

Biological invasions as disruptors of plant reproductive mutualisms

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Invasive alien species affect the composition and functioning of invaded ecosystems in many ways, altering ecological interactions that have arisen over evolutionary timescales. Specifically, disruptions to pollination and seed-dispersal mutualistic interactions are often documented, although the profound implications of such impacts are not widely recognized. Such disruptions can occur via the introduction of alien pollinators, seed dispersers, herbivores, predators or plants, and we define here the many potential outcomes of each situation. The frequency and circumstances under which each category of mechanisms operates are also poorly known. Most evidence is from population-level studies, and the implications for global biodiversity are difficult to predict. Further insights are needed on the degree of resilience in interaction networks, but the preliminary picture suggests that invasive species frequently cause profound disruptions to plant reproductive mutualisms.

Introduction

Biological invasions threaten global biodiversity by altering the structure and functioning of ecosystems [1,2]. Invasive plant species (see Glossary) often modify system-level flows and the availability and/or quality of space and resources [2,3]. Many studies have focused on the impacts of invaders on species diversity and community composition and functioning, but only a few have explored the underlying mechanisms [2]. Although invasive species can cause the extinction of native ones, good-quality supporting data are scarce [4]. It is known, however, that invaders can alter ecological interactions that have arisen over evolutionary timescales and, thus, could modify evolutionary trajectories. In particular, alien species can disrupt mutualistic plant–animal interactions, such as pollination or seed dispersal [5–8]. Here, we review the information available on this subject and identify the range of mechanisms by which invaders can interfere with mutualistic interactions. In so doing, we evaluate the vulnerability of such interactions at a global scale. However, insufficient information is available to enable us to compare the impacts of invasive species on mutualisms with those of direct competition for space, light, soil nutrients or water.

Pollination and seed-dispersal mutualisms can have a fundamental role in the regeneration of natural communities and are crucial for maintaining the structure and diversity of some ecosystems [5,9,10]. We thus must be able to predict the ecological and evolutionary impact of any factor that can disrupt them. Most information available about mutualistic disruptions owing to biological invasions is from islands, although an increasing number of studies provide data from continental areas. Biological invasions appear to pose a greater hazard on islands than on continents mainly because of the intrinsic characteristics of the island biota, such as smaller population sizes and isolated evolution [8,11,12].

Disruption of plant–pollinator interactions

Most angiosperm species rely either facultatively or obligatorily on animals for seed production. Many of those plants are generalists, being visited by a wide

Glossary

Allelopathy: the production of specific biomolecules by one plant, mostly secondary metabolites, that can influence the growth and development of other neighbouring plants.

Invasive species: here, ‘invasive’ always refers to alien species (those whose occurrence in an area is due to their introduction, intentionally or accidentally, as a result of human activity) that recruit reproductive offspring, often in large numbers, at considerable distances from parent plants and, thus, can spread at a considerable rate.

Disruption of pollinator–plant or seed disperser–plant interactions: the effect that any factor (habitat fragmentation, introduction of alien species, hunting, etc.) could have on the quantitative and/or qualitative components of pollination or dispersal effectiveness and, ultimately, on plant fitness. Quantitative aspects refer to the number of pollen grains deposited or the number of seeds dispersed. Qualitative changes involve the value of either the pollen (in genetic terms) or the microhabitat where seeds are left [10],[10]

Endozoochory: seed dispersal carried out by frugivorous animals that ingest fleshy fruits and defecate or regurgitate viable seeds intact.

Invasional meltdown: process by which a group of alien species facilitate one another’s invasion in various ways, increasing the likelihood of survival and/or of ecological impact, and possibly the magnitude of impact [50],[50]

Legitimate pollination or dispersal: pollination or dispersal that is effective. A legitimate pollinator contacts the reproductive organs of the flowers and transports pollen among flowers. A legitimate disperser consumes the fruits and transports their seeds to adequate sites for germination and seedling growth.

Mutualistic compartments: functional groups of species linked by exclusive or frequent mutualisms (e.g. deep-corolla plants pollinated by long-tongued bees).

Native taxa: those that have originated in a given area without human involvement or that arrived there without intentional or unintentional intervention of humans from an area in which they are native (synonyms: indigenous taxa).

Seed set: number of seeds produced relative to the number of flowers.

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diversity of pollinators that, in turn, visit flowers of a great variety of species [13]. Therefore, introduced pollinators [14,15] or plants [16] have a good chance of integrating within pollination webs in the newly invaded ecosystems. Here, we explore the mechanisms whereby invaders in four broad categories could modify the outcome of native plant–pollinator mutualisms, and we give examples of systems already disrupted (Table 1).

