

*Perspectives and paradigms*

## Can invasive species facilitate native species? Evidence of how, when, and why these impacts occur\*

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Received 6 July 2005; accepted in revised form 14 November 2005

**Key words:** competitive release, facilitation, habitat modification, indirect facilitation, invasive species, novel facilitation, pollination, predatory release, substitutive facilitation, trophic subsidy

### Abstract

Although the predatory and competitive impacts of biological invasions are well documented, facilitation of native species by non-indigenous species is frequently overlooked. A search through recent ecological literature found that facilitative interactions between invasive and native species occur in a wide range of habitats, can have cascading effects across trophic levels, can re-structure communities, and can lead to evolutionary changes. These are critical findings that, until now, have been mostly absent from analyses of ecological impacts of biological invasions. Here I present evidence for several mechanisms that exemplify *how* exotic species can facilitate native species. These mechanisms include habitat modification, trophic subsidy, pollination, competitive release, and predatory release. Habitat modification is the most frequently documented mechanism, reflecting the drastic changes generated by the invasion of functionally novel habitat engineers. Further, I predict that facilitative impacts on native species will be most likely *when* invasive species provide a limiting resource, increase habitat complexity, functionally replace a native species, or ameliorate predation or competition. Finally, three types of facilitation (novel, substitutive, and indirect) define *why* exotic species can lead to facilitation of native species. It is evident that understanding biological invasions at the community and ecosystem levels will be more accurate if we integrate facilitative interactions into future ecological research. Since facilitative impacts of biological invasions can occur with native endangered species, and can have wide-ranging impacts, these results also have important implications for management, eradication, and restoration.

### Introduction

Facilitation, defined as an interaction between two species that results in an increase in the density or biomass of at least one of the species, is not frequently addressed in the biological invasion literature. In non-invaded communities, the

role of facilitation as a structuring force has been well documented (Bertness and Leonard 1997; Callaway and Walker 1997; Hacker and Gaines 1997; Menge 2000; Stachowicz 2001). Specifically, facilitation plays a key role in ecosystems that are physically stressful (Clements 1936; Bertness and Leonard 1997; Bertness et al. 1999; Bruno and Kennedy 2000; Stachowicz 2001), as a result of habitat modification (Jones et al. 1997; Stachowicz 2001; Coleman and Williams 2002;

\* Contribution Number 2293, Bodega Marine Laboratory, University of California at Davis.

Crooks 2002), and through indirect interactions (Levine 1999; Batzer et al. 2000). Facilitation can be as biologically significant as other factors (e.g. competition, predation, physical stress) in establishing and maintaining community dynamics (Callaway and Walker 1997; Bertness et al. 1999; Goldberg et al. 1999; Arsenault and Owen-Smith 2002), and needs to be incorporated into future ecological testing and theory (Kareiva and Bertness 1997; Stachowicz 2001; Bruno et al. 2003).

The invasion of ecosystems by non-indigenous species is one of the greatest threats to biodiversity and community structure (Elton 1958; Carlton 1989; Vitousek et al. 1996; Wilcove et al. 1998; Mack et al. 2000). Most studies of biological invasions have focused solely on the direct negative impacts of non-indigenous species on native biota. Ecological impacts of non-indigenous species include competition with, and predation on, native species, hybridization with native species, changes in ecosystem processes, loss of biodiversity, and an increase of pests and diseases (Vitousek et al. 1996; Ruiz et al. 1997; Mack et al. 2000; Crooks 2002; Grosholz 2002; Bruno et al. 2005). As invasive species integrate into recipient communities, the number and type of species interactions are predicted to increase (Vermeij 1996; Pearson and Callaway 2003). Further, there are documented synergistic interactions and impacts that result from multiple species invasions (i.e. 'invasional meltdown') (Simberloff and Von Holle 1999; Ricciardi 2001; Grosholz 2005). Recent reviews provide important starting points by affirming that facilitative interactions are likely more widespread than expected (Richardson et al. 2000; Crooks 2002; Bruno et al. 2005; Sax et al. 2005). The question is why, if they can be so diverse and frequent in non-invaded communities, are facilitative interactions not widely documented as resulting from biological invasions?

Incorporating facilitative interactions of invasive species into future ecological research will be crucial to determine their relative strength in comparison to competition, predation, and changes in ecosystem processes and biodiversity. In addition, facilitative impacts present management dilemmas in conservation and restoration efforts (Myers et al. 2000a, b; Van Riel et al. 2000; Zavaleta et al. 2001; D'Antonio and Meyerson 2002). For example, what is the 'correct'

management decision when an invasive species is detrimental to several native species but facilitates an endemic, endangered species? What if an invasive species provides a novel ecological function, which facilitates native species? In addition, how do we manage an invasive species that is very harmful to resident species, but provides a critical ecosystem service?

