Positive interactions of nonindigenous species: invasional meltdown?

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Abstract

Study of interactions between pairs or larger groups of nonindigenous species has been subordinated in the literature to study of interactions between nonindigenous and native species. To the extent that interactions among introduced species are depicted at all, the emphasis has been on negative interactions, primarily resource competition and interference. However, a literature search reveals that introduced species frequently interact with one another and that facilitative interactions are at least as common as detrimental ones. The population significance of these interactions has rarely been determined, but a great variety of types of direct and indirect interactions among individuals of different nonindigenous species is observed, and many are plausibly believed to have consequences at the population level. In particular, mutualisms between plants and the animals that disperse and/or pollinate them and modification of habitat by both animals and plants seem common and often important in facilitating invasions. There is little evidence that interference among introduced species at levels currently observed significantly impedes further invasions, and synergistic interactions among invaders may well lead to accelerated impacts on native ecosystems – an invasional 'meltdown' process.

Introduction

The concept of 'environmental resistance' was introduced by Chapman (1931) to describe the forces, primarily biotic, that hinder the establishment of species in a new location. The emphasis (e.g., Elton 1958; Udvardy 1969) has been on the biological aspects of this resistance – the complex of native predators, parasites, pathogens, and competitors, as well as previously introduced species, that oppose a newly arrived, nonindigenous propagule. Thus, the notion is perhaps more accurately described as 'biotic resistance', and it has dominated thinking on why some introduced species survive and spread while others die out or persist tenuously and perhaps temporarily (Simberloff 1986). For example, two of the commonest generalizations claimed for introduction success – that islands are more easily invaded than mainland, and that disturbed habitats are more readily invaded than pristine ones – are both usually interpreted as at least partly due to differences in species richness of the recipient community (Simberloff 1986 and references therein). Islands usually have fewer species than mainland, and disturbed areas have fewer species than undisturbed ones. Similarly, occasional claims have been voiced that species introduced earlier to a site have excluded one or more of those introduced later. For example, in the biological control literature, a debate raged about whether some introductions of natural enemies of Homoptera, Coleoptera, and Lepidoptera failed because the species were excluded by others previously introduced for the same purpose (references in Simberloff and Boecklen 1988). For the introduced Hawaiian avifauna, Moulton and Pimm (1983) argued that species introduced later had a higher probability of going extinct precisely because of competition with species introduced earlier.

The view that biotic resistance determines invasion success or failure fits well with the dynamic equilibrium model of island biogeography (MacArthur and Wilson 1963, 1967), which became enormously popular for some 20 years after its publication (Simberloff 1974; Williamson 1989). The model posits that the

arrival of a new species on a real or habitat island will be compensated for by the extinction of a species already present, so that the number of species remains constant. The model refers only to species richness, not species' identities, though implicitly the notion in the original papers and most successors was that extinction would likely occur in a species taxonomically related to the invader. This view was consistent with the dominant interpretation that the main force causing the extinction was competition, especially diffuse competition (Simberloff 1981). Some of the papers invoking biotic resistance to explain the failure of biological control introductions (e.g., Tallamy 1983) specifically relate the failure to the island biogeographic model, as does the study of the introduced Hawaiian birds (Moulton and Pimm 1983). Additionally, the original and almost all subsequent depictions of the extinction curve in the equilibrium theory were concave upward – that is, the per-species rate of extinction rose faster than the number of species did. This approximately exponential shape was partly attributed to the 'increasing probability of interference among species' with a resultant 'accelerating detrimental effect' (MacArthur and Wilson 1967, p. 22).

However, a diametrically opposite conception of invasion success is also possible, one in which non-indigenous species, instead of interfering with one another, facilitate each other's establishment and/or continued existence. Thus, for example, Crosby (1986) depicts the colonization of the Americas, Australia, New Zealand, and the Canary Islands by European animals, plants, and pathogens as a mutualistic process. The European species, including European humans, are seen as biological allies that together constituted a synergistic juggernaut crushing native peoples and their ecosystems because the European species had coevolved with humans and with one another. For instance, European weeds, having coevolved with pigs, sheep, and cattle, were adapted to their activities, while North American plants were devastated by them.

Similarly, many classic examples of the ravages of introduced species include facets that entail facilitation, either one-way or two-way, between different introduced species. Elton (1958) describes how the Argentine ant, *Linepithema humile*, tends the Asian red scale insect, *Aonidiella aurantii*, in California citrus orchards. Ant removal demonstrated that scale densities were several times higher on trees with ants than on trees without them; ants remove some scale natural enemies. The population impact of the scale on the ant is not described, but it surely is not negative.