Introduction of an alien pollinator

An alien pollinator is likely to have negative effects on plant populations if it decreases the quantity and/or quality of pollen transferred among plants, resulting in reduced seed set and decreased plant fitness (Figure 1). Plants that are usually seed limited are likely to be the most vulnerable [17,18]. Moreover, a quantitatively important pollinator (with high flower visitation rates) might be a poor-quality pollinator if it does not transfer pollen effectively [19–21]. The same properties that make a pollinator invasive (e.g. high rates of intrinsic population increase) might also be associated with the proportion of pollen that is fed to young instead of being transferred among plants. Nevertheless, alien pollinators might either increase plant fitness by increasing pollen transfer among plants [6,22,23], or have no effect if flower visitation rate is relatively low [24] or if such increased pollen transfer does not increase reproductive success.

That most invasive pollinators are generalists facilitates their integration into native mutualistic webs and, in turn, their establishment and spread within the invaded ecosystems [15,22,24]. Such a generalized foraging syndrome makes the interactions with native plants diffuse and relatively weak and, thus, the impact on native mutualisms might be weaker than expected. Native plants visited by several native pollinators are likely to be more buffered from any negative (or positive) impacts of an alien pollinator than are plants that depend upon only one or two pollinators. However, a highly coevolved specialist mutualism might be more protected against any alien entering the pollination web. The scarce data currently available preclude testing such hypotheses. Traits other than the degree of generalism and pollinator-limited seed set that could make plants more susceptible to the influence of alien pollinators include a low native pollinator constancy, a restricted flowering period, few floral rewards, or low flower and seed crops [17].

Honeybees *Apis mellifera* are a typical example of a successful worldwide pollinator invasion. They visit many plant species and are quantitatively effective pollinators in several mutualistic systems [22,23,25,26], although are qualitatively poorer pollinators than are natives in others [6,12,19,20,27]. Honeybees often decrease flower visitation rate by native pollinators through exploitative or interference competition [12,23,28] and can alter plant genetic structure by promoting greater levels of selfing [12,28,29]. Such competition has a potentially negative impact on plant fitness [12,19,20,28], although no cascading consequences have yet been demonstrated [22,26].

Native pollinators might be outcompeted by an invasive pollinator depending upon the competitive superiority of

the invader and whether resources were limiting. Different studies have claimed competition between introduced honeybees and native pollinators, although only a few have measured competition directly [5,22,25]. Other invasive insects, such as bumblebees *Bombus terrestris*, the alfalfa leafcutter bee *Megachile rotundata* and wasps in the genus *Vespula*, are also potentially harmful to native pollinators [14,24,26]. Long-term studies on fecundity, survival or population density of native pollinators are lacking but are essential for assessing the threat that such invasive insects pose to native pollinators [25,26,30]. Likewise, the long-term consequences of changes in the local pollinator fauna for the native flora also require investigation.

Invasive pollinators can also replace lost or declining native pollinators to some extent. This has been found in fragmented landscapes [23,29] and in several oceanic islands: for example, in Hawaii, the vine *Freycinetia arborea* (originally pollinated by now-extinct bird species) survives thanks to the Japanese silveryeye *Zosterops japonica* [11]; in Mauritius, the introduced red-whiskered bulbul *Pycnonotus jocosus* visits the flowers of the extremely rare endemic *Nesocodon mauritanus* more frequently than do native birds [31]; and in New Zealand, the recently arrived silveryeye *Zosterops lateralis* has replaced several species of extinct or declining native bird pollinators [24]. The ecological and evolutionary consequences of such replacements for the plants are still unknown.

Introduction of an alien herbivore

An animal that consumes vegetative or reproductive parts of a plant can exert considerable influence on plant–pollinator mutualisms. Such influence can be directly negative for the plant (e.g. by consuming flowers) and/or for the pollinator (by reducing resources such as nectar and pollen). For example, in New Zealand, the eradication of introduced possums *Trichosurus vulpecula* and wallabies *Petrogale penicillata* from some islands has led to significant increases in the flowering of several plant species that, in turn, have increased the population sizes of their bird pollinators [32]. Introduced herbivores, particularly ungulates, are usually generalists and can significantly affect plant–pollinator mutualisms in invaded areas [33]. The simple impact of trampling can result in smaller population sizes and, thus, indirectly affect patterns of pollination visits and plant reproductive success [33]. From an evolutionary perspective, herbivores could also counteract pollinator-mediated selection on floral traits, such as flowering phenology, quantity and quality of floral nectar, pollen performance or flower number [34].