This review addresses the following questions: is there evidence in the primary literature that non-indigenous species facilitate native species? If so, *how* do these interactions take place? Are there situations *when* these interactions are most likely to occur? And finally, *why* do some native species respond to invasions this way?

## Methods

To answer these questions, I searched the primary literature using the electronic database BIOSIS (1993–2004). I raised extensive queries using all possible terms for both invasive species (invasive, invader, introduced, non-native, non-indigenous, alien, exotic), and facilitative interactions (facilitation, habitat modification, pollination, positive, release, habitat, modification, engineer, indirect, commensalism, refugia, amelioration, pollination, fertilization, mutualism) and then limited the results using the BIOSIS major concept 'Ecology'. When appropriate, I used word roots to locate all possible associated keywords. The initial search yielded 1293 articles, for which I read every abstract to identify evidence of facilitative effects. Articles that appeared to contain evidence of facilitative interactions between a non-indigenous species and a native species were read in full. Additional articles were found by looking through references cited. A total of 172 articles were read, and of these articles, those containing information (survey, experimental, or other) regarding facilitative interactions are presented. Certain articles were eliminated, such as those articles containing only theoretical information, articles dealing with single species population dynamics, articles that dealt with invasion dynamics relating to glaciation periods and other paleontological issues, and meeting abstracts. Although this literature search yielded a large diversity of examples, it is likely that some

articles were not located either because of the restriction imposed by keyword searches, or because the focal species was not identified as an invasive species.

## Results

A total of 61 studies yielded evidence of facilitative impacts of non-indigenous species on native populations. Any article with graphic, numeric or descriptive evidence of facilitation was included. The number of articles published per year increased (Figure 1), a pattern which parallels the number of articles on invasive species published per year (Simberloff and Von Holle 1999). The decrease in articles found in 2003 and 2004 is likely due to the lag between publication date and date of BIOSIS reporting.

There is a broad diversity of both invasive facilitator species and native facilitated species which were documented to interact (Figure 2a). Further, facilitative impacts were found to occur almost equally in terrestrial (39%, 24 studies) and freshwater (36%, 22 studies) environments, with slightly fewer examples documented

from marine environments (25%, 15 studies) (Figure 2b).

### *How do these facilitative interactions take place?*

From the 61 articles reviewed, several mechanisms document *how* facilitation of native species by invasive species occurs. These mechanisms include direct (habitat modification, trophic subsidy and pollination) and indirect (competitive release and predatory release) interactions (Table 1).

#### *Habitat modification*

Habitat modification was the most frequently reported mechanism by which invasive species facilitate native species. Habitat modification, which can also be referred to as ecosystem engineering, is defined as 'the physical modification, maintenance and creation of habitats' (Jones et al. 1997). For the purposes of this review habitat modification is defined broadly, encompassing a range of effects from creation of entirely novel habitats to slight changes in abiotic conditions due to the presence or biological activity of a species.