This example of interaction between a neotropical ant and an Asian scale in California suggests that facilitation among nonindigenous species need not be generated by a coevolutionary history. Also, the fact that some successful biological control programs entail new associations between parasitoid and host or predator and prey (Hokkanen and Pimentel 1984, 1989) indicates that at least some introduced species can benefit from interactions with others even if they are not coevolved.

In short, it is possible to imagine an invasion model very different from the dominant scenario of biotic resistance. At the most basic level, positive interactions among invaders may, for at least some of them, enhance the probability of survival and/or increase population size. In such instances, there may or may not be synergy – that is, a greater impact of a group of invaders on the recipient community than would have been predicted by the summed impacts of the individual species. Howarth (1985) foresaw this possibility:

> Often two or more harmful alien species may act in consort so that their joint impact is more severe than that of the several species acting separately. Even an otherwise innocuous or seemingly beneficial alien may, in fact, act in consort with other aliens with a consequent synergistic effect, causing great harm to the native biota. (p. 163)

We suggest the term 'invasional meltdown' for the process by which a group of nonindigenous 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. Thus, there is an accelerating accumulation of introduced species and effects rather than a deceleration as envisioned in the biotic resistance model. The analogy to mutational meltdown (Lynch et al. 1995) is evident. Our purpose in this paper is to determine the frequency of invasional meltdown and the variety of processes that can contribute to it. Is it a rare phenomenon generated by a few sorts of interactions, or is it occurring all around us?

Methods

To assess the frequency of facilitative interactions – that is, enhanced survival and/or population size – among nonindigenous species, we used a data base, compiled by Ingrid Parker, consisting of all papers between the years 1993 and 1997 in the Biosis data base that had the key words 'species AND inva# OR introduced OR

alien OR exotic OR non-native OR non-indigenous'. These keywords did not specifically address impact or effect of introduced species, and the majority of papers did not. The data base excluded any reports of biological control agents on their target organisms but included those of biological control agents on non-targets. There were over 5,000 papers. We determined the journals represented by the greatest number of papers for one year in this data base. Three journals (*Biodiversity and Conservation*, *Biological Conservation*, and *Ecology*) each had approximately twice as many papers as did any other journal. In addition to these three journals, we choose four of the twelve journals that fell in the next frequency category (*Conservation Biology*, *Journal of Animal Ecology*, *Journal of Applied Ecology*, and *Natural Areas Journal*) because it was clear from the titles in the data base that these journals tended to have articles that dealt with effects of introduced species in addition to just presence and absence data. For these seven journals, we examined all 254 articles in the data base to determine the extent and nature of facilitative interactions among two or more introduced species.

The articles fell into four categories. In those denoted '+/+', individuals of two or more nonindigenous species each benefited from the presence of the other(s). The '+/0' category described situations in which individuals of one species benefited from the presence of the other, while the second species was not known to affect individuals of the first. The category '+/−' included invasions in which individuals of one nonindigenous species benefit from the presence of a second species, while the individuals of the second were negatively affected by those of the first. Finally, to represent a sort of interaction envisioned as frequent in the governing paradigm, competition or other forms of mutual detriment between individuals of pairs of species, we used the category '−/−'. In the great majority of tabulated studies, the population impact of one species on another was not demonstrated. For example, in cases recorded as '+/+', the activities of individuals of each species were shown to benefit individuals of the other, but there was generally no evidence on the effect of these activities on the population of either species, though often an effect was reasonably inferred. Thus, the quantitative evidence for facilitation – and even more so for synergy – is usually absent or weak. For example, grazing nonindigenous mammals may disperse the seeds of a nonindigenous plant, and may even aid their germination, but replicated, quantitative, probably experimental study would be required to show that the population of either species

is therefore more likely to survive or be greater than it would have been without the other species. Of course, the same caveat applies to arguments that two nonindigenous species negatively affect one another.

In addition to the classification of articles from the data base, we sought examples from the literature (including the data base, but also other journal articles, books, and gray literature sources) to depict the range of ways in which nonindigenous species can facilitate one another.

Results

The numbers of different types of interactions are depicted in Table 1. Of the 254 articles reviewed, 30 recorded at least one interaction between two introduced species, and one recorded a great number: an introduced phytophage eating many introduced plant species. The majority of perceived introductions (156) are of the latter sort – at least at the individual level, one species benefits and the other is harmed (+/−), as when one species eats another. However, it is noteworthy that almost as many +/+ cases were adduced (10), in which two species facilitate one another, as −/− cases (12) that accord with the governing paradigm of mutual interference or competition. In addition, 12 instances were recorded in which individuals of one introduced species benefit, while individuals of the other are unaffected (+/0). No case of amensalism (−/0) was found. Table 1 also lists the more specific nature of the interactions of the four types. With respect to the preponderance of +/− interactions entailing plants and phytophagous insects, it should be noted that 128 of these were reported in a single study. No other study reported even ten interactions, and most reported just one.