Introduction of an alien predator

An introduced invasive predator can alter the population growth of pollinators and, in turn, indirectly affect the fitness of plants that strongly depend upon them. In the Canary and Balearic Islands, alien carnivores have led to the extinction of native lizards that were important pollinators for a variety of plant species [35,36]. Introduced rats, cats and stoats in New Zealand have reduced

Table 1. Invasive species that have altered native plant–pollinator mutualisms and the presumable magnitude of the effect based on available data

Invasive species	Plant–pollinator mutualism altered ^a	Region	Magnitude of the effect	Refs	
Insects					
Honeybee <i>Apis mellifera</i>	<i>Sideroxylon</i> spp.–native birds	Mauritius	Moderate for plants; unknown for native birds	[12]	
	<i>Zosterops</i> spp.	Bonin Islands	Unknown for plants; strong for native bees	[52]	
	Native plants–native bees	New Caledonia	Unknown for plants; strong for native bees	[30]	
	Native plants–native ants and native bees	Santa Cruz Island	Unknown for plants; strong for native bees	[60]	
	<i>Echium wildpretii</i> –native birds and insects	Canary Islands	Weak for plant; unknown for pollinators	[28]	
	<i>Grevillea barklyana</i> –native birds	Australia	Moderate for plant; unknown for pollinators	[27,61]	
	<i>Callistemon rugulosus</i> –native bees and/or birds	Australia	Moderate for plants; strong for some pollinators	[6]	
	<i>Correa reflexa</i> –native bees and/or birds	South America	Weak for plant; unknown for pollinators	[62]	
	<i>Prosopis nigra</i> –native insects	Australia	Weak for plant; unknown for pollinators	[23]	
	<i>Cercidium australe</i> –native insects	Australia	Moderate for plant; unknown for pollinators	[19]	
	<i>Dillwynia juniperina</i> –native bees	Australia	Moderate for plant; strong for native bees	[20]	
	<i>Brachyloma ericoides</i> –native birds	French Guiana	Unknown for most plants; strong for native bees	[59]	
	Bumblebee <i>Bombus terrestris</i>	At least 26 native plants pollinated by native insects and/or birds	Tasmania	Unknown for plants and pollinators	[14]
		Native plants–native insects and/or birds	Australia	Unknown for plants and pollinators	[63]
Native plants–native bees		Israel	Unknown for plants; strong for some native bees	[64]	
Little fire ant <i>Wasmannia auropunctata</i>	Native plants–native geckos	New Caledonia	Unknown for plants and pollinators	[37]	
	Argentine ant <i>Linepithema humile</i>	Western Med. Basin	Moderate on plant; strong for pollinators	[65]	
Mammals					
Weasel <i>Mustela nivalis</i>	<i>Euphorbia dendroides</i> – <i>Podarcis lilfordi</i>	Balearic Islands	Weak for plant; strong for endemic lizards	[36]	
Pine marten <i>Martes martes</i>					
Genet <i>Genetta genetta</i>					
Stoat <i>Mustela erminea</i>	Native plants–short-tailed bats <i>Mystacina</i> spp.	New Zealand	Unknown for most plants; strong for pollinators	[24]	
Rat <i>Rattus</i> spp.	Native plants–native birds				
Possum <i>Trichosurus vulpecula</i>	(e.g. stitchbirds <i>Notiomystis cincta</i>)				
Reptiles					
<i>Boiga irregularis</i>	<i>Freycinetia reineckeii</i> – <i>Pteropus</i> spp.;	Guam Island (South Pacific)	Unknown for plants and pollinators	[66]	
	Native plants–native birds and bats				
Plants					
Tagasaste <i>Cytisus palmensis</i>	<i>Vaccinium calicimum</i> –native birds	Hawaii	Unknown for plants and pollinators	[67]	
	<i>Metrosideros polymorpha</i> –native birds				
Himalayan balsam <i>Impatiens glandulifera</i>	<i>Stachys palustris</i> –native insects	Central Europe	Moderate for plant; unknown for pollinators	[68]	
Purple loosestrife <i>Lythrum salicaria</i>	<i>L. alatum</i> –native insects	Continental USA	Moderate for plant; unknown for pollinators	[41]	
Christmas bush <i>Chromolaena odorata</i>	<i>Dipterocarpus obtusifolius</i> –native butterflies	Thailand	Weak for plant; unknown for pollinators	[69]	
<i>Carpobrotus acinaciformis</i>	Native plants–native insects	Balearic Islands	Weak for plants; unknown for pollinators	[40]	

^aWhen no specific names are given, several or many species are involved.

populations of endemic nectarivorous birds and bats that pollinate a diverse array of plants, some of which are now pollen limited [24]. In New Caledonia, the invasive ant *Wasmannia auropunctata* is threatening populations of

several species of geckos [37] that pollinate and disperse several plant species (T. Whitaker, personal communication). Given the global importance of such ant invasions [38], it is necessary to determine how they influence the