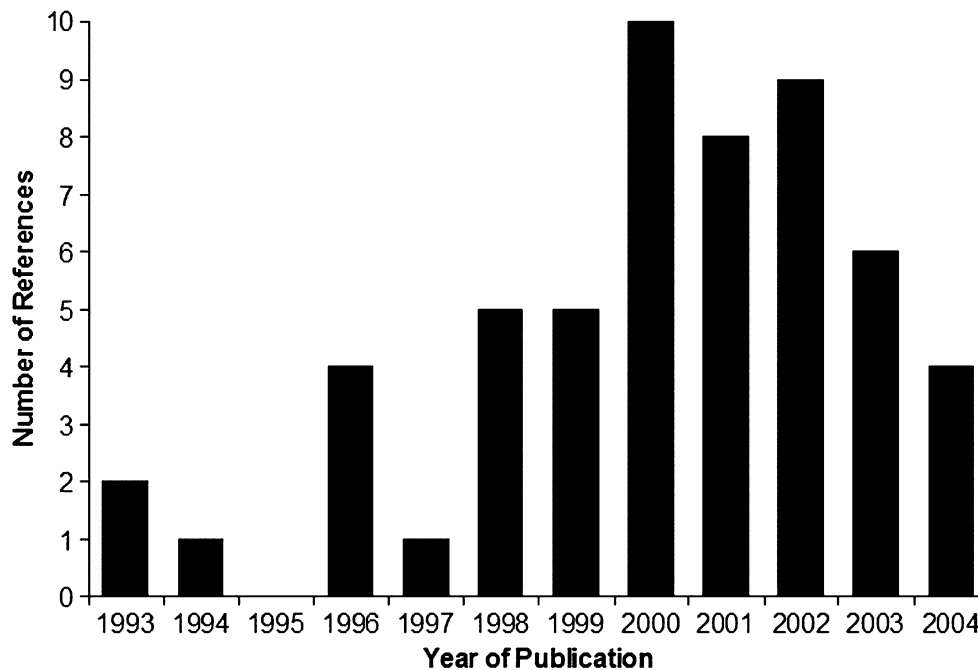


Figure 1. Number of references found with BIOSIS search that contain evidence of facilitative interactions between non-indigenous and native species. The decrease in 2003/2004 is likely due to the lag between publication date and date of BIOSIS reporting.

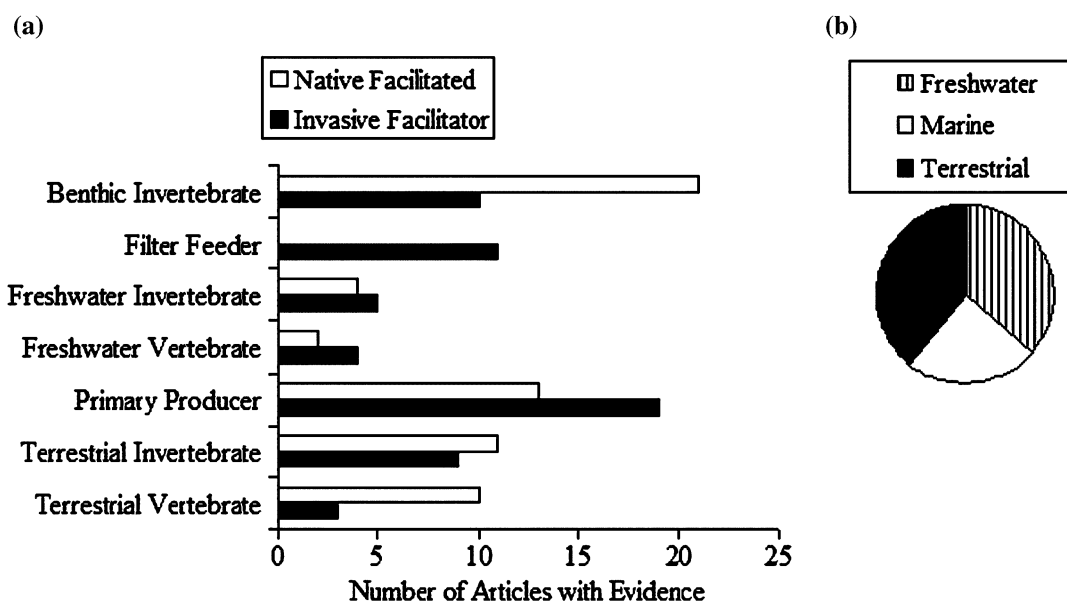


Figure 2. Categorization of evidence by (a) general type of species (for both the native facilitated and invasive facilitator), and (b) habitat where these interactions occur.

*Creation of novel habitats.* Introducing novel physical structure can change abiotic conditions (temperature, shading, fluid flow, etc.), or provide refugia or substrata. Facilitative interactions between invasive habitat engineers and native species develop when the novel habitats created are persistent and stable, and native species use the habitat with increasing frequency and dependence (Van Riel et al. 2000).

Table 1. Number of references found as evidence for each mechanism and type of facilitation.

Mechanisms	# References
Habitat modification	
Creation of novel habitat	25% (15)
Replacement of habitat	10% (6)
Trophic subsidy	
Nutrient enrichment	3% (2)
Food source diversification	21% (13)
Novel hosts	13% (8)
Pollination	10% (6)
Competitive release	7% (4)
Predatory release	11% (7)
Facilitation type	# References
Novel	34% (21)
Substitutive	48% (29)
Indirect	18% (11)

Extensive impacts have resulted in fresh- and saltwater soft sediment systems due to the invasion of the bivalves *Dreissena polymorpha* (Stewart and Haynes 1994; Johnson and Padilla 1996; Thayer et al. 1996; Bially and MacIsaac 2000; Ricciardi 2001), *Musculista senhousia* (Crooks 1998; Crooks and Khim 1999) and *Limnoperna fortunei* (Darrigran 2002). These invaders form dense, complex, colonies which provide refuge and greatly increase invertebrate diversity and abundance as compared to adjacent habitats (Crooks 1998; Bially and MacIsaac 2000). Bially and MacIsaac (2000) found that zebra mussel (*D. polymorpha*) colonies support up to 700% more taxa than neighboring mussel-free habitat. These changes not only re-structure benthic communities (Ricciardi et al. 1997; Darrigran 2002), but also cascade up the food-web. For example, yellow perch (*Perca flavescens*) have higher growth rates due to increased availability of invertebrate prey associated with zebra mussel colonies (Thayer et al. 1996).

