Chapter 12

MUTUALISMS: KEY DRIVERS OF INVASIONS … KEY CASUALTIES OF INVASIONS

Anna Traveset and David M. Richardson

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143

12.1 INTRODUCTION

The reigning paradigm over much of the history of the study of biological invasions has been that communities have 'biotic resistance' to invaders, a notion that was central to Charles Elton's (1958) understanding of invasions. This view is based on the assumption that natural communities are mainly structured by negative interactions; it thus emphasizes the biotic relationships between native and invasive alien species mediated through competition, herbivory, parasitism, etc. It predicts (i) the risk of invasions decreases when resource capture by the native community increases, for instance when species diversity in the community is higher, and (ii) the establishment of invasive species is favoured by the absence of natural enemies (herbivores, predators, pathogens) (Simberloff 1986; Rejmánek 1998); the enemy-release hypothesis (see, for example, Keane & Crawley 2002) proposes that introduced species have better opportunities for establishment when freed from the negative effects of natural enemies that, in their native range, lead to high mortality rates and reduced productivity.

This longstanding paradigm has, however, been increasingly challenged recently as many studies have shown that positive (facilitative) interactions are as important, or even more so, than negative interactions in structuring communities and ecosystems (Bertness & Callaway 1994; Callaway 1995; Bruno et al. 2003, 2005; Valiente-Banuet et al. 2006; Brooker et al. 2008). Facilitation can have strong effects at the level of individuals (on fitness), populations (on growth and distribution), communities (on species composition and diversity) and even landscapes (see, for example, Valiente-Banuet et al. 2006; Brooker et al. 2008).

When positive interactions among species are incorporated in population and community models, they change many fundamental assumptions and predictions (Bruno et al. 2005; Bulleri et al. 2008). Clearly, a robust predictive framework for invasion biology demands an improved understanding of the role of facilitation in mediating biotic resistance of communities to the incursion of introduced species. In particular, it is important to consider (i) the effect that the establishment of such positive interactions between the invasive alien species and already-present biota (native or alien) can have from overcoming such biotic resistance, and (ii) that such positive interactions can bring about significant changes to invaded ecosystems. Much evidence has accumulated in the last decade from terrestrial and aquatic ecosystems to show that native species frequently promote (facilitate) the colonization and establishment of introduced species through a variety of mechanisms (Richardson et al. 2000a; Bruno et al. 2005; Badano et al. 2007; Milton et al. 2007; Olyarnik et al. 2008). Simberloff and von Holle (1999) were the first to incorporate facilitation explicitly in an invasion biology framework; they coined the term 'invasional meltdown' for the process whereby two or more introduced species facilitate establishment and/or spread of each other (and potentially other species). This contributes to increased invasibility and accelerated invasion rates and to a synergic amplification of the disruptive effects of invasive species.

Mutualisms are a type of facilitative interaction in which the two (or more) species involved both benefit. Pollinator and seed dispersal mutualisms are especially important for plant invasions, as the production and dispersal of propagules are usually fundamental requirements for invasion (see reviews in Davis 2009; Simberloff 2009). Native and alien animals clearly assist the spread of alien plants by pollinating their flowers or by dispersing their seeds (reviewed in Richardson et al. 2000a). Native and alien plants also facilitate the spread of alien animals (pollinators and seed dispersers) by providing them with important food resources (pollen, nectar, resins, fruit pulp, etc.). In this chapter we deal mostly with plant–animal mutualistic interactions involving pollination (for which most data are available) and seed dispersal. Plant–fungal mutualistic interactions (see, for example, Callaway et al. 2004, Kottke et al. 2008, Collier & Bidartondo 2009) and plant–plant interactions (e.g. Badano et al. 2007) are also crucial for the success of many plant invasions, as has been documented in several systems.

Another established concept in ecology is that invasion success is influenced by the phylogenetic relationships between biological invaders and residents of the target community. In *The Origin of Species*, Darwin (1859) explored whether species with a common evolutionary history interact with each other more closely than unrelated species. He predicted that introduced species with close relatives were less likely to succeed owing to fiercer competition

resulting from their similarity to residents. Using data from eastern North America, Darwin found that most naturalized tree genera had no native counterparts, suggesting that aliens may be handicapped by more intense competition from established congenerics. A century later, Elton (1958) supported this view by arguing that unique traits allow invaders to exploit 'empty niches' in species-poor island communities. There has been a lack of consensus among studies that have tested 'Darwin's naturalization hypothesis', some finding support for it and others not (reviewed in Proches̗ et al. 2008; see also Thuiller et al. 2010).

Considering mutualistic interactions, we might predict that plant invaders similar to natives in morphological traits (flower/fruit colour, size, shape, etc.) and physiological traits (chemical composition of nectar, fruit pulp, etc.) are more likely to share pollinators/seed dispersers with native plants. This could lead to successful establishment in the receptive community. Similarly, an invader pollinator/disperser might 'fit better' in the new environment if its requirements are similar to those of the resident/native pollinators. Therefore, when considering positive interactions, predictions about invasive success based on the phylogenetic relatedness between invaders and residents might differ from those made when considering negative interactions. Recent developments in coexistence theory demonstrate that invasion success can result either from fitness differences between invader and residents that favour the former, or from niche differences that allow the establishment of the invader despite having a lower fitness (MacDougall et al. 2009).

Mutualisms have received increasing attention recently, and are now widely accepted to be important mediators of ecosystem functioning (Bruno et al. 2003, 2005; Agrawal et al. 2007; Brooker et al. 2008; Bronstein 2009). There has been a rapid increase in the number of published papers linking mutualisms and invasions. A literature search in the ISI Web of Knowledge including the terms 'mutualis' and 'invasi' showed only three papers dealing with both topics in 1999, but 50 in 2009. In this chapter we review studies that have examined the importance of mutualistic interactions in determining the success and impact of invasive species. Our goal is to identify general patterns as well as topics that need more research.

