2013) found. Moreover, many native arbuscular mycorrhizal fungi rapidly adapt to new invasive plant species. Ongoing research is exploring how much genetic variability within and among fungal species contributes to the mycorrhizal response to changing environments (Johnson et al. 2013).

The introduction of alien symbiotic microbes that can shift hosts in the new range can also disrupt native mutualistic networks. This largely unexplored effect has been documented for alien symbiotic bacteria in areas invaded by *Acacia longifolia*. These alien bacteria could become the dominant microsymbionts for native co-occurring legumes, but they may be less effective than native rhizobia (Rodríguez-Echeverría 2010, Rodríguez-Echeverría et al. 2012). Alien bacteria can thus facilitate plant invasion not only by enhancing the growth of the invader, but also by detrimentally affecting the growth of native species in response to the disruption of plant-rhizobia mutualisms.

## **4. A FRAMEWORK OF MUTUALISTIC NETWORKS TO BETTER UNDERSTAND INVASION PROCESSES AND IMPACTS**

Further progress in understanding how mutualisms enhance and/or are influenced by biological invasions requires us to move beyond the study of pairwise interactions toward a network approach encompassing entire communities. Network theory offers a highly informative foundation for exploring the structural and functional attributes of complex interaction networks. In studies of biological invasions, network theory specifically helps us to assess how new species are incorporated in the community and how the community responds to additions. Most studies following such an approach have detailed pollination interactions, but a few have focused on seed dispersal. Vacher et al. (2010) provided the first study to explore the integration of aliens into a plant-fungus network; however, their study included an antagonistic network. As far as we know, this issue has yet to be addressed for networks involving plants and mutualistic bacteria or fungi.

### **4.1. Integration of Alien Species into Mutualistic Networks**

Mutualistic networks usually consist of a core of native generalized species that facilitate the incorporation of alien species. Invaded natural communities provide confirmation of this for native plants and pollinators (e.g., Aizen et al. 2008, Kaiser-Bunbury et al. 2011, Traveset et al. 2013a) and also for seed dispersers (Spotswood et al. 2012; Heleno et al. 2013a,b). In turn, the most successful animal-pollinated or animal-dispersed invasive plants tend to be highly generalized, often acting as main network hubs. Alien mutualists have, on average, more connections than do natives in the community, as found with insect pollinators in the Galápagos (Traveset et al. 2013a) or with avian seed dispersers in the Azores (Heleno et al. 2013b) or in French Polynesia (Spotswood et al. 2012). This result suggests that such higher generalization levels may enhance the spread of alien mutualists by increasing their competitive advantage over natives.

Phylogenetic signals also shape mutualistic networks (Bascompte & Jordano 2007), which may be important in determining the vulnerability to specific invasive species that can be more or

less phylogenetically related to the native species (Valiente-Banuet & Verdú 2013). The phylogenetic relatedness of an invader to members of the native community provides a tool for predicting invasiveness (e.g., Strauss et al. 2006, Vacher et al. 2010) as well as the overall effect on the mutualistic network. Further analyses are needed to find phylogenetic signals in invaded networks.

#### 4.2. Effects of Alien Species on the Structure of Mutualistic Networks

A network approach has been most frequently used to assess the impact of alien species at the community level. The interaction structure within a network can determine its resistance to the extinction of particular species. Consequently, compared with species diversity measures, metrics that describe such structures are better for detecting subtle shifts in entire communities, as interactions can be lost well before species are lost (Bond 1994, Kearns et al. 1998, Tylianakis 2008).

Most available evidence shows no changes in connectance (proportion of links relative to all those possible) between invaded and noninvaded networks (Memmott & Waser 2002, Olesen et al. 2002, Aizen et al. 2008, Padrón et al. 2009, Heleno et al. 2013a), but alien species often promote rearrangements of links within the networks (Aizen et al. 2008, Padrón et al. 2009, Kaiser-Bunbury et al. 2011). Links are usually transferred from generalist natives to highly linked invaders, and thus the entire network topology is modified. As the invasion progresses, such alien supergeneralists become central nodes (Aizen et al. 2008, Kaiser-Bunbury et al. 2011, Santos et al. 2012), thus playing a pivotal role in shaping the network structure. By being generalized species and/or by linking to generalized species, aliens may also increase network nestedness (Aizen et al. 2008, Traveset et al. 2013a), which provides stability to networks (Bascompte et al. 2003). Likewise, aliens can enhance network cohesiveness if they play an important role in binding modules (i.e., subgroups of frequently interacting species) (Santos et al. 2012, Traveset et al. 2013a, Albrecht et al. 2014), with potential effects on network functioning, reciprocal selection regimes, and the cascade of perturbations throughout the network.