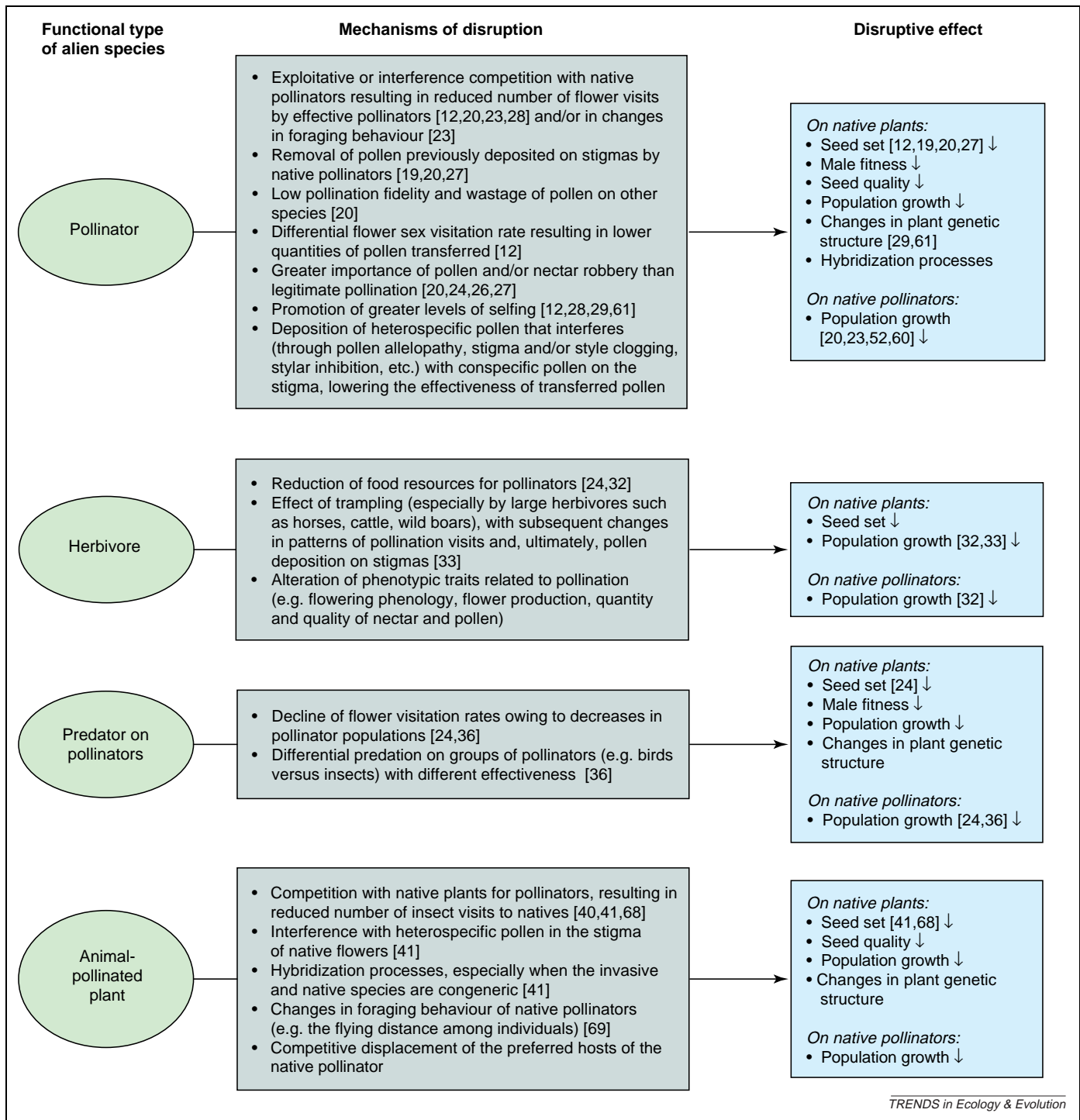


Figure 1. List of possible mechanisms by which alien (invasive or not) species belonging to different functional types might disrupt mutualistic pollination interactions. More than one mechanism of disruption might act on a particular system. References are given only when such mechanisms of disruption or the disruptive effect (on different components of plant and pollinator fitness) have been reported in studies involving alien species. Arrows indicate the possible consequences that such disruption mechanisms can lead to.

outcome of plant–animal mutualisms. Predator species, such as carnivorous species on islands, that can displace native fauna from their habitats are perhaps the most likely to disrupt native plant–pollinator interactions, especially in specialized systems [8].

Moreover, the indirect effects on native mutualists through the introduction of diseases or parasites carried by alien species require further investigation. Malaria transmitted by introduced mosquitoes in Hawaii, for

instance, has contributed to the extinction of over a third of the endemic bird species, with probable cascading effects on many endemic ornithophilous plants [11].