12.2 MUTUALISMS AS DRIVERS OF INVASIONS

The role of mutualists in the naturalization–invasion continuum

To colonize, survive, regenerate and disperse, a species introduced to a new area must negotiate several biotic and abiotic filters/barriers (Richardson et al. 2000b; Mitchell et al. 2006). This, and the fact that the introduction of species and their mutualistic or antagonistic partners often do not take place simultaneously (see, for example, Richardson et al. 2000b; Grosholz 2005), greatly reduces the probability of an alien species interacting with the same mutualistic and antagonistic species in the new environment as in their native range. An increasing body of literature demonstrates that positive interactions between species, specifically those established among plants and animals, are crucial for the integration of invasive species into native communities, and that these can mediate the impacts of introduced species.

Mutualisms are important at all stages of the invasion process (Fig. 12.1). An alien plant introduced by humans can be transported to new areas far from the original site through dispersal by animals; such a plant may in turn establish in that area owing to symbiotic microorganisms in the soil and/or because pollinators mediate seed production. A plant species can spread and become invasive because frugivorous animals disperse its seeds far from where the plant was originally established. The same dispersal vector may be implicated at more than one stage. Human activities, for instance, are by definition the vector of arrival for alien species, but can also disseminate the invader within the introduced region. The rate of spread is influenced by mean dispersal distance and more importantly by unpredictable, rare long-distance dispersal events that have a disproportionate effect on population growth and aerial spread (Trakhtenbrot et al. 2005). Moreover, disturbances (whether natural or anthropogenic) can also influence the initial establishment of invasive mutualists.

The importance of mutualistic interactions during the invasion process depends on different traits/requirements of the invader. In the case of invasive plants, we expect these interactions to determine invasion success when the plant:

1 Is an obligate outcrosser (e.g. owing to self-incompatibility or dioecy, or if self-compatible has no
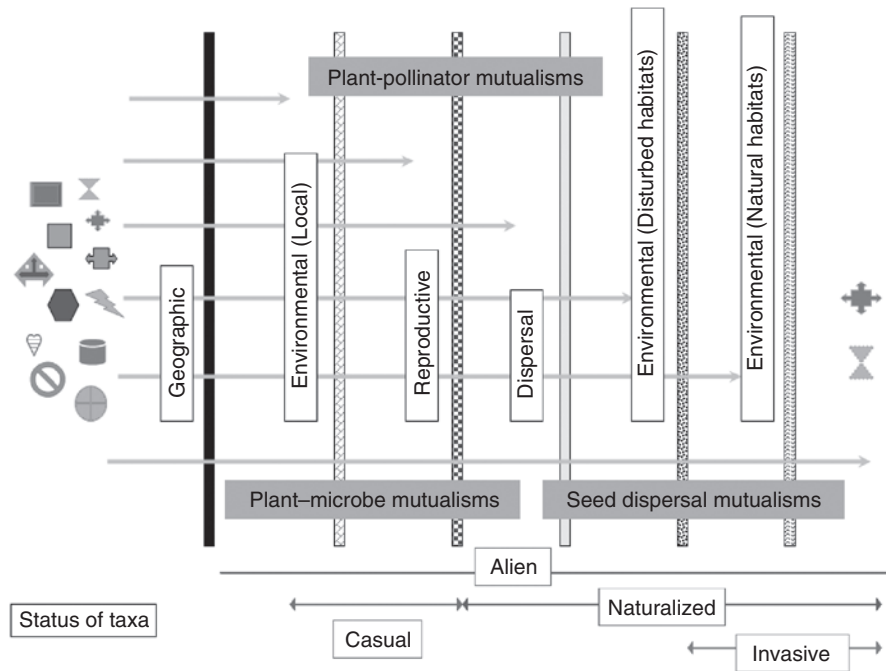
Fig. 12.1 Schematic representation of the naturalization–invasion continuum, depicting various barriers that an introduced plant must negotiate to be become 'casual', 'naturalized' or 'invasive' (based on Richardson et al. 2000). Bars show the main phases and stages at which different categories of mutualisms are influential in invasion dynamics. Once species become 'invasive' they often become widespread and abundant and may affect a wide range of naturally occurring mutualisms.

capacity for autonomous self-pollination), and therefore requires pollinators to set seeds. Examples include the obligate outcrossers *Centaurea diffusa* and *C. maculosa* (Harrod & Taylor 1995) and purple loosestrife, *Lythrum salicaria* (Mal et al. 1992), both invasive in North America.

2 Needs animals to disperse its seeds. For instance, *Crataegus monogyna* produces larger fruit displays of higher quality than a native congener, and this has contributed to the rapid spread of this shrub in western North America (Sallabanks 1993).

3 Needs specific microorganisms (nitrogen-fixing bacteria or mycorrhizal fungi) to establish and grow. Examples include many introduced conifers in the Southern hemisphere (which failed until appropriate fungal symbionts were introduced; Richardson et al. 2000a) and many herbs (Reinhart & Callaway 2006).

Because mutualistic interactions, specifically plant–animal mutualisms, are more prevalent in the tropics

than in the temperate zones (Schemske et al. 2009), they are more likely to influence invasion success at lower latitudes. Unfortunately, this hypothesis has yet to be tested, as most data elucidating the role of mutualisms on invasions are from temperate areas. Likewise, we would expect a stronger influence of pollinators and seed dispersers on plant invasions at lower altitudes owing to the declining diversity of such animals with increasing elevation.

Several studies have shown that systems rich in native species often support large numbers of alien species (see, for example, Rejmánek 1996; Stohlgren et al. 1999; Richardson et al. 2005). In fact, if plant invasions are facilitated by a diverse array of pollinators, dispersers, fungi and bacteria. So, if disturbance and/or fluctuations in resource availability create windows of opportunity, we should expect invasibility to be positively correlated with native species richness (Richardson et al. 2000a).