Because interactions of low reciprocal dependence are the most robust against disturbances (Bascompte et al. 2003), an invasive species and its mutualists may be more resistant to disturbances, thereby increasing the probability of permanence and survival of such an invasive in the network. Some studies show that invaders are important for network persistence (Valdovinos et al. 2009, Traveset et al. 2013a), implying that invader-dominated networks could hinder the restoration of interactions among natives. Added to a preferential interaction among invasive species, this effect could cause a positive-feedback loop (invasional meltdown) that precipitates an even higher impact of the invasion on the native community.

In terms of maintaining ecosystem functions, such as pollination or seed dispersal, whether the mutualist is native or alien may be irrelevant as long as the diversity of service providers is maintained. Regarding plant fitness (measured as fertilization, plant dispersal success, or plant growth), the integration of alien species into mutualistic networks provides intriguing natural experiments. It is not straightforward to predict in which cases alien species will dominate the interactions within the networks, to what extent they will alter the ability of native plants to interact with their mutualists, and the demographic consequences that alteration will have on them. Further research is especially needed at the community level to compare the efficiency of alien and native mutualists, as most information we have now is at the species level. As previously mentioned, empirical evidence on the evolutionary responses of native mutualists in the community to invasive dominance is scarce, though they are probably profound (Tylianakis 2008, Kiers et al. 2010, Moran & Alexander 2014).

## 5. MUTUALISTIC INTERACTIONS IN INVASION ECOLOGY: IMPLICATIONS FOR ECOSYSTEM MANAGEMENT

This review outlines the pervasive and complex influence of mutualisms on community structure and functioning and their pivotal role in facilitating biological invasions and mediating their impacts. Invasive species threaten the integrity of many communities by altering prevailing mutualistic interactions. In other cases, however, invaders seem to play a positive role in the survival and maintenance of some species and may enhance community stability in the face of continued anthropogenic changes. What seems certain is that all forms of ecosystem management will increasingly require interventions to manipulate interactions among species. Restoration ecology, for example, needs to consider mutualisms more explicitly, in particular those involving keystone species (“hubs” in network terminology) and ecosystem engineers (species—either native or alien—that create or modify habitats). In simple ecosystems (e.g., oceanic islands), such species are usually vertebrate seed dispersers, but they can also be insect pollinators (Kaiser-Bunbury et al. 2010). Sometimes, radical conservation strategies may be needed, such as managed relocation and “rewilding” of ecosystems, via the introduction of extant species (taxon substitutions) as functional replacements or ecological analogs for extinct native species. For example, by acting as pollinators and dispersers, some alien species may contribute positively to the fitness of native plant species in heavily degraded island systems. Different mutualistic processes (microbial, pollination, seed dispersal) operate at different spatial and temporal scales; thus, conservation measures and restoration methods that focus on one process will not necessarily ensure the maintenance of others. Studying the spatiotemporal dynamics of such interactions will surely contribute to the improvement of ecosystem management.

## 6. FUTURE AVENUES OF RESEARCH

Biological invasions provide superb natural experiments for exploring many aspects of ecology, including the factors that influence ecosystem functioning and stability. The past decade has seen radical advances in our understanding of the role of mutualisms in structuring communities and of the fragility of many interactions. The impacts of invasive species on naturally occurring mutualisms are increasingly being documented, and the emerging picture shows that these often have profound implications for ecosystem structure and functioning. Observations provide most insights, and more manipulative experiments are needed to elucidate the complexity of species interactions to understand fully the mechanisms involved.