Table 1. Numbers of different types of interactions between introduced species cited in 254 articles in seven journals during a five-year period (see text).

Interaction type	Number	Nature of interaction
+/+	10	Disturbance = 6, indirect effects = 3, pollination = 1
+/0	12	Disturbance = 9, commensalism = 1, host/parasite and similar interactions = 2
+/−	156	Predator/prey = 23, phytophagous insect/plant = 131, other = 2
−/−	12	Competition = 12

The data base plus the literature search turned up a great variety of types of interactions in which introduced species facilitate one another, at least at the individual level. Although there are many idiosyncratic varieties of facilitative interactions, most examples can be broadly classified as follows:

Animals pollinating and dispersing plants

There is some evidence that introduced plants may alter pollination regimes for native plants (e.g., Butz Huryn 1997), but the introduction of non-native pollinators does not have such a big effect. Nor is it clear that a newly introduced pollinator will automatically enhance the reproduction of introduced plants it can pollinate. Although the introduced honey bee is a major pollinator of such weeds as yellow star thistle (*Centaurea solstitialis*) (Barthell et al. 1994) and purple loosestrife (*Lythrum salicaria*) (Mal et al. 1992) in North America and barberry shrub (*Berberis darwinii*) in New Zealand (Butz Huryn 1997), these weeds would all be pollinated by other insects in the absence of honey bees. Whether or not the pollination regime is altered by the introduction of honey bees and whether altered seed set and gene flow occurs are, for the most part, unknown. The examples presented by Butz Huryn (1997) are clearly system-specific, and population impact should be studied by assessing both the specific plant species present and the particular nonindigenous pollinator. Although there are many highly coevolved plant–insect interactions, the majority of insect pollinators are generalist pollinators, not systematically favoring the pollination of nonindigenous or native plants (Waser et al. 1996).

Highly coevolved plant–insect interactions are the exception to most pollination regimes, but such highly coevolved species complexes do exist and their introduction can generate major impacts. When a coevolved plant is introduced into an area, it may become a virtual time bomb, requiring only the arrival of the associated insect to set off an invasion. Over sixty species of introduced *Ficus* occur in south Florida; twenty of these fig species are frequently planted. If the pollinating wasp associated with a *Ficus* species in its natural range is not present, the fig species cannot reproduce. Within the last 15 years breeding populations of three host-specific pollinating wasps have been introduced in south Florida; thus the three associated *Ficus* species regularly produce viable seeds. A variety of birds and mammals are thought to disperse these seeds. *Ficus micropcarpa* is spreading most rapidly (Kauffman et al. 1991). This aggressive spread is thought to be due to the small fruits, which can be effectively exploited and dispersed by the small-gaped frugivorous birds in Florida (McKey and Kaufmann 1991) and secondarily by ants (Kauffman et al. 1991). The synergistic spread of the same coevolved plant–pollinator complex (*Ficus microcarpa–Parapristina verticillata*) is also occurring in Bermuda (Monkman 1984; Dow and Terceira 1985; Hilburn 1987) and Mexico and Central America (B.W. Ramirez and S. Montero, in press).

Another example of a coevolved species complex in which the spread of each species depends on the spread of the other is that of the solitary bee species of *Peponapis* and *Xenoglossa* with the cultivation of the genus *Cucurbita* (squashes, gourds and pumpkins) (Hurd and Linsley 1964, 1966, 1967a, b). Even though *Cucurbita* is not native to the eastern US north of Florida, three squash and gourd bee species (*Peponapis pruinosa*, *Xenoglossa* (*Eoxenoglossa*) *kansensis*, and *Xenoglossa* (*Eoxenoglossa*) *strenua*) that pollinate and feed on *Cucurbita* are abundant in these areas, apparently because of the introduction and spread of the cultivated *Cucurbita* (Hurd et al. 1971).