The importance of mutualisms as mediators of invasion success

Baker's rule states that plants capable of uniparental reproduction, especially self-compatible species, are more likely to be successful colonists than are self-incompatible or dioecious species (Baker 1955). Unfortunately, we still have rather little information on the reproductive systems of most invasive alien plants (but see Barrett, this volume). A study of 17 invasive alien woody and herb species in South Africa using controlled pollination experiments revealed that all were either self-compatible or apomictic, and that 72% of species were capable of autonomous self polli-nation (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 introduced plant species, although of those that differed, the introduced species were more autoga-mous than their native congeners (Harmon-Threatt et al. 2009). Other surveys in different areas, however, show that many introduced plant species, particularly woody ones, require pollinator mutualisms to become invasive (Richardson et al. 2000a).

Pollen limitation does not seem to represent a major barrier to the success of introduced plants (Richardson et al. 2000a; Rambuda & Johnson 2004). This may be because of the high level of generalization of pollina-tors (see section 'Mechanisms whereby mutualisms can drive invasions'). Among the few exceptions reported so far are *Trifolium pratense* (red clover), which did not set seed in New Zealand before bumblebees were introduced, and *Cytisus scoparius*, *Ficus* spp. and *Melilotus* sp. (details in Richardson et al. 2000a). Figs are the best-studied case of pollinator-mediated con-straints on invasion. Several species have spread in alien habitats only after their specific wasp pollinators arrived, either through accidental introduction by humans or by long-distance dispersal (Gardner & Early 1996). Assuming that pollinator specificity is greater in tropical than in temperate forests (Bawa 1990), and given the significant positive relationship between pollen limitation and plant species richness (Vamosi et al. 2006), we predict that invasive plants should be more pollen limited in the former, but more data are needed to test this hypothesis.

An example of how a plant-seed dispersal interac-tion may drive an invasion is provided by Milton et al. (2007). They report that birds drive the invasion of arid savannas in South Africa when alien fleshy-fruited plants infiltrate prevailing seed-dispersal networks. Once infiltrated, the natural dispersal network is dis-rupted because some invasive plants transform the savannas by overtopping and suppressing native trees that act as crucial perch sites and foci for directed dis-persal (Iponga et al. 2008).

The importance of mutualistic interactions is also emphasized in the invasion ecology of ectomycorrhizal plants, such as Northern hemisphere conifers intro-duced to the Southern hemisphere. For instance, the establishment and spread of *Pinus* species in many parts of the Southern hemisphere was initially thwarted by the absence of appropriate fungal symbionts (Richardson et al. 2000a; Nuñez et al. 2009). In the Galápagos Islands, the invasion by the obligately arbus-cular mycorrhizal *Psidium guajava* was only possible because arbuscular mycorrhizas were already natu-rally present on the islands (Schmidt & Scow 1986).

Towards a framework of ecological networks to study integration (and impact) of invasive species at the community level

Understanding the evolution and diversification of eco-logical interactions requires more than an elucidation of interactions between pairs of species. Mutualisms between plants and pollinators or plants and seed dis-persers must be considered as networks of interactions involving many species, some with high degrees of generalization (Jordano 1987; Waser et al. 1996). The formalization of interactions between plant communi-ties and their mutualistic animals, using analytical methods developed for the ecology of trophic webs, provides an appropriate conceptual framework for studying the dynamics of such interactions. Such an approach helps us to understand how new species are incorporated into the community and how the com-munity responds to new members (see, for example, Memmot & Waser 2002; Olesen et al. 2002, Olesen & Jordano 2002; Bascompte et al. 2003, Aizen et al. 2008; Padrón et al. 2009). Nonetheless, most informa-tion derived using this network approach to date is based on qualitative data (presence/absence of interac-tions) and assumes that all interactions between plants and animals have similar weights, at least regarding the quality of the interaction (i.e., assumes all pollinator/disperser visits are equally effective from the plant's viewpoint). A functional approach is needed to make more robust predictions about the impact of a
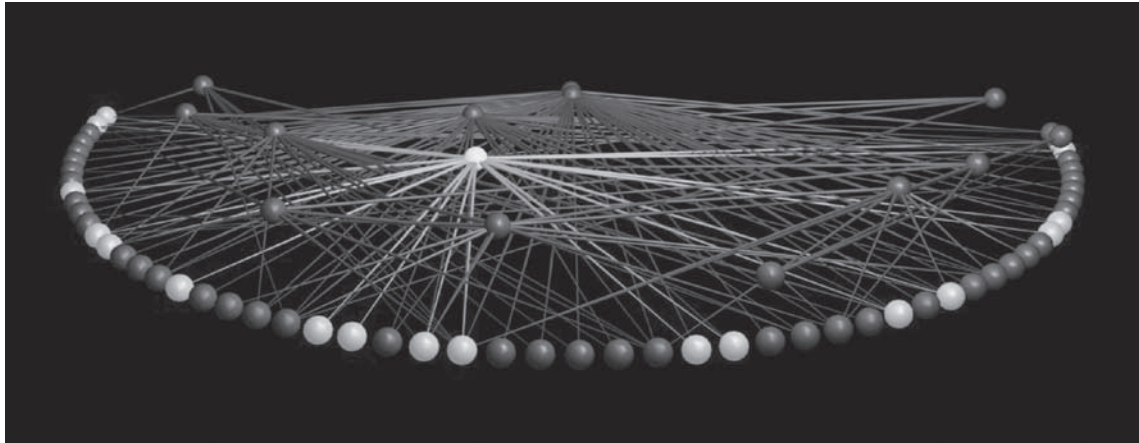
Fig. 12.2 Example of a plant–flower visitor network. The nodes in the lower part represent the insect species in the web; nodes in the upper part represent plant species that are visited by them. Lines between nodes symbolize links between species pairs. The yellow node is the invasive species *Opuntia maxima*, which is integrated in the community and which interacts with a high number of flower-visiting insects (lines indicated in green). Data from Padrón et al. (2009). The image was produced using FoodWeb3D, written by R.J. Williams and provided by the Pacific Ecoinformatics and Computational Ecology Laboratory (www.foodwebs.org; Yoon et al. 2004), courtesy of B. Padrón.

disturbance (the entrance of an invader, for instance) on the entire community. We must obtain good quantitative data to assess whether the patterns that have emerged so far hold when the different effectiveness of mutualists are considered.