Introduction of an alien plant

An animal-pollinated invasive plant has great potential to disrupt interactions between native plants and pollinators in various ways (Figure 1). As most invasive plants are pollinator generalists, their integration into

pollination webs is facilitated and, in turn, their establishment and spread can be enhanced, by such mutualists [39]. An invasive plant bearing rich floral resources, with large or prolonged floral displays (e.g. *Carpobrotus* spp., *Lantana camara*, *Mimosa pigra*), could have a strong impact on a native plant if it was preferred by pollinators and this resulted in a lower reproductive success of the native. Only a few studies have investigated the competition for pollinators between alien and native plants (Table 1) and most have found evidence for it, although a facilitative effect is also possible [40]. Competition has been reported with the invasive Asian *Impatiens glandulifera*, which reduces the number of pollinators and seed set of the native *Stachys palustris* by ~50% and ~25%, respectively; the invader *Chromolaena odorata* in a tropical dry forest in Thailand also reduces the frequency of butterfly visits to flowers of the native *Dipterocarpus obtusifolius* (Table 1). Sharing pollinators can also imply hybridisation processes, especially between congeneric species, with implications for the native plant fitness, as reported for the genus *Lythrum* in the continental USA [41]. Other potential pollinator-mediated effects of invasive plants on native flora include changes in gene flow and decreased quality of pollen delivered, with subsequent reduction in seed set [41].

Invasive plants can also have direct effects on the native pollinator fauna. Plants benefit from the mutualism established with native fauna [39], but pollinators, in turn, benefit from the new resources. In northern New South Wales, plant invasions appear important for maintaining animal populations in fragmented systems (C.R. Gosper, PhD thesis, University of Wollongong, 2004) and the butterfly fauna of an urban Californian area depends mainly on naturalized weeds [42]. However, alien plants can also reduce the reproductive success of pollinators if, for instance, the plants are toxic to larvae of the insects that visit and oviposit on them [42]. An invasive plant might also indirectly impact the pollinator fauna of the invaded area if it competitively displaces the preferred hosts of the native pollinators.

Disruption of plant–seed disperser interactions

Animal dispersers contribute significantly to maintaining the structure and diversity of different natural communities (e.g. flying foxes in the South Pacific islands [11] or ants in South African fynbos [7]) and can have an important role in many others, for example in humid tropical forests, where vertebrates disperse 75–90% of the woody taxa [10]. Despite the loss of native dispersers as a result of widespread invasions [7,11,24], impacts on seed dispersal mutualisms are still poorly documented (Table 2).

Table 2. Invasive species that have altered native plant-dispersal mutualisms and the presumable magnitude of the effect based on available data

Invasive species	Plant–dispersal mutualism altered ^a	Region	Magnitude of effect	Refs
Insects				
Argentine ant <i>Linepithema humile</i>	Native plants–native ants	South African fynbos; Western Med. Basin; California	Strong for some plants; strong for dispersers	[7,70,71]
Little fire ant <i>Wasmannia auropunctata</i>	Native plants–native geckos	New Caledonia	Unknown for plants and dispersers	[37]
Birds				
Starling <i>Sturnus vulgaris</i>	Native plants–native birds	New Zealand	Unknown for plants and dispersers	[43]
Blackbird <i>Turdus merula</i>				
Song thrush <i>Turdus philomelos</i>				
White-eye <i>Zosterops japonicus</i>	Native plants–endemic White-eye <i>Apalopteron familiare</i>	Bonin Islands	Weak for plants and birds	[72]
Mammals				
Stoat <i>Mustela erminea</i>	Native plants–short-tailed bats <i>Mystacina</i> spp.	New Zealand	Unknown for most plants; strong for endemic dispersers (in severe decline)	[24,32]
Rat <i>Rattus</i> spp.	Native plants–native birds			
Possum <i>Trichosurus vulpecula</i>	(e.g. kokako <i>Callaeas cinerea</i> , kereru <i>Hemiphaga novaeseelandiae</i>)			
Cat <i>Felis catus</i>	Native plants–native birds/lizards (<i>Podarcis</i> spp.)	Balearic Islands	Strong for some plants; strong for dispersers (extinct from some islands)	[8,45]
Pine marten <i>Martes martes</i>				
Genet <i>Genetta genetta</i>				
Weasel <i>Mustela nivalis</i>				
Cat <i>F. catus</i>	Native plants– <i>Gallotia</i> spp. (endemic lizards)	Canary Islands	Unknown for most plants; strong for dispersers	[35]
Cat <i>F. catus</i>				
Plants				
Wild tobacco bush <i>Solanum mauritianum</i>	Native plants–Rameron pigeon <i>Columba arquatrix</i>	South Africa	Strong for most plants; unknown for dispersers	[48]
Hawthorn <i>Crataegus monogyna</i>	<i>Crataegus douglassii</i> <i>suksdorfii</i> –native birds	Continental USA	Unknown for plant and dispersers	[47]
<i>Chrysanthemoides monilifera</i>	Native plants–native birds	New South Wales, Australia	Strong for most plants; unknown for dispersers	^b

^aWhen no specific names are given, several or many species are involved.