For microbial symbionts, in particular, there have been major advances in recent years, though much work remains to be done on their ecology, biogeography, and taxonomy. The intentional introductions of symbionts have clearly altered the invasiveness of many species and the invasibility of many ecosystems. Strains such as the rhizobia TAL 1145 have been widely introduced throughout the tropics to grow economically important woody legumes and spread rapidly (Burleigh & Dawson 1994). The implications of such changes on the distribution and ecology of these microbiota are only beginning to be assessed.

In an increasingly fragmented and homogenized world, the role of evolution cannot be ignored if we are to understand the dynamics of species interactions, in general, and mutualistic interactions, in particular. New interactions established between species in invaded communities can evolve rapidly, sometimes over a few decades and across complex geographical landscapes. We urgently need more and better information on the geographical scales at which mutualistic interactions function ecologically and evolutionarily.

With increasing environmental changes occurring at all scales, we need to be able to predict when communities are likely to collapse in response to different combinations of pressures. Because they may be nonadditive, the effects of invasions on mutualistic interactions need to be examined together with those caused by other drivers of global change (e.g., changes in land use) (Didham et al. 2007). Empirical knowledge of such combined effects remains scarce and is far from meeting the needs of conservation management, but our knowledge is growing (Tylianakis 2008, Potts et al. 2010, Hoover et al. 2012, Grass et al. 2013; also see the review by Colwell et al. 2012). The use of complex network approaches, together with phylogenetic methods, is improving our understanding of the complexity of ecological interactions that occur in nature, in general, and between native and alien species, in particular. Network studies also help researchers predict extinction cascades following the disappearance of species from ecosystems and evaluate the degree of community resilience with respect to different types of disturbance.

### SUMMARY POINTS

1. Mutualistic interactions provide important ecosystem services, occur in all ecosystems, and enhance many biological invasions worldwide.
2. Mutualistic soil microorganisms, pollinators, and seed dispersers mediate the naturalization, invasion, and impacts of most introduced plants. Likewise, many animal and microbial invasions are mediated by the mutualisms they establish with plants, both native and introduced.
3. “Invasional meltdown,” whereby alien species enhance other invasions, is common in disturbed habitats, and a growing number of studies are showing the positive feedback between invaders that amplifies their impacts. These invasive complexes are probably more common and influential in simple ecosystems, such as islands.
4. Invasions that add and often remove species (e.g., when the invader outcompetes or otherwise excludes a native) offer new insights into the strength, resilience, and robustness of mutualistic networks.
5. Integrating the study of mutualistic interactions with invasion ecology may shed light on the possibility of using extant species as functional replacements—or ecological analogs—for extinct native species, potentially avoiding a cascade of extinctions.
6. Because such effects are nonadditive, the impact of invasions on mutualistic interactions cannot be considered separately from the effects of other drivers of global change.

### DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

### ACKNOWLEDGMENTS

We are grateful to Miguel Verdú, Ruben Heleno, and Susana Rodríguez-Echeverría for valuable comments on the manuscript as well as the latter two, Pedro Jordano, and Chris Kaiser-Bunbury for kindly providing pictures for **Figure 1**. We also thank Sharon Strauss and Dan Simberloff for useful suggestions on a previous version. A.T. acknowledges support from the Ministry of

Economy and Competitiveness (Project CGL2010-18759BOS). D.M.R. receives support from the DST-NRF Center of Excellence for Invasion Biology, the National Research Foundation (grant 85417), and the Oppenheimer Memorial Trust.

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Shows that, as invasion progresses, aliens can shape network structure, usurping links to generalist natives.

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Provides the first review of evidence for promotion of invasive species by novel plant-microbe-insect interactions.

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Shows that some alien species may play crucial roles in the regeneration of native ecosystems.

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Provides the first network approach assessing the combined effects of invasions and land-use changes on plant–pollinator interactions.

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Provides the first experimental approach to assess the impact of alien species on a pollination network.

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Shows how invasive species can change the dispersal dynamics of natives and have ecosystem-level impacts.

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First review showing the importance of mutualisms in promoting plant invasions.

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Demonstrates that mutualistic disruptions can lead to underappreciated cascading coextinctions in a community.

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First evidence of invasional meltdown in a plant-bacteria mutualism.

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Provides the first review of the impact of invasive alien species on plant reproductive mutualisms.

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