Other mutualistic interactions, such as those established between plants and soil biota (mycorrhizas or nitrogen-fixing bacteria) should also be studied at a community level (see, for example, Kottke et al. 2008; Collier & Bidartondo 2009; van der Heijden & Horton 2009). Recent research has highlighted their important role, either facilitating or inhibiting plant invasions (Callaway & Rout, this volume). These underground interactions can in turn affect the aboveground mutualisms. For instance, arbuscular mycorrhizas in some plants can promote an increase in floral display and/or in the quantity and quality of nectar which directly affects the pollination visitation rates to flowers (Wolfe et al. 2005). Similarly, underground mutualisms can alter plant–herbivore interactions, as observed in the invasive *Ammophila arenaria*, a dominant species in many dune systems around the world whose mycorrhizas improve resistance to the attack of parasitic nematodes to its roots (Beckstead & Parker 2003).

An alien species is incorporated in a mutualistic plant–animal network when it establishes a link with another species, native or alien, forming a new node in the web. The new interactions between alien and native species affect the demographic success of the former, and influence interactions among natives with subsequent consequences for them. Figure 12.2 shows a network of plant-flower visitor interactions in a plant community in the Balearic Islands that has been invaded by the alien cactus *Opuntia maxima*. This species has become integrated in the community and interacts with many native insects (Padrón et al. 2009).

Pollination and seed dispersal systems tend to be dominated by generalists. Consequently, it has been predicted that alien species are easily accommodated in such networks (Waser et al. 1996). Studies in invaded natural communities seem to confirm this prediction in the case of native pollinators, because their level of generalization is positively correlated with the probability of servicing a given invasive plant (Lopezaraiza-Mikel et al. 2007), or with the number of alien species included in their diet (Memmott & Waser 2002). In turn, most successful animal-pollinated invasive plants are pollinated by generalist species (Richardson et al. 2000a). Less information is available on seed dispersal assemblages of alien species.

Mechanisms whereby mutualisms can drive invasions

Species niche width may be one of the traits that determines the success of an invader (Vázquez 2005). If we apply this hypothesis to mutualistic interactions, the prediction is that generalist alien species have a higher probability of receiving more visits, in the case of plants, or of acquiring more resources in the case of animals, than specialist species (Richardson et al. 2000a). As result, generalist aliens are more likely to integrate into local networks. Validation of this hypothesis requires the comparison, from a biogeographical perspective, of the generalization level of invasive alien species with those of non-invasive aliens (Vázquez 2005). Available evidence suggests that even if reproduction of some highly invasive plant species is limited by pollen availability (Parker et al. 2002), only a small proportion of potentially invasive introduced plants seem to have failed because of the absence of pollinators (Richardson et al. 2000a). This is the case of many species with highly specialized flowers, such as orchids or *Ficus*, emblematic examples that represent examples of mutual specialization.

We may also ask whether, in a given community, invasive species are more generalist than native species. Intra-community comparisons have not shed much light on this so far. Whereas some communities show similar levels of generalization between native and alien mutualists, either for plants or pollinators (see Morales & Aizen 2002, 2006; Olesen et al. 2002), others show differences between them. For instance, Memmott and Waser (2002) found alien flower visitors to be the most generalist species in the community, including super-generalist species such as *Apis mellifera*, whereas alien plants were on average less generalist than natives.

In mutualistic networks, the distribution of the generalization level (or degree) is highly asymmetrical (Vázquez & Aizen 2004), leading to a nested pattern that in turn confers a high coherence to the network (Bascompte et al. 2003). This implies that specialist species tend to interact exclusively with generalist species, whereas generalist species interact both with specialists and generalists. The former might raise the possibility of integration of specialist alien species into mutualistic networks more than would be expected by random. This might indeed explain the similar generalization levels in native and alien species.

Given that the number of links that an alien plant species can establish is partly explained by the phylogenetic affinity of that species with the native flora (Memmott & Waser 2002), it seems likely that specialist alien species connect to those generalist natives that have some taxonomic affinity with their original mutualists. For example, the European native *Cytisus scoparius*, with zygomorphic flowers specialized for bumblebee pollination, is visited almost exclusively by native and generalist bumblebees in the invaded range in South America (Morales & Aizen 2002). The ornithophilous *Nicotiana glauca* is pollinated by hummingbirds in its native range in central and northern Argentina (Nattero & Cocucci 2007), and receives visits of other hummingbird species in Venezuela (Grases & Ramírez 1998) and of sunbirds in South Africa (Geerts & Pauw 2009). By contrast, *Kalanchoe* sp., another ornithophilous species introduced to Venezuela, pollinated by passeriforms in its native region (South Africa), is not visited by hummingbirds in Venezuela (N. Ramírez, personal communication).