The complex coevolved systems that characterize some non-indigenous pollinators and plants do not occur with the many frugivorous invasive animals that preferentially spread non-native fruit-bearing trees and shrubs. The red-whiskered bulbul (*Pycnonotus jocosus*) is a cosmopolitan, frugivorous invader that has disrupted plant communities in many habitats. This bulbul colonized the southeastern part of La Réunion island and became a 'common and efficient seed-disperser of alien species such as *Rubus alceifolius*' (C. Thebaud, unpublished data) (Macdonald et al. 1991). Cheke (1987) described the damage in the Mascarene islands caused by the introduction of a dispersal agent for a plant already present but quiescent until the introduction of the red-whiskered bulbul (Wiehé 1946), which now spreads the ubiquitous weed *Cordia interrupta*. This bulbul is also thought to be the principal dispersal agent of privet, *Ligustrum robustum* (Vaughan and Wiehé 1939). In Florida, *Pycnonotus jocosus* eats fruits and berries of over 24 exotic species including loquat (*Eriobotrya japonica*), various jasmines (*Oleaceae*), and *Lantana* spp., and feeds extensively on Brazilian pepper (*Schinus terebinthifolius*) and the syconia of fig trees (*Ficus*) (Carleton and Owre 1975). Owing to the extreme anthropogenic modification of southeastern Florida in the last century, this bird species has the opportunity to use virtually identical food and nesting material to those it uses in its native India (Carleton and Owre 1975).

Cheke elegantly summarized the complex relationship of frugivorous pigs and the Mascarene plant communities they invade:

> The afflictions of the native forests are synergistic. Invasive plants need dispersal agents and reduced competition by selective browsing to help them spread. In turn it seems likely that the extraordinarily high fruit production of the Strawberry Guava has helped sustain high populations of pigs (Owadilly 1980) and monkeys, forcing them to continue damaging the native flora outside the guava's fruiting season. (Cheke 1987, p. 14)

Exotic pigs in Hawaii also spread exotic plants (Loope and Scowcroft 1985), selectively eat some native plants (Stone 1985), and their rooting and defecation favor exotic invertebrates (Stone 1985). Pigs do not reach large sizes without significant protein in their diet (Stone 1985). There is evidence that the current large size of feral pigs is due to the introduction of protein-rich European earthworms. Also the role of pigs in spreading *Passiflora mollisma* (Ramakrishnan and Vitousek 1989) is much the same as in the Mascarene islands.

Woodward et al. (1990; cf. Vitousek and Walker 1989) concluded that introduced Japanese white-eye, *Zosterops japonicus*, was the primary disperser of *Myrica faya* seeds in the natural areas of Hawai'i Volcanoes National Park. Other native and exotic birds visited the trees, but this was the only species to ingest and to disperse viable seeds. Feral pigs and rats also disperse the seeds of *Myrica faya* (Stone and Taylor 1984).

Knight (1986) suggested that alien species that produce fleshy fruits and/or nectar can change naturally occurring patterns of frugivory and nectarivory. Dispersal of exotic plants by frugivorous birds may be the largest of all facilitation categories. This type of interaction should be of special management concern when the introduction of either a fruit-bearing plant or a frugivorous animal is into a system with the other component already present. Of the 90 major weeds in Hawaii, 33 (37%) are dispersed by predominantly alien, frugivorous birds and 9 (10%) by mammals (on clothing or hides). A surprising result is that a mere 23 (25%) are dispersed only by man (Smith 1991).

Animals modifying habitat

Exotic animals altering the habitat is the best studied of all the facilitation categories. This is probably due to the economic importance of the habitat that most non-indigenous animals alter: rangeland. Westman (1986) suggested the terms 'endogenous disturbance' for those disturbances that the ecosystem has been subject to through evolutionary time and 'exogenous disturbance' for disturbances outside the range the ecosystem has experienced. Invasion of non-indigenous species increases in ecosystems subject to exogenous disturbance regimes (Elton 1958; Fox and Fox 1986). Physical disturbance of habitat by invasive species constitutes a major exogenous disturbance.

The two key shared characteristics of several temperate grasslands vulnerable to plant invasion are the lack of large, hooved, congregating animals in the Holocene or longer and dominance by caespitose (tussock) grasses. The morphology and phenology of tussock grasses explain their sensitivity to large, congregating herbivores (Mack 1989). Mack (1986) documents this facilitation of invasive weeds by domestic herbivores in the intermountain region of western North America, attributing the establishment of alien plants in grasslands to the increase in disturbance. Native grassland plants evolved without the influence of frequent disturbance by large congregating animals or their functional equivalents. North American bison were found only in small, isolated herds in the intermountain West and did not play a large part in the evolution of the native grassland vegetation (Mack and Thompson 1982). Mack (1981, 1986) pinpoints the most common mechanism of introduction of non-native grasses as the contamination of agricultural seed; and less commonly, as the attachment to and dispersal by the coats of domesticated animals. However, trampling by ungulates facilitated the establishment of the dispersed seed. This same facilitation occurred in the grasslands of temperate South America, the Central Valley of California, and temperate Australia:

> Whether through grazing or trampling, or both, the common consequences of the introduction of livestock in the four vulnerable grasslands were destruction of the native caespitose grasses, dispersal of alien plants in fur or feces, and continual preparation of a seed bed for aliens that evolved with large mammals in Eurasia and Africa. (Mack 1989, p. 158)

The Asian water buffalo was introduced into northeastern Australia as a beast of burden and meat for early European settlers. The water buffalo dispersed from military settlements in the first half of the nineteenth century and spread throughout the flood plains of the Adelaide River (Lonsdale and Braithewaite 1988).