Facilitation by novel habitat creation has also been documented for other marine invaders. For example the invasive 'reef' building polychaete *Ficopomatus enigmaticus* provides refuge for a native crab species (Schwindt et al. 2001). Also,

in its invaded range the seagrass, *Zostera japonica*, is associated with increased abundance of benthic invertebrates that find refuge within its extensive root matrices (Posey 1988). Dense colonies of the intertidal ascidian *Pyura praeputialis*, a recent invader to the rocky coast of Chile, harbor 79 species of invertebrates, 55% of which are not found outside the ascidian matrices (Castilla et al. 2004). Finally, the invasion of Chesapeake Bay by the plant *Hydrilla ventricillata* leads to enhanced survival and growth of native benthic invertebrates, attributed to a possible reduction in predator efficiency with increased habitat complexity (Posey et al. 1993).

However, creation of a unique habitat needs to be considered in light of other factors. First, facilitation via habitat modification almost always occurs at the expense of other species. For example, while the reefs created by the exotic polychaete *Ficopomatus enigmaticus* create refugia for one crab species, ultimately several associated native infaunal species decline due to intensified crab predation (Schwindt et al. 2001). Second, novel habitats can also facilitate other invasive species. The shells of the Asian horn-nail (*Batillaria atramentaria*), invasive to the Northwest Pacific coast of the United States, provide habitat for two native hermit crabs. But, because the shells also provide up to 600 cm<sup>2</sup> of hard substrata in a mudflat system, they also facilitate several populations of benthic invasive species (Wonham et al. 2005).

*Replacement of existing habitats.* Species replacements can have varying impacts on native species and their richness (Sax et al. 2005). For example, the reed *Phragmites australis* has extensively invaded marsh areas replacing the native cordgrass *Spartina alterniflora*. Changes in vegetative biomass, water velocities, and microhabitat conditions result in higher abundances of nematodes and polychaetes, but a net reduction in total invertebrate density and species richness (Angradi et al. 2001). In another example, the marine tube-building polychaete, *Sabella spallanzanii*, creates a canopy above the substratum with its feeding structures. These structures increase the recruitment and abundance of select species, but these facilitative effects are transitory, disappearing after only 6 months (Holloway and Keough 2002). In

Australian coastal habitats invasion by the shrub *Mimosa pigra* results in the increase of a small flycatcher and a small rodent, but occur in conjunction with decreases in several other birds, lizards, herbaceous and woody plant species (Braithwaite et al. 1989). Subtle species-specific facilitative interactions for small freshwater fish occur as the invasive Eurasian milfoil, *Myriophyllum spicatum* replaces native freshwater macrophytes. (Duffy and Baltz 1998).

Facilitative interactions can also develop between endangered native species and invasive species, presenting a conundrum for conservation and management efforts (D'Antonio and Meyerson 2002). Such is the case with the endangered native willow flycatcher, *Empidonax trailii extimus*, whose native nesting habitat has been replaced by saltcedars (*Tamarix* spp.). The willow flycatcher will nest successfully in both habitats, albeit with lowered breeding success in the invasive habitat (Zavaleta et al. 2001). Nevertheless, since most of the native habitat has been lost, and restoration has not been fully successful due to hydrodynamic changes, survival of the willow flycatcher depends on the presence of the invasive species. Similarly, seven species of endemic land snails of the Azores and Madeira islands now depend on the habitat provided by the non-native plant community that has completely replaced the native endemic forest (Van Riel et al. 2000).

#### *Trophic subsidy*

Invasive species can provide limiting resources to higher trophic levels. Trophic subsidy is broadly defined for this review as the enhanced availability of an exploitable food source (i.e., nutrients, prey, host). For primary producers, the biological activity of certain invasive species can provide limiting nutrients. Invasive species can also lead to an increase in the diversity of available prey. In addition, by providing both a source of food and habitat, invasive species can be utilized as hosts.