Facilitation among invasive species and evidence for invasional meltdown

A preferential interaction between alien mutualists in which species interact with a higher frequency than expected by chance can lead to a core of alien generalists, or what has been termed an invasion complex (D'Antonio 1990). Positive interactions among invasive species are relatively frequent, especially plant–pollinator and plant–seed disperser interactions. However, there is no evidence to date that such a core of alien generalists within networks is the rule. Indeed, Bruno et al., (2005) showed that alien species are not more likely to benefit alien species than natives. More recently, Aizen et al. (2008) have suggested that the existence of differential interactions among invaders might take place in the most advanced stages of invasion; at the early stages, invasives are integrated in the webs by interacting with natives.

Examples of such invader complexes have been reported from many different types of ecosystems, but especially islands (Traveset & Richardson 2006). The honeybee is an important pollinator of many invasive plants on islands where it has been introduced, such as the Bonin Islands, New Zealand, Tasmania, Azores, Santa Cruz and Tenerife. Some species of bumblebees and *Megachile rotundata* show a preference for alien

plants in New Zealand and Australia, respectively. Alien wasps have favoured the spread of introduced *Ficus* species in continental areas of North America, in Hawaii and New Zealand (references in Richardson et al. 2000a). The same intrinsic plant traits (for example a large floral display, high nectar and/or pollen production) can promote more frequent interactions with invasive pollinators (usually social insects, mainly owing to their high energetic demand to maintain their colonies) than with native pollinators. Likewise, invasive plants that produce large fruit crops can also be mainly dispersed by alien invasive animals. For instance, on Mediterranean islands, rats and rabbits, introduced thousands of years ago, are important dispersers of invasive plants such as *Carpobrotus* spp. In the Canary Islands, the alien squirrel *Atlantoxerus getulus* is dispersing the also invasive *Opuntia maxima* (López-Darias & Nogales 2008). In island ecosystems specifically, mainly because of the lower species richness, we may expect a greater effect of invasion complexes on native biodiversity than in the mainland. More data are, however, needed for a robust test of this hypothesis.

Invader complexes can lead to a process whereby the species involved in the interaction reciprocally improve conditions for survival and spread (invasional meltdown; Simberloff & Von Holle 1999). Many authors have suggested that such processes may be operating in a wide range of ecosystems (references in Simberloff & Von Holle 1999; Traveset & Richardson 2006). We need more research to determine how widespread such invasion complexes are, and how they impact on pollination and seed dispersal networks. Much research is currently underway in this area and a clearer picture should emerge soon.

12.3 THE OTHER SIDE OF THE COIN: MUTUALIMS DISRUPTED – CASUALTIES OF INVASIONS

The dynamics of disruption

Invasive alien species can bring about substantial changes to prevailing mutualistic interactions (Traveset & Richardson 2006), and such alterations can, in turn, mediate subsequent invasion dynamics (Mitchell et al. 2006). The most dramatic changes have been documented in island ecosystems such as those on Hawaii (Waring et al. 1993) and New Zealand

(Kelly et al. 2006), but also in continental situations, such as in South African fynbos (Christian 2001), the dry forests of Thailand (Ghazoul 2004) or the rainforest of Mexico (Roubik & Villanueva-Gutierrez 2009). Such mutualistic disruptions may be caused by plants, animals or pathogens. An example of the last-mentioned was recently reported by McKinney et al. (2009) from the northern Rocky Mountains, where an invasive alien fungus is disrupting the obligate seed-dispersal mutualism involving *Pinus albicaulis*, a keystone subalpine tree species, and the only bird capable of dispersing its large, wingless seeds, the Clark's Nutckacker (*Nucifraga columbiana*). The fungus kills tree branches and significantly reduces cone production, which influences the nutcracker's occurrence and seed dispersal success.

One of the best documented categories of mutualistic disruptions caused by invasions has been widespread changes to plant–animal mutualisms that affect pollination and reproductive success of native plant species. Competitive interactions between native and alien species can involve different, not mutually exclusive mechanisms, which mainly imply changes in the frequency of visits and in interspecific pollen transfer (reviewed in Morales & Traveset 2008). In the presence of more attractive alien species, natives can experience fewer pollinator visits (see, for example, Brown et al. 2002), and/or a reduction in the quality (Ghazoul 2004; Lopezaraiza-Mikel et al. 2007) of visits of some pollinator species owing to changes in their abundance or behaviour (Ghazoul 2002, 2004). In either case, this may lead to a subsequent decrease in pollination levels and seed production of native plants. Research is needed to investigate whether such reductions in seed set have demographic consequences.

Alternatively, the presence of a highly attractive invasive species may facilitate visits to the less attractive native species by means of an 'overall attraction' of pollinators (see Rathcke 1983; Moeller 2005). In the past decade, an increasing number of studies have experimentally evaluated changes in pollination levels and in reproductive success of natives in response to the presence of aliens. A recent meta-analysis found an overall significantly negative effect of alien plants on visitation to and reproduction of native species (Morales & Traveset 2009). The negative effect increased at high relative densities of alien plants and, interestingly, their effect on visitation and reproductive success was most detrimental when alien and native plants had similar flower symmetry or colour, thus highlighting

the importance of phenotypic similarity between aliens and natives in determining the outcome of the interaction. Such a finding is indeed consistent with a prediction of niche theory: that functionally similar invaders should impose the greatest harm on native communities (MacDougall et al. 2009).

Once an alien species is integrated into a network of mutualistic interactions, it can modify key parameters that describe network structure or topology. In natural systems with a nested interaction structure (Bascompte et al. 2003) the impact of an alien species may rapidly cascade through the entire network because all species are closely interlinked (Lopezaraiza-Mikel et al. 2007). Thus, the importance of aliens at the level of network is expected to be pronounced. However, research in this area of invasion biology is in its infancy, both for alien plants and alien pollinators (see Lopezaraiza-Mikel et al. 2007; Aizen et al. 2008; Padrón et al. 2009; Valdovinos et al. 2009; Vilà et al. 2009).