These enormous ungulates devastated native plant communities, compacted the soil, altered the hydrology of the forests causing tree mortality, and eroded creek banks. A Central American shrub, *Mimosa pigra*, had been in abeyance in the surroundings of Darwin, Australia as a minor weed for a century (Lonsdale and Braithewaite 1988). This tall, shrubby legume produces large amounts of small, bristly, pod-covered seeds that are readily dispersed by water (Lonsdale 1993). The sundering of the flood plains by the Asian water buffalo created ideal germination ground for *Mimosa pigra* seedlings (Lonsdale and Braithewaite 1988). The switch from native sedgelands to a monoculture of *M. pigra* caused the decline of native waterbirds, lizards, and insectivorous birds. The only benefit of *Mimosa* for natives is that it provides refugia for rodents and shrew-like marsupials (Lonsdale and Braithewaite 1988; Lonsdale 1993). These woody shrubs did serve as protection for the water buffalo from aerial hunters trying to exterminate these animals in 1980s (W.M. Lonsdale, personal communication). Once a large majority of the estimated 250,000 water buffalo were extinguished from northeastern Australia, the spread of *M. pigra* abruptly terminated (Lonsdale 1993; W.M. Lonsdale, personal communication). This leveling of the rate of spread of *M. pigra* in the mid-1980s was primarily due to the drastic decline in water buffalo numbers, as biocontrol agents for *M. pigra* were not yet widespread (W.M. Lonsdale, personal communication).

Another woody shrub causing huge ecological damage to the recipient habitat is *Rhododendron ponticum* in the woods in southwestern Ireland. *Rhododendron ponticum* was introduced from the Mediterranean to Ireland in 1763 (Elton 1958) to serve as an ornamental around houses and in the surrounding woods (Cross 1981). *Rhododendron ponticum* saturates the woodland understory and displaces holly (*Ilex aquifolium*) and other native shrub species. These woods were heavily disturbed by logging activities for the last four centuries. The introduction of the Japanese sika deer (*Cervus nippon*) in 1860 initiated a new form of woodland disturbance. Sika deer have augmented and replaced native red deer (*Cervus elaphus*) in forest habitat. *Rhododendron ponticum* establishes in the oakwoods of Killarney through the production of 'safe sites' (Harper et al. 1965) created when the sika deer overgraze or humans log an area that eventually becomes covered with primary bryophyte successors. These bryophyte-covered patches become ideal germination sites for *R. ponticum* (Cross 1981). Thus,

the creation of patches by the Japanese sika deer and logging throughout the forest, the unpalatibility of *Rhododendron ponticum*, and its tolerance of shade cause the spread and dominance of this shrub in Irish oak woodland. This is a classic mutualism, as *R. ponticum* serves as shelter for this invasive deer species. It appears to constitute a synergistic invasion, as the net impact of the two species likely far exceeds the sum of the individual impacts each would generate in the absence of the other.

The zebra mussel *Dreissena polymorpha*, introduced to the Great Lakes in the mid-1980s, has had huge ecological impacts (US Congress 1993; Lowe and Pillsbury 1995; MacIsaac 1996; Dermott and Kerec 1997; Ricciardi et al. 1998). Owing to their high fertility and filtering ability, these mussels have caused a huge shift in energy from planktonic to benthic food webs wherever they have invaded. *Dreissena* profoundly influences phytoplankton biomass. Reeders et al. (1993) recorded a 46% decline in phytoplankton volume in a pond containing *Dreissena* relative to a control pond. MacIsaac (1996) suggests that this drastic energy shift may greatly affect invertebrate communities. This mussel serves as a sediment trap by converting large amounts of seston into excreted feces, creating a soft substrate of rich organic material highly suitable for deposit-feeding infaunal species (Leppäkoski 1984). In Lake Ontario, invertebrate diversity increased from at most 22 species to between 27 and 32 species at a cobble site, and from at most 15 species to between 19 and 26 species at an artificial reef site following *Dreissena* invasion (Stewart and Haynes 1994). (However, macroinvertebrate richness increased at sites in Lake St. Clair that lacked the zebra mussel [Griffiths 1993; MacIsaac 1996].) An experimental study on the Saint Lawrence River (Ricciardi et al. 1997) showed great change in composition and numbers of macroinvertebrates on hard substrates colonized by the zebra mussel. Further, live mussels had an even greater impact than dead shells, so several factors are probably at play here – not only does the surface area and spatial heterogeneity increase, giving settling sites, providing refuge, and trapping sediment and biodeposits, but also filtration currents generated by *Dreissena* may be exploited by some invertebrates. Among the species whose populations were enhanced by the presence of *Dreissena* is the invasive Eurasian faucet snail *Bithynia tentaculata* (Ricciardi et al. 1997; A. Ricciardi, personal communication).