*Nutrient enrichment.* Increased availability of limiting nutrients due to the biological activities of non-indigenous species can facilitate primary producers. In terrestrial systems, the invasion of nitrogen-fixing plants can facilitate neighboring

plants. For example, in the lowland pampas of Argentina the vegetative growth and above-ground biomass of native perennial grasses increases in the presence of non-indigenous *Lotus tenuis* (Quinos et al. 1998). In a marine system, the invasive mussel *Musculista senhousia* fertilizes sediments by depositing nutrient rich feces, resulting in increased leaf growth rates of the native seagrass (*Zostera marina*). Nevertheless, rhizome growth, the main means by which seagrass expands its population, is inhibited by the presence of the mussels (Reusch and Williams 1998).

*Food source diversification.* As invaders become more abundant in a habitat the probability increases that native predators, herbivores, and detritivores will utilize it as a food resource. For example, native predatory birds and mammals of the Flathead Lake (Montana) region prey on the abundant Kokanee salmon, introduced as a recreational fishery (Spencer et al. 1991). Non-indigenous Pacific oysters (*Crassostrea gigas*) fall prey to native herring gulls (*Larus argentatus*) in the Wadden Sea (Cadee 2001), and blue crabs (*Callinectes sapidus*) in the Chesapeake Bay prey upon the invasive rapa whelk, *Rapana venosa* (Harding 2003). Also, the invasion of freshwater lakes in Ireland by exotic amphipods has increased the availability of a readily consumed prey for a native predatory amphipod (Dick 1996).

Biological control measures also introduce species that can become prey (Pearson and Callaway 2003). Two gall fly species of the genus *Urophora*, introduced in an effort to control the spotted knapweed, *Centaurea maculosa*, compose up to 85% of the winter diet of native mice, *Peromyscus maniculatus* (Pearson et al. 2000). Mice consume on average 247 larvae per day, leading to increased mouse survival and population size (Pearson et al. 2000; Ortega et al. 2004). This predation of biological control species will decrease the efficiency with which the target pest is reduced.

Herbivory of non-indigenous species has also been documented. Two introduced subspecies of the algae *Codium fragile* are preferred over native *Codium* species by herbivorous sea slugs in the British Isles and Australia, a switch that occurred within a few years of introduction (Trowbridge 2004). And, a plant community composed almost

entirely of non-indigenous species in the Azores now provides the largest winter food source for the endemic bullfinch, *Pyrrhula murian* (Van Riel et al. 2000). Invasive plants are also be exploited for their leaves and nectar by native phytophages and pollinators (Memmott et al. 2000; Richardson et al. 2000; Memmott and Waser 2002).

Finally, invasion by the New Zealand mud snail, *Potamopyrgus antipodarum*, is significantly correlated with an increase in the densities of several native benthic stream fauna. The suggested mechanism for this correlation is via the production of feces by the snails, considered a highly nutritious food source for native detritivores (Schreiber et al. 2002).

*Novel hosts.* Invasive species can also act as host species, a condition that provides both food and habitat for native species. In California, 34% of the 236 native butterfly species oviposit or feed on introduced plant species (Graves and Shapiro 2003). Shapiro (2002) found that over 40% of the native butterfly fauna in a suburban–urban environment in California have no native hosts. Further, in a tropical lowland forest two non-indigenous plants of the genus *Piper* hosted on average more species of caterpillars than native plants (Novotny et al. 2003). The development of pest communities which use introduced crops (i.e. cacao and sugarcane) as hosts has also been well documented (Strong 1974, 1977). Rapid evolution of the checkerspot butterfly (*Euphydryas editha*) occurred during a host-switch to the invasive weed *Plantago lanceolata* (Singer et al. 1993). In only 8 years the butterfly evolved a genetic preference for the invader, refusing the ancestral host.

Novel hosts are also exploited by native parasites and parasitoids. Acanthocephalan parasites of freshwater amphipods are more prevalent in non-indigenous amphipod species, and interestingly are thought to allow coexistence of native and invasive species (MacNeil et al. 2003). Finally, four species of non-indigenous gall wasps in Britain have become the main, and sometimes sole, host for native parasitoids (Schonrogge and Crawley 2000).

#### *Pollination*

Non-indigenous species can facilitate native species by acting as pollinators. On the Hawaiian

islands, where several native bird species have gone extinct, the Japanese white-eye (*Zosterops japonica*) has become the main pollinator of the ieie vine (*Freycinetia arborea*) (Cox 1983). Honeybees (*Apis mellifera*) are transferred around the world to provide pollination services for domesticated crops. There is evidence that honeybees also pollinate native plants (Horskins and Turner 1999; Kato et al. 1999), and in some habitats are the dominant pollinator (Roitman 1999; Gross 2001). However, facilitative effects of this invader are not community-wide, since honeybees displace the foraging behavior of native bees, reducing their reproductive success (Kato et al. 1999; Thomson 2004).