^bC.R. Gosper, PhD thesis, University of Wollongong, 2004.

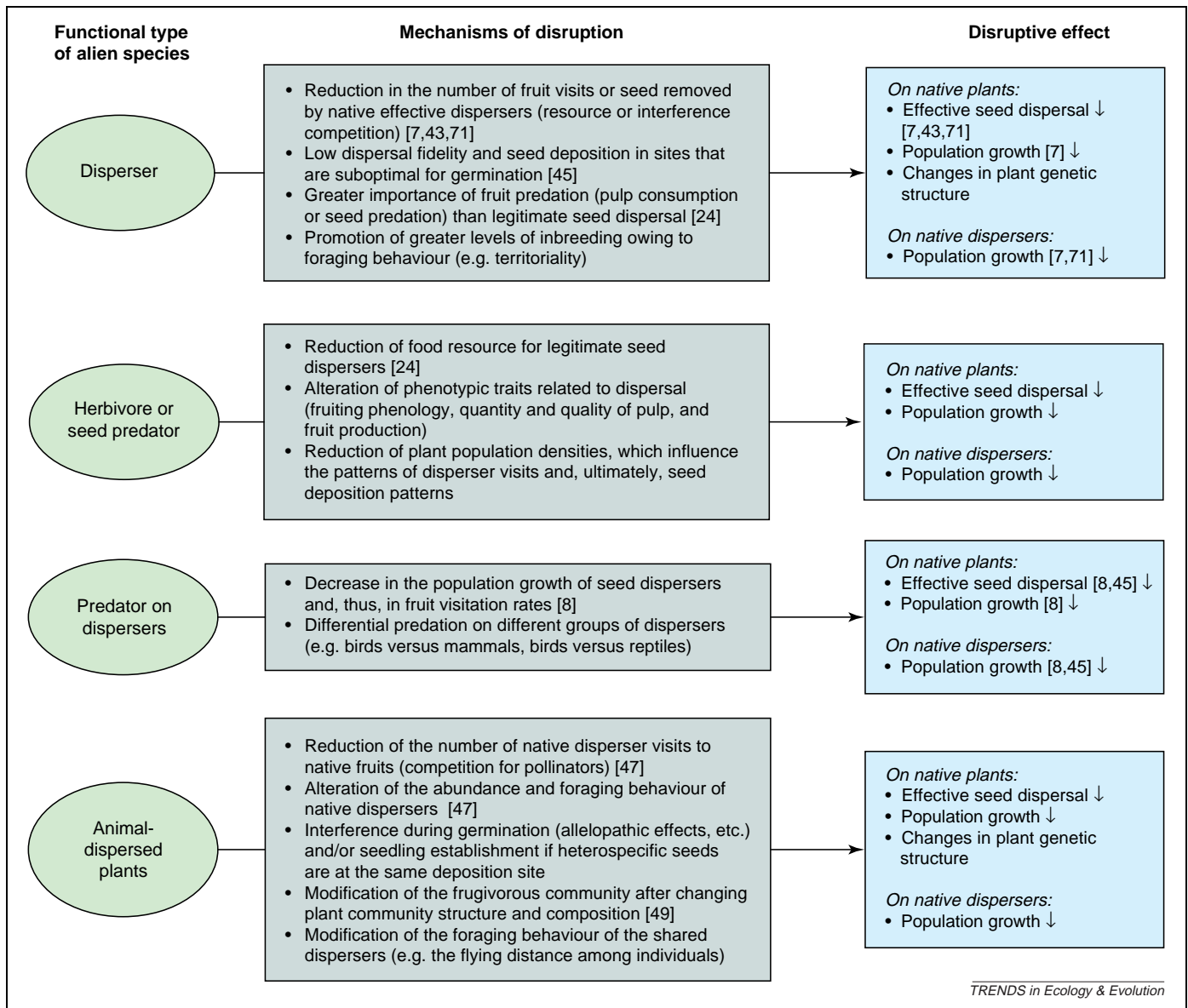


Figure 2. List of possible mechanisms by which alien species belonging to different functional types might disrupt mutualistic seed-dispersal interactions. More than one mechanism of disruption might act on a particular system. References are given only when such mechanisms of disruption or the disruptive effect (on different components of plant and disperser fitness) has been reported for alien species. Arrows indicate the possible consequences that such disruption mechanisms can lead to.