Zebra mussels may also generate a mutual facilitation with macrophytes, including introduced ones, in

shallow, light-limited waters (MacIsaac 1996). High mussel abundance increases water clarity, which in turn promotes macrophyte growth. The macrophyte growth, in turn, provides additional settling substrate for *Dreissena* (Lewandowski 1982) and can help disperse zebra mussels between water bodies (Johnson and Carlton 1996). Eurasian watermilfoil (*Myriophyllum spicatum*), an invasive aquatic weed, has greatly increased because of the *Dreissena* invasion (MacIsaac 1996). The zebra mussel also is a key food source for several native fishes as well as two introduced species, white bass (*Morone chrysops*) and round goby (*Neogobius melanostomus*) in the Great Lakes (French 1993). The round goby co-occurs with the zebra mussel in littoral and lower tributary habitats in their native Black and Caspian Seas and, in feeding trials, preferred zebra mussels (Ghedotti et al. 1995).

Plants modifying habitat

Nonindigenous plant species that alter soil nutrients may facilitate the invasion of other nonindigenous species. For example, the Atlantic nitrogen-fixing shrub, *Myrica faya*, has been studied extensively in Hawaii, where it has invaded very nitrogen-poor volcanic soils (Vitousek 1986; Vitousek and Walker 1989). Because there are no native symbiotic nitrogen-fixers in these habitats, and because invasions by many nonindigenous plant species in Hawaii are most successful on more fertile soils (Gerrish and Mueller-Dombois 1980), there is a high likelihood that *Myrica faya* facilitates further plant invasions (Vitousek 1986). Experimental research in Hawaii with the aggressively invading introduced strawberry guava tree (*Psidium cattleianum*) showed biomass accumulation in soil from under *Myrica faya* highly significantly increased over that in soil from under the native *Metrosideros polymorpha* (Hughes et al. 1991), suggesting that a broad range of invasive nonindigenous species will ultimately be favored (Vitousek and Walker 1989). *Myrica faya* enhances populations of nonindigenous earthworms, which in turn enhance the rate of nitrogen burial and thus increase the impact on nutrient cycling (Aplet 1990). Further, the introduced white-eye (*Zopsterops japonicus*) was the most frequent visitor to *Myrica faya* in two closely monitored sites, and it dispersed large numbers of seeds (Vitousek and Walker 1989); this observation resembles that of Woodward et al. (1990) cited above. Thus, it appears that a complex set of facilitative interactions among a variety of introduced species centered on *Myrica faya* aids the invasion of all of them.

Many invasive nonindigenous plants enhance fire frequency and/or intensity; they are adapted to the new regime, as are other nonindigenous species, but native plants are not. Thus, the fire-enhancers aid their own invasion and that of other exotic species and simultaneously harm the native species. Old World grasses that have come to dominate many New World grasslands exemplify this facilitation (D'Antonio and Vitousek 1992). For example, in Hawaii the nonindigenous perennial grass *Schizachyrium condensatum* invaded seasonal submontane shrub-dominated woodland. This grass filled the interstices and canopy of the shrubs with abundant fuel, thus fostering much more frequent fires over much larger areas. These fires killed most native trees and shrubs, but *S. condensatum* recovered rapidly and the even more flammable exotic perennial grass *Melinis minutiflora* also invaded (Hughes et al. 1991). Fires were subsequently more frequent and severe, generating a positive feedback cycle that led to increasing replacement of a native-dominated woodland by a low-diversity, exotic-dominated grassland (D'Antonio and Vitousek 1992). A similar scenario arises in many rangelands of the US West (Mack 1981, 1989). Here the importation of livestock, particularly cattle and sheep, facilitated the invasion of Eurasian grasses adapted to congregating, hooved grazers that destroyed native bunchgrasses. Some of these invading grasses, such as the annual cheatgrass (*Bromus tectorum*), were highly flammable and fueled immense fires that damaged or killed native shrubs and perennial grasses (references in D'Antonio and Vitousek 1992). Cheatgrass also suppresses growth of some native species (Melgoza et al. 1990), and other nonindigenous, fire-enhancing grasses such as *Tainiatherum asperum* invade areas burned by fires fueled by cheatgrass (references in D'Antonio and Vitousek 1992). Thus a positive feedback cycle is established similar to that in Hawaii.