#### *Competitive release*

The reduction in the abundance of a competitive dominant can indirectly facilitate competitively inferior native species. For example, on the Channel Islands of California, populations of an endemic skunk (*Spilogale gracilis amphiala*) have increased, correlated with reduced populations of their main competitor, the island fox (*Urocyon littoralis*), due to preferential fox predation by golden eagles (Roemer et al. 2002). Invasive European green crabs (*Carcinus maenas*) preferentially prey on dominant infaunal clam species, resulting in greater abundances of several benthic invertebrates (Grosholz et al. 2000; Grosholz 2005). Also, preferential feeding of Dreissenid mussels correlates with species-specific changes in zooplankton abundances (Thorpe and Casper 2002).

#### *Predatory release*

The reduction of native consumers by invasive species can indirectly result in increased abundance or biomass of native prey. For the purposes of this paper, consumption is defined as either predation or herbivory. The introduced toad, *Bufo marinus*, indirectly facilitates native anuran prey by reducing populations of a native predatory anuran (Crossland 2000). In alpine lake systems, the introduction of recreational sport fish results in increased mosquito larvae (*Culex* sp.), due to the reduction of invertebrate predators (Knapp et al. 2001). Introduced freshwater consumers, such as crayfish and trout, prey on native herbivores, resulting in increased algal biomass (Townsend 1996; Huryh 1998; Nystrom

et al. 1999; Biggs et al. 2000). Finally, primary productivity has increased in Lake Ontario after the predatory cladoceran (*Cercopagis pengoi*) was introduced and began to consume native herbivorous zooplankton (Laxson et al. 2003).

#### *When are facilitative interactions between exotic and native species most likely to occur?*

From the summarized evidence, facilitative effects of invasive species on native species can be predicted to be most likely *when* invasive species: (1) provide a limiting resource, (2) increase habitat complexity, (3) replace a native species and fulfill their functional role, or (4) provide significant escape from enemies or competitors. Although these are very broad generalizations, they begin to provide a framework that can be useful to predict both which invasive species might have facilitative impacts, as well as what habitat conditions lend themselves to the development of these interactions.

#### *Why are some native species facilitated by invasive species?*

As non-indigenous species invade a habitat, they will generally reduce population of native species either through predation or competition. Evidence presented in this review finds that some species increase in abundance or biomass in the presence of an invader. It is possible to generalize *why* these facilitative interactions develop between native and exotic species through three scenarios: Novel, Substitutive and Indirect facilitation (Figure 3). From the evidence found in this review, substitutive facilitation was the most common type of interaction, followed by novel and indirect (Table 1).

Novel Facilitation (Figure 3a) develops if invasive species is functionally unique in comparison to native resident species, and hence provides a new exploitable resource that is utilized by native species. Novel facilitation can be exemplified by the invasion of freshwater systems by the zebra mussel, *D. polymorpha*, which creates novel and unique habitat matrices that act as habitat for native species (Ricciardi et al. 1997; Bially and MacIsaac 2000; Darrigran 2002).