One of the consequences of the asymmetry of mutualistic networks is a low reciprocal dependence between mutualists: if a pollinator, for instance, is strongly reliant on a given plant species, this plant species typically depends only weakly on the services of that pollinator species, and vice versa. Such asymmetry confers stability and robustness to the networks against the loss of species (Vázquez & Aizen 2004; Bascompte et al. 2006). In a study of the impact of invasive plants and pollinators on network architecture, Aizen et al., (2008) analysed the connectivity of 10 networks characterized by contrasting levels in the incidence of invasive species and in their mutual dependence among the interacting species. There were no differences in connectivity (proportion of links relative to all those possible) between invaded and uninvaded networks (as also found by Memmott & Waser (2002) and Olesen et al. (2002)), but the invasive species were found to promote a 'redistribution' of links between plants and animals in the network: a high number of links were transferred from generalist native species to invasive super-generalist species, and therefore the entire network topology was modified. In other words, the invasive species usurp interactions among native mutualists in the process of invasion. In this way, at least at advanced stages of the invasion, supergeneralist invasives can alter the 'foundations' of the network architecture itself, becoming central nodes in it (Aizen et al. 2008), and their removal might significantly alter network topology (Valdovinos et al. 2009). Moreover, because interactions of a low reciprocal

dependence are the most robust against disturbances promoting extinctions (Ollerton et al. 2003), such results suggest that the invasive species and its mutualists might be more resistant to disturbances, which would increase the probability of permanence and survival of such invasive in the network. This, added to a preferential interaction among invasive species, might lead to invasional meltdown, precipitating an even higher impact of the invasion on the native community, similar to those reported for other systems and interactions (see, for example, Grosholz 2005; Griffen et al. 2008; Belote & Jones 2009).

The presence of an invasive species can affect the patterns of pollen flow if pollinators transfer pollen interspecifically, depositing pollen of the invasive on the stigmas of the native, or vice versa, generating a decrease in the quality of pollination. Such a decrease may be due to the deposition of heterospecific pollen on their stigmas, which can interfere with the deposition and/or germination of conspecific pollen and/or to a loss of conspecific pollen on flowers of other species (Morales & Traveset 2008). Such changes can occur independently of changes in the absolute frequency of visits, although sometimes both phenomena occur simultaneously (see, for example, Brown et al. 2002; Ghazoul 2002; Lopezaraiza-Mikel et al. 2007). Only a few studies have evaluated changes in pollen deposition in the presence of an invasive species. Some have found reductions in the deposition of conspecific pollen (Ghazoul 2002; Larson et al. 2006), others have found increases in the deposition of heterospecific pollen (Ghazoul 2002), whereas yet others reported no consistent changes (Grabas & Laverty 1999; Moragues & Traveset 2005; Larson et al. 2006). Although the amount of heterospecific pollen on native stigmas is generally too low to interfere with the deposition of conspecific pollen (Morales & Traveset 2008), it might affect the reproduction of closely related native species if it produces hybrid seeds (Wolf et al. 2001; Burgess et al. 2008). So far, these mechanisms (changes in the frequency of visits and interspecific pollen transfer) have been evaluated separately, and the difference in the approaches used has hampered the evaluation of the relative importance of both mechanisms and their interaction.

Although individual invasive alien species may have a negative impact on particular mutualistic interactions, their effect on the overall community may be neutral or even positive for mutualistic interactions. It is also important to consider that the spatial scale of

investigation affects the estimated strength of competition for pollinators between invasive and native plant species. For instance, the alien geophyte *Oxalis pes-caprae* appears to compete for pollinators with the native *Diplotaxis erucoides* at a scale of a few metres, but at larger scales the presence of *Oxalis* flowers in invaded fields attracts pollinators, facilitating visits to *Diplotaxis* (Jakobsson et al. 2009). Consistent with the arguments of Bulleri et al. (2008), it might well be that competition could operate inherently at a smaller spatial scale than facilitation and thus be more likely to produce results observed in fine-scale studies.

Can invasive alien species replace extinct or declining native mutualists?

Native island pollinators and seed dispersers, which tend to be more prone to extinction than plants (at least at the time scale of years or decades), have been occasionally and unintentionally, replaced by 'ecologically similar' alien species. For instance, in Hawaii, the widespread alien bird *Zosterops japonica* has replaced the extinct native honeycreepers (see Cox & Elmqvist 2000), whereas *Z. lateralis* has replaced native bird pollinators in New Zealand (Kelly et al. 2006). On Mauritius, the ornithophilous flowers of *Nesocodon mauritianus* (Campanulaceae) are currently visited almost exclusively by the introduced red-whiskered bulbul (*Pycnonotus jocosus*) (Linnebjerg et al. 2009). In Mallorca (Balearic Islands, western Mediterranean), the main disperser of the native shrub *Cneorum tricoccon* is the alien pine marten *Martes martes*, which appears to have replaced the extinct endemic lizards that performed this role before carnivores arrived on these islands (Traveset 1995). Given that the decline in native species and the arrival of alien species is frequently associated with habitat disturbance, it is often difficult to discern the relation of causality between a native species regression and an alien invasion.

An illustrative case of a functional replacement is the invasion of the alien bumblebee *Bombus ruderatus* in the Andean forests of Patagonia, after their deliberate introduction to southern Chile in 1982. This species was detected in native communities in 1994, and since then its abundance and distribution range have increased (Morales 2007). In 1996, a census of flower visitors to the native *Alstroemeria aurea* along a gradient of anthropogenic disturbance showed a decrease in the relative frequency of its main pollina-

tor, the native bumblebee *B. dahlbomii*, parallel to an increase in the frequency of the invasive pollinator, suggesting that such disturbance would favour the invasive species and hamper the native one. Later, a long-term study on the same plant species in a non-disturbed area confirmed that the invasive species is favoured by habitat alteration but also that it has indeed displaced the native species (Madjidian et al. 2008). This study highlights the necessity of long-term studies that consider different factors that can co-vary with changes in abundance of invasive and native species at the time that they evaluate the impact of the former on the latter (Stout & Morales 2009). This will allow distinguishing between passive replacements and competitive displacements of native by the invasive alien species. The study also highlights that these replacement processes can occur very quickly, in just a few years.