Various Eurasian species of salt cedar (*Tamarix*) have invaded the riparian zones of rivers, as well as other wet areas, in the US Southwest (Vitousek 1986 and references therein) and Australia (Griffin et al. 1989; Anonymous 1991). Generally, they are deeply rooted and transpire rapidly, thus drying up surface water and lowering the water table. Further, their foliage concentrates high salt concentrations, so the litter is saline. A consequence of these changes is the elimination of almost all native vegetation and associated animals. In the Southwest, among the few species that thrive in this situation

are three non-native species of *Bromus* (L. Stevens, personal communication). Further, a non-indigenous, honeydew-producing leafhopper (*Opsius stactogalus*) interacts with a fungus to change soil characteristics so that plant recruitment is virtually eliminated under a *Tamarix* canopy (L. Stevens, personal communication). On the Finke River in Australia, the main beneficiaries of the replacement of native *Eucalyptus* trees by *Tamarix* were several native chenopods and introduced grass species able to tolerate the saline soil (Griffin et al. 1989).

A final example of a nonindigenous plant that modifies the environment to favor other introduced species is the African crystalline ice plant, *Mesembryanthemum crystallinum*, in California (Philbrick 1972; Vivrette and Muller 1977) and Australia (Kloot 1983). In California, this ice plant invades existing plant communities through preferential grazing by animals on native plants. For example, on Santa Barbara Island, Philbrick (1972) observed the initial invasion of native vegetation by *M. crystallinum* to have been fostered by introduced rabbits, which removed native plants. Once *M. crystallinum* is established, it accumulates salt, which is released when the plant dies through leaching by fog and rain. The salt, in turn, produces an osmotic environment intolerable to the native plants (Vivrette and Muller 1977; Kloot 1983). On Santa Barbara Island, when wind or other disturbance creates openings in the ice-plant carpet, these are colonized not by native plants, but by the ice plant itself or by weedy introduced plants such as *Malva parviflora* or *Erodium cicutarium* (Philbrick 1972).

Indirect effects

The above categories, and in fact almost all the examples of facilitation in the literature, concern direct effects, at least at the individual level, of one introduced species on another. However, species can affect one another indirectly in myriad ways (Menge 1995; Stiling 1996). Traditionally, indirect effects are defined as how one species modifies the impact a second species has on a third species. For example, introduced *Pheidole megacephala* ants in the Hawaiian islands tend an introduced scale insect, *Coccus viridis* (Bach 1991) on the introduced plant *Pluchea indica*; among other activities, they hinder introduced predatory coccinellid beetles and parasitic wasps. These interactions, at least at the individual level, are direct ($+/+$ for the ant and scale, $+/-$ for the ant and beetle or ant and wasps). But there is also an indirect effect ($+/+$) of the ant on the scale by virtue of its suppression of the enemies of the scale. And the subsequent increased rate of honeydew production by the scales results in increased colonization by a sooty mold (an indirect $+/+$ interaction between ant and mold) and greater rates of leaf death and abscission by the plant (an indirect $+/-$ interaction between ant and plant).

Facilitation can occur in many other ways. Some researchers consider habitat change that affects another species an indirect effect, as opposed to direct trophic interactions and interference. Some examples cited above can be construed this way, as, for example, when an introduced grazer facilitates an introduced weed by its suppression of native plants (rather than simply by dispersing the seeds of the invader). But various kinds of indirect mutualisms and commensalisms (Menge 1995) do not fall into this category. Almost certainly, intensive natural historic study would uncover many such examples among introduced species. Currently, the overwhelming majority of such potential effects are just intriguing hypotheses.

Discussion

It is a commonplace that mutualistic interactions between species are not nearly as frequently discussed in the general literature as competitive interactions are, and the dominant view is that this lack of study and reporting is not because mutualisms themselves are so infrequent (e.g., Risch and Boucher 1976; DeAngelis et al. 1980; Boucher et al. 1982; Boucher 1985; Kareiva and Bertness 1997). Although a number of reasons have been proposed for the lack of attention, from the sociopolitical (e.g., Boucher 1985) through the mathematical (cf. Kareiva and Bertness 1997), and the reasons are not mutually exclusive, our concern here is not with why mutualism is not as carefully studied and reported as would be warranted by its frequency. Rather, we wish to stress that the figures reported above probably underestimate the extent of the positive interactions among species. Whatever causes researchers to deemphasize mutualism in general is likely to have the same influence in the study of mutualism between nonindigenous species.