As in the case of pollination, there is a high level of generalism in seed-dispersal systems; endozoochorous plants usually rely on a wide range of species that, in turn, consume the fruits of a variety of plants [13]. Therefore, alien dispersers or plants encounter few obstacles to infiltrating native seed dispersal networks. We explore here the possible mechanisms whereby invaders can disrupt the native plant-disperser interactions (Figure 2).

Introduction of an alien seed disperser

An introduced frugivorous animal can be an effective seed disperser of many native plants [24,43–45] and might even increase plant fitness when seed dispersal is limiting [44]. By contrast, its effect on plant populations might be either low [24], or even detrimental, if it is an inefficient disperser that, for example, deposits most seeds on sites that are unsuitable for germination [45], if it outcompetes legitimate native dispersers [43], and/or it modifies either

the seed shadow or the germination patterns generated by native dispersers [45]. As in pollination systems, the quantity and quality components of dispersal effectiveness might not be correlated and, thus, both need to be assessed to determine the relative importance of an alien disperser for plant dispersal [24]. The impact of such a disperser is likely to be low if fruits are abundant and not limiting, if its fruit visitation rates are relatively low, if it has similar foraging behaviour to natives, and/or if the plant does not strongly rely on dispersers for regeneration.

Native dispersers might be negatively affected by an alien seed disperser that is competitively superior to them, especially if resources are scarce. Alien grey squirrels *Sciurus carolinensis*, for instance, displace native squirrels *S. vulgaris* in Europe [46], with probable negative (but as yet unconfirmed) consequences for the plants dispersed by the latter. If there is no competition between alien and native dispersers, the impact will be minimal [47].

Introduction of a herbivore (including seed predators)

The dispersal success of a plant can be modified by introduced herbivores (e.g. parrots, rats and goats) either directly by consuming vegetative or reproductive parts and decreasing seed dispersal rates [24], or indirectly by negatively affecting populations of native legitimate dispersers, as found in the South African fynbos, where the Argentine ant *Linepithema humile* has displaced native ants, subsequently reducing plant densities of large-seeded Proteaceae that depended upon them and, ultimately, altering plant community composition [7]. The impact of the ant *W. auropunctata* in many parts of the world [37,38] might be shown to be as strong.

Introduction of an alien predator

Alien animals that prey on native dispersers can influence plant dispersal success. To date, all evidence is from island systems. In New Zealand, introduced possums, ship rats, cats and stoats are altering the populations of native seed dispersers, such as stitchbirds and short-tailed bats *Mystacina robusta* and *M. tuberculata* [24,32]. Carnivorous mammals introduced in the Balearics led to the extinction of the lacertid *Podarcis lilfordi* from some of these islands, causing, in turn, the regression of *Daphne rodriguezii*, an endemic shrub that depends upon the lizard for dispersal [8].

Introduction of an alien plant

A fleshy fruited invasive plant that reaches a new area could alter in many ways the dispersal patterns of native plants that fruit simultaneously but that have either less attractive or more concentrated fruit displays. Such competition for dispersers has been documented in Australia (C.R. Gosper, PhD thesis, University of Wollongong, 2004), Oregon [47] and South Africa [48]. Moreover, a mixed diet of alien and native fruits might result in native seeds being dispersed in microhabitats that are unsuitable for germination. Germination of native seeds might be altered further as a result of allelopathic effects caused by alien species. In addition, an invasive plant might alter the composition, morphology and structure of the native plant community, resulting in the modification of the animal community that feeds upon fruits or seeds. For instance, the invasive gorse *Ulex europaeus* has replaced New Zealand communities dominated by the native kanuka *Kunzea ericoides*, changing the proportion of seed-dispersing mammals and birds [49].

Invasional meltdowns

Positive interactions among alien species are increasingly common, particularly plant–pollinator and dispersal interactions [39,50]. For instance, introduced honeybees are important pollinators of several alien species, both on continents [50,51] and islands such as Bonin [52], New Zealand [26], Tasmania [53] Azores [15] and Santa Cruz [54]. Several *Bombus* species and *Megachile rotundata* often prefer alien flowers in New Zealand and Australia, respectively [26]. Alien fig wasps also trigger the expansion of invasive fig species in continental USA, Hawaii and New Zealand [50]. Rats and rabbits disperse the seeds of the invasive ice plant *Carpobrotus* spp., contributing to its

expansion along the Californian coast [54] and on Mediterranean islands [55]. European starlings *Sturnus vulgaris* in New Zealand are important dispersers of alien plants such as *Solanum* spp., *Phytolacca americana* and *Rubus fruticosus* [43]. The red-whiskered bulbul *P. jocosus* disperses many alien species in La Réunion Island and in Florida, whereas *Z. japonica* in Hawaii is a primary disperser of the invasive *Myrica faya* [50].