In general, we have rather little information on whether alien species act as functional surrogates of, and occupy the same niches as, extinct native species. Regarding pollinators, several studies have shown that introduced pollinators are not as effective as natives they have replaced (see Traveset & Richardson 2006). For instance, they may promote reduced outcrossing rates which can result in a reduced gene flow and/or promote hybridization between native plants (England et al. 2001; Dick et al. 2003). Introduced bees can affect plant fitness by actively reducing pollination of native plants (physical interference with native pollinators on the flowers; Gross & Mackay 1998) or by altering pollen dispersal (see, for example, Westerkamp 1991; Paton 1993; Celebrezze & Paton 2004).

Hansen et al. (2002) showed experimentally that the exclusion of bird pollinators reduced seed set in two Mauritian trees that were otherwise visited primarily by alien honeybees, possibly owing to higher levels of within-plant foraging behaviour of honeybees. Likewise, the introduced *Bombus ruderatus* is not as effective for *Alstroemeria* as is *B. dahlbomi* (Madjidian et al. 2008). For seed dispersers, we do not know to what extent they have similar foraging behaviours and move seeds to similar sites as extinct native species. Many oceanic islands, for instance, have lost a large proportion of native frugivorous avifauna, although avian species richness has remained fairly constant because extinction has been balanced by colonization and naturalization of alien bird species (see, for example, Sax et al. 2002; Foster & Robinson 2007; Cheke & Hume 2008). Despite this, alien birds

often act as legitimate, and highly effective, dispersers of native plants. We do not know exactly how these alien birds influence the dispersal of native plants. In Hawaii, alien birds disperse many native understorey shrubs (Foster & Robinson 2007), but elsewhere alien birds disperse mainly alien plant species, like the red-whiskered bulbul on La Reunion (Mandon-Dalger et al. 2004). In New Zealand, the contribution of alien birds to seed dispersal of native plants is unexpectedly small (Kelly et al. 2006). In the Bonin Islands, Kawakami et al. (2009) found that introduced white-eyes appear to compensate for extinct native seed dispersers.

The magnitude of the current biodiversity crisis calls for radical conservation measures in some cases (e.g. rewilding in North America; 'managed relocation' involving the planned movement of threatened species to areas outside their current range where prospects of long-term survival are improved; habitat restoration using alien birds in Hawaii). Native species that have recently become extinct or those in which populations are declining might be replaced by functionally equivalent species. This might be especially necessary to buffer ecosystems against the loss of keystone species (*hubs* in the community networks).

Invasions and mutualisms in fragile ecosystems (islands)

The integration of invasive species into receptive communities by means of facilitative interactions with native species is likely to occur frequently in island ecosystems, where many native mutualists have wider trophic niches than in mainland systems. On islands, all possible detrimental effects are magnified exponentially, with reduced population sizes, absence of specialization in the native interactions or the unpredictability of resource production (see review in Kaiser-Bunbury et al. 2010). Many cases have been documented on islands where alien species have strongly negative impacts on native communities; both the magnitude and the mechanisms of the impacts vary depending on the functional group to which the alien species belongs and its abundance (Traveset & Richardson 2006; Traveset et al. 2009a). In any case, the invasive species has the capacity to alter significantly the reproductive success of the natives at the same time as altering the structure of pollination or disperser networks.

The introduction of *Apis mellifera* and *Bombus terrestris* to many islands around the world has had devastating effects on native bees (Goulson 2003) as a direct result of competition for floral resources (see, for example, Kato et al. 1999) or competition for nest sites (see, for example, Wenner & Thorp 1994), and even on the reproductive success of plants that depended upon them. This is because such alien species may reduce seed production, modify gene flow and promote hybridization between closely related species (see Traveset & Richardson 2006). Honeybees are already reported to have displaced native pollinators on many islands. For instance, small endemic solitary bees and white-eyes have been replaced in the Bonin Islands, Japan (Kato et al. 1999) and in Mauritius (Hansen et al. 2002), respectively. Similarly, honeyeaters have decreased in numbers in Australia, which has been attributed to the introduction of honeybees (Paton 1993) or bumblebees (Hingston et al. 2002; Hingston 2005). These two alien species have integrated well into the pollinator networks of many invaded island communities in Japan (Abe 2006), Tasmania (Hingston et al. 2002), the Mascarene Islands (Olesen et al. 2002) and the Canary Islands (Dupont et al. 2004). Invasive ants, such as *Anoplolepis gracilipes*, *Technomyrmex albipes* and *Wasmannia auropunctata* are also having dramatic effects on the biota of different islands where they have been introduced, such as New Caledonia (Jourdan et al. 2001), Mauritius (Hansen & Müller 2009) and Samoa (Savage et al. 2009). The Argentine ant *Linepithema humile* has significantly reduced the abundance of two important pollinators in Hawaii, the moth *Agrotis* sp. and the solitary bee *Hylaeus volcanica*, with potentially severe negative effects on the seed set of many native plant species (Cole et al. 1992). Moreover, a recent review by Rodríguez-Cabal et al., (2009) on the impact of this invasive ant on seed dispersal shows that it displaces native ants in most invaded areas and that it does not act as a legitimate disperser, although this depends upon seed traits such as size and percent reward. This suggests that Argentine ant invasions may drive shifts in community diversity (e.g. Christian 2001) and parallel changes in ecosystem functioning.