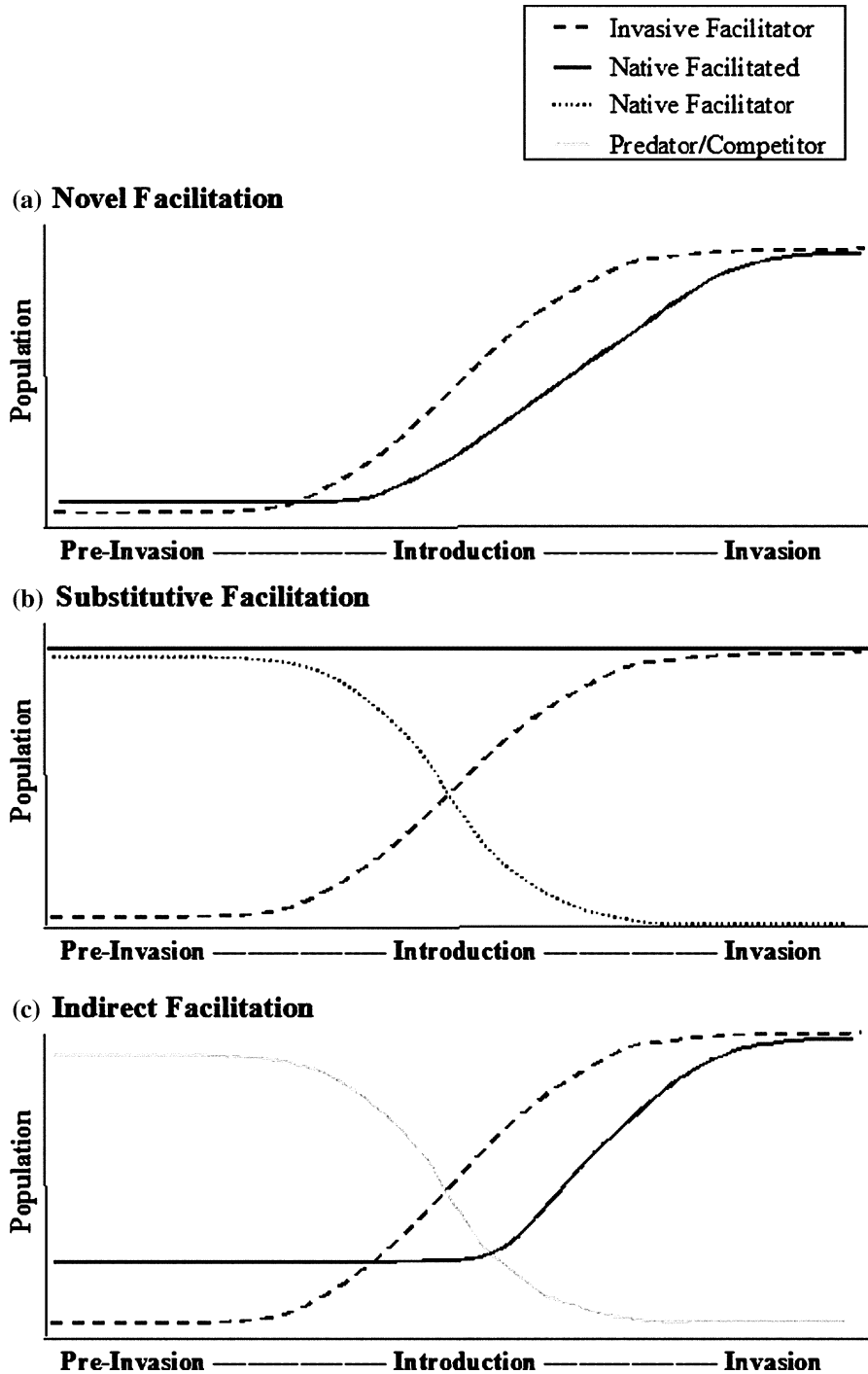


Figure 3. Conceptual models for three scenarios that define why invasive species can facilitate native species. Depicted along a timeline of invasion events is the relative population size of different interacting species: invasive facilitator, native facilitated, native facilitator, and predator/competitor. Scenarios are: (a) Novel facilitation which occurs when no native facilitator existed; (b) Substitutive facilitation which occurs when an invader functionally replaces a native facilitator; (c) Indirect facilitation which occurs when the reduction of a predator or dominant competitor indirectly results in the facilitation of a native.



Substitutive Facilitation (Figure 3b) occurs if an invasive species functionally replaces a native facilitator species. This condition occurs because the invader outcompetes the native facilitator. One important point to note is that the native species being facilitated can likely have the same abundance/biomass in both the pre- and post-invasion conditions. Therefore, in cases where the native and invader are highly functionally redundant, there might not be an observable 'increase in the abundance or biomass' of the native species. However, if the invader is removed, and the native facilitator not restored, the dependant native species will suffer. This is clearly exemplified by the dynamics of *Tamarix* spp. invasion, which has replaced native riparian vegetation, providing the only nesting habitat for the endangered native willow flycatcher, *Empidonax trailii extimus*. (Zavaleta et al. 2001). Since restoration of native habitat has been difficult, survival of the willow flycatcher is dependent on the presence of this invader.

Finally, Indirect Facilitation (Figure 3c), which occurs if a native competitor or predator is reduced (either numerically or behaviorally) by an invasive species, results in an increase in the native prey or native competitively inferior species. For example, facilitative impacts of the invasion of the European green crab (*Carcinus maenas*) occurred because of preferential predation on dominant clam species, which resulted in increased populations of other benthic invertebrates (Grosholz et al. 2000; Grosholz 2005).

## Discussion

In order to understand the role of facilitation by invasive species, and to weigh the relative importance of facilitation against predatory and competitive impacts, it will be necessary to address several questions.

(1) First and foremost, what are the comparative strengths of predation, competition, and facilitation by non-indigenous species? Although there is recent evidence that facilitative interactions are as frequent as other interspecific interactions including competition, predation and parasitism (Bruno et al. 2005), what is yet undetermined is the relative strength of each

of these interactions. Meta-analysis (Hedges and Olkin 1985; Osenberg et al. 1999; Gurevitch and Hedges 2001) and path analysis (Wootton 1994) techniques could be used to decipher the systemwide net effects of invasions. For some systems, these types of analyses are timely and feasible.