Such invasional meltdowns disrupt native plant–animal mutualisms because they modify the structure of native plant communities and the foraging behaviour and movement patterns of the animal mutualists. On islands, because of the relatively lower species richness and the presence of endemic generalists [15], we would expect a stronger effect of such invader complexes. Further studies that explore the impact of such invasive species on the structures of either pollination or dispersal webs are needed as ecologists have only just begun to explore this facet of biological invasions [15].

Implications of mutualistic disruptions for conservation

Mutualistic interactions are important for maintaining and generating biodiversity [10] and conservation efforts should aim to ensure the continued functioning of these processes. As well as determining how an alien species enters the pollination or dispersal web, with what kind of species it interacts, how frequently, and the implications of the interactions it establishes, we need to evaluate to what extent it is competitively superior to native species, not only in terms of resource and/or space acquisition, but also in terms of attracting dispersers and pollinators. If an alien is preferred by animal mutualists, its invasiveness and potential impact on the invaded community are amplified [17]. Furthermore, we need to consider that alien species can influence not only the population density and growth, but also the capacity for long-distance dispersal of native species [29,56]. The implications of such disruptions for biodiversity conservation are only beginning to be discussed [57].

Given the levels of generalism found in plant–pollinator and plant–disperser interactions, it seems appropriate to consider them as networks of interactions involving many species [13,15]. Such generalism implies resilience to linked extinctions, but also enables introduced generalists to displace native species, leading to a net loss of diversity. Many of these generalist pollinators and seed dispersers are becoming more abundant as a result of human-aided dispersal and habitat modification [25,26,39,50].

Several relevant hypotheses worth testing emerge from the fact that most interactions in pollination or dispersal networks are asymmetrical, that is, specialist pollinators or dispersers tend to visit plants that accept many pollinator or disperser species, whereas specialist plants are pollinated or dispersed by animals that are themselves generalists [13]: (i) the introduction of an invasive pollinator or disperser that can displace native ones is expected to affect specialist plants more than it does generalist plants, which are more buffered against mutualist losses; (ii) specialist pollinators or dispersers are more prone than are generalist ones to disruptions by

invasive pollinators or dispersers (which often are competitively superior) as the generalists rely on a wider array of floral or fruit resources; (iii) Invasive alien plants offer more floral or fruit resources than do native plants, and more-rewarding flowers or fruits attract greater numbers of pollinators or seed dispersers, especially the most generalist ones. Thus, in nested communities, specialist plants are more likely to be affected than generalist plants; (iv) plants that depend upon an array of pollinators or dispersers might be less vulnerable to the introduction of an invasive herbivore that decreases plant attractiveness (to at least some of those mutualists) or to the introduction of an invasive predator that causes declines in the populations of such mutualists. Only in the case of a two-way specialist interaction might a herbivore have little impact on the mutualism itself as pollinators or dispersers do not have other alternatives; (v) an invasive herbivore (usually generalist) poses a major risk to specialist pollinators or dispersers as these depend on only a few plant species. Similarly, an invasive predator is also more likely to affect specialist pollinators or dispersers as these might be more easily encountered in the few plant species they pollinate or disperse. Finally, (vi) two-way specialist mutualistic interactions among native plants and pollinators or dispersers will be the least vulnerable to disruption by invasive pollinators or dispersers or by invasive plants because, by definition, specialist pollinators or dispersers are unlikely to share plants whereas specialist plants are unlikely to share pollinators or dispersers.

Landscape restoration programs should explicitly consider mutualistic interactions, paying particular attention to the keystone species in the plant communities that interact with large number of pollinators or dispersers [57]. Special effort should also be invested in maintaining vulnerable 'mutualistic compartments', such as long-tongued bees–deep-corolla flowers [58] or large-gaped birds–large fruits [24], rather than protecting species that might have little effect on ecosystem functioning. Special attention should also be paid to highly generalist pollinators, particularly those favoured and introduced by humans (e.g. honeybees). Such pollinators can displace others and have negative effects on plant recruitment, but they can also increase recruitment in other species that have lost their native pollinators [26]. Hence, each particular system will need to be examined to develop an appropriate management strategy.

Conclusions

The most important causes of plant–animal mutualistic disruptions are shared among different regions of the planet, although their consequences can vary widely. The restoration of 'pristine' pollination and dispersal systems is probably impossible, as changes in land use and species introductions are likely to be irreversible as a result of their natural dynamics as well as the persistence of socio-economical factors that drive them. As Roubik pointed out [59], the key question is whether such 'new' systems can absorb new species and interactions while simultaneously sustaining complex interactions of native species. Obtaining appropriate knowledge to formulate management

plans for the preservation of the functioning of those mutualisms is a challenge for researchers and conservation managers alike.

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