The integration of invasives into island communities is usually facilitated by generalist (sometimes supergeneralist) pollinators and dispersers that include nectar and pollen or fleshy fruits in their diets (Olesen et al. 2002; Morales & Aizen 2006; Traveset & Richardson 2006; Aizen et al. 2008;

Linnebjerg et al. 2009). For instance, *Carpobrotus* spp. are highly invasive on many Mediterranean islands, and are pollinated by a large diversity of native insects that are attracted by their abundant and attractive flowers (Moragues & Traveset 2005). A different situation occurs with the invasive *Kalanchoe pinnata* (Crassulaceae) in the Galápagos Islands. This plant, with a great capacity for vegetative growth, has complex flowers, which are not effectively visited by native pollinators in these islands (L. Navarro, personal communication). Kueffer et al. (2009) compared fruit traits between native and invasive alien plants on oceanic islands. They found fruit quality to be more variable in the latter, suggesting that this might represent an advantage for them during the invasion process. They also proposed that island plants produce fruits of lower energy content than invasives, probably because of reduced competition for dispersal. Further work is needed on more oceanic islands to examine this idea.

Introduced vertebrates are the animal group with most detrimental effects on the native island floras and faunas (Sax & Gaines 2008), including indirect effects on native mutualisms (see, for example, Nogales et al. 2004, 2005, 2006; Traveset & Riera 2005; Kelly et al. 2006; Traveset et al. 2009b). The negative impacts of, for example, introduced goats, rats and parrots on plant fitness and dispersal can be multifold. These include the direct consumption of native plants and, more indirectly, the reduction of populations of legitimate seed dispersers (see Riera et al. 2002; Traveset & Richardson 2006). There is also much evidence that rodents, cats and opossums have overwhelming effects on native seed dispersers (see, for example, Jourdan et al. 2001; García 2002; Nogales et al. 2004; Kelly et al. 2006; Towns et al. 2006; Hansen & Müller 2009).

Given the alarming increase in disturbances in island ecosystems, further studies are needed to determine the range of impacts of invasive species on mutualistic interactions at different levels (population, species, community and ecosystem). The loss of some mutualistic interactions often leads to decreases in recruitment rates of plants that depend upon them, even cascading into local or total extinctions. The lack of studies at community level precludes us from making global estimates of the impact of the loss of such mutualisms and from evaluating the degree of resilience of mutualistic networks possess with respect to different types of disturbance.

12.4   CHALLENGES FOR THE FUTURE

Biological invasions provide superb natural experiments at a global scale, offering exciting new insights on many aspects of ecology, including the factors that mediate ecosystem functioning and stability. Ecologists have begun to grasp this opportunity in the past decade, resulting in substantial 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 still poorly documented, but the picture that is emerging is that they are often profound. Most insights are still from observations, and more manipulative experiments are needed to disentangle the full complexity of species interactions and to unravel the implications of the multiple interactive factors for community and ecosystem stability. Assessments of actual and potential impacts of introduced species have until recently all but ignored effects on mutualisms: a revised framework for incorporating such effects in impact assessments is needed.

Many restoration projects are underway to address degradation of ecosystems due to invasions and other factors. Too few such projects consider positive species interactions explicitly, or pay enough attention to keystone species (e.g. species that interact with large number of pollinators or dispersers; 'hubs' in network terminology) and ecosystem engineers (species that create or modify habitats). The integration of results such as those reviewed in this chapter is crucial for improving the efficiency of restoration efforts in yielding sustainable restored communities and landscapes. The use of ecosystem engineers (either native or alien) can enhance recruitment of native species, either directly or indirectly. For instance, many studies have shown the important effect of plant facilitation for the recruitment of many plant species, especially in stressful environments (Brooker et al. 2008). Such engineers can also create new opportunities for invaders, and there are examples of this both for terrestrial (Badano et al. 2007) and marine systems (Tweedley et al. 2008). Pollination and seed dispersal processes operate on very different spatial and temporal scales, as pollination is mainly dominated by invertebrates whereas seed dispersal is largely carried out by vertebrates. Therefore, restoration programmes that focus mainly on pollination may not necessarily favour the maintenance of seed dispersal interactions, and vice versa.

Insights from invasions can inform decisions on radical conservation strategies, such as managed relocation and 'rewilding' of ecosystems by introducing extant species, taxon substitutions, as functional replacements or ecological analogues for extinct native species. Using alien species as a management tool can in some cases provide beneficial interactions in systems where native mutualists have disappeared. For example, in some heavily degraded island systems, honeybees may act as pollinators of native species, thus contributing positively to the native plant fitness. In Mauritius, honeybees were the major flower visitors of 43 out of 74 plant species (58%) in a weeded conservation management area (Kaiser-Bunbury et al. 2010).

When trying to understand the dynamics of plant–animal interactions in an increasingly fragmented and homogenized world, we also need to consider the role of evolution. Some of the new interactions established between species in invaded communities can evolve quickly, sometimes over a few decades and across complex geographical landscapes (Thompson 2002). We need much better information on the geographical scales at which mutualistic interactions are organized ecologically and evolutionarily.

It is increasingly accepted by conservation managers that what we need to preserve is the 'interaction biodiversity' of communities. Interactions are the glue of biodiversity, linking species locally and over broader geographical scales. Entire community networks can collapse if such interactions weaken or if a fraction of them disappear. A network framework may improve many conservation efforts and help to take better management decisions. We need remnants of relatively pristine, geographically complex landscapes as benchmarks for interaction biodiversity (Thompson 1996). Such landscapes are becoming scarce; maintaining interaction biodiversity must therefore also require a better understanding of how to minimize the increasingly pervasive influence of the different drivers of global change, one of them being invasive species. This comes back to understanding species interactions and evolution of specialization in such interactions.

ACKNOWLEDGEMENTS

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