- (2) Are facilitative interactions density dependent and to what extent? And, how do facilitative interactions vary temporally and spatially? There might be a threshold density of the facilitating invader which needs to be reached before facilitative mechanisms are expressed. For example, novel habitat creation might only impact native species when a dense 'matrix' of habitat has been formed. Temporally, we do not know if facilitative impacts are transient or lasting. Furthermore, temporal dynamics such as time-lags before population explosions (Crooks and Soulé 1999), or boom–bust population cycles (Simberloff and Gibbons 2004) will affect the development and strength of facilitative impacts.
- (3) Do facilitative impacts occur as frequently on island ecosystems? Island communities can be especially damaged by invasive species if they either have a low level of diversity and/or a high level of endemism. Also, if islands have a high level of endemism, it is likely that an invader will be 'taxonomically distinct', and have a greater impact on island communities (Ricciardi and Atkinson 2004).
- (4) What are other mechanisms of facilitation of native species by non-indigenous species? There are likely to be more facilitative interactions than are reported in this review. The literature searches conducted for this review were limited to only one database, and only a certain span of years. Further, there are several articles that were located, but do not present evidence of increases in native species. For example, horses and cattle are thought to be the main seed dispersers in the New World neotropical forests, in which most large herbivores have gone extinct (Janzen and Martin 1982). Although there are no data on increased tree abundances correlated with horse behavior, seed dispersal is very likely another mechanism through which invasive species can facilitate native species.

- (5) How do we weigh the ecological impacts of invasive species against anthropogenically 'profitable' uses? We should focus attention on facilitative impacts of exotic species on native species not only to develop a broader understanding of ecological dynamics, but also because in some cases these interactions are valuable tools for ecosystem management and conservation. For example, two methods take advantage of the facilitative effects of non-indigenous species: biological control and forest restoration. Biological control capitalizes indirect facilitative interactions to restore populations of native species. In other words, 'direct effects of the biological control agent on its intended host translate into an indirect positive effect on native species' (Pearson and Callaway 2003). Forest restoration efforts utilize facilitative effects of non-indigenous species to modify habitats and catalyze establishment of natives (D'Antonio and Meyerson 2002). For example, fast growing non-native trees facilitate native seedlings in tropical forests (Otsamo 2000). Also, plantation pines have been used to stabilize dunes and increase the succession of forests in blowout areas (Leege and Murphy 2001). Success of both biological control and forest restoration depends on a working understanding of facilitative and indirect interactions. Hence, utilization of invasive species for anthropogenic means should only proceed when other alternatives are not viable, and with utmost caution.
- (6) Finally, how will facilitative impacts interact with already existing anthropogenic stressors? As invasive species become established, facilitative interactions could possibly mitigate native species population declines that have occurred due to anthropogenic disturbance. For example, the Hawaiian ieie vine (*Freycinetia arborea*) is now mainly pollinated by an exotic bird after the extinction of several native bird species (Cox 1983). Alternatively, the presence and permanence of populations of non-indigenous species may interact synergistically with habitat loss to prevent the re-establishment of native species. For example, the invasion of riparian habitats by *Tamarix* sp., which has led to further deterioration of

habitat quality, preventing the re-establishment of the native nesting habitat for the willow flycatcher (Zavaleta et al. 2001).

## Conclusion

This review develops a framework to analyze *how*, *when* and *why* invasive species can facilitate native species. The facilitative impacts of invasive species on native species can have cascading effects across trophic levels, can re-structure communities, and can lead to evolutionary changes. Specific patterns emerge from this review, most importantly that facilitative impacts never happen in isolation, rather they occur concomitantly with competition, predation, herbivory, and/or parasitism. It is imperative that invasion biologists incorporate facilitative interactions of non-indigenous species into future ecological research if we wish to determine their relative strength in comparison to competitive and predatory effects, and the resulting response of native populations and communities. Knowledge of all interactions with invasive species, including facilitation, will be increasingly important as we strive to ameliorate environmental degradation and prevent future invasions.

## Acknowledgements

I offer my sincere gratitude to S. Williams, J. Stachowicz, E. Grosholz, G. Vermeij, A. Shapiro and three anonymous reviewers who provided invaluable comments and mentorship. Thanks are also due to M. Harker, M. Frey, K. Hultgren, S. Olyarnik, H. Swarts, H. Weiskel, C. Harley, and M. Swarner. Funding for L. Rodriguez for this work provided through NSF Pre-Doctoral Fellowship and UC MEXUS Dissertation Research Grant.

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