Any sorts of interactions introduced species have with one another are also probably less likely to be sought and reported than are the effects of introduced species on native ones. After all, the predominant concern with introduced species, for researchers as for conservationists and resource managers, is with the

potential damage they may inflict on native species. That is, they are pests and otherwise would not be of great interest in their own right. Certainly to the extent that facilitative interactions among nonindigenous species increase the likelihood that at least some of them will harm native species, researchers will seek and be sensitive to these interactions. However, although we do not want to explore here the issue of exactly what fraction of introduced species affect native species and ecosystems, it seems clear that it is at most a rather small minority (e.g., Williamson 1996). Thus, for most nonindigenous species, there is probably not much motivation to look for interactions with other nonindigenous species. This is yet another reason why our above estimates of frequency of different types of interactions are probably underestimates.

In spite of probable tendencies to overlook interactions between introduced species, 12% of the articles surveyed, which were delimited to focus on nonindigenous species but not particularly on interactions (with either native or non-native species), did show interactions between different nonindigenous species. Few if any produced hard evidence that these interactions had a population effect, but in many cases such an effect was at least plausible. We do not take the numbers of various sorts of interactions detected in our data base search to represent actual frequencies. The tabulated studies were insufficient for such estimation. Rather, we hope they can serve as a rough, preliminary indication of the relative frequencies. Of the 190 pairwise interactions described, 82% consisted of $+/-$ interactions in which individuals of one species benefited and those of the other species were harmed; 82% of these were a single sort of interaction reported in one study. However, of the remainder, almost as many were mutualistic $(+/+)$ as were competitive $(-/-)$: 10 vs. 12. And many more were commensal $(+/0)$ than were amensal $(-/0)$: 12 vs. 0. It seems clear that there is no prima facie case for the biotic resistance paradigm, in which successively introduced species generally harm one another. And, given the historical trend towards neglect of mutualistic interactions, it is probably fair to say that a substantial part of the impact of introduced species as a whole arises from situations in which one invader aids another.

Conclusions

There are a great variety of ways in which different nonindigenous species can aid one another, with numerous idiosyncratic interactions described in the literature. Sometimes the interactions may be synergistic – the impact of several species together is greater than the sum of the impacts of the individual species. However, the key types of facilitative interactions appear to be animals pollinating and dispersing plants (and getting food in return) and animals and plants modifying the habitat in a way that favors other introduced species over natives (such as by grazing or fostering more numerous or intense fires).

Although the invasion literature is underlain largely by a paradigm of 'biotic resistance', and this paradigm in turn suggests that introduced species are more likely to hinder than to aid one another, there is little evidence that this is so. Very few published reports actually document the population impact of one nonindigenous species on another, but over 10% of a large sample of recent papers on nonindigenous species at least mention impacts of individuals of one nonindigenous species on individuals of another, and several of these suggest that the population effect could be substantial, even crucial. More papers depict individuals of nonindigenous species helping individuals of other nonindigenous species than hindering them, in spite of a likely pervasive tendency for the literature to emphasize interfering rather than facilitative interactions.

In the introduction, we stated that one purpose of this survey was to determine the frequency of invasional meltdown. We were unable to do this, though we present preliminary evidence that it is not uncommon. Our failure in this regard is because the invasion literature is usually too anecdotal to sustain the quantitative analysis that would be necessary. This fact suggests that quantification of population-level impacts of nonindigenous species on one another, and on native species, is an urgent research need. Although qualitative reports are useful, and one cannot expect quantitative population studies of the invader and potentially affected species for every reported invasion, a larger catalog of such studies is needed in order to assess the importance of the meltdown phenomenon. Parker et al. (1999) have recently reviewed several approaches to quantifying impacts of invaders and suggested research directions to develop these approaches.

Even without such intensive study of particular invasions, examination of the current literature on invasions could provide some insights. For example, a search to find the order of various invasions, both failed and successful ones, might provide evidence for the importance of one species for the survival of a second. In this regard, temporally or spatially replicated invasions

of the same species but in different order would be most convincing. The literature on successful control of invaders, including local or regional eradications, may also contain information relevant to facilitation, as there is occasional mention of impacts of a removal on other species. Of course, such reports are generally anecdotal, so again we are driven back to the main need, quantified information on population-level impacts.

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