

MINI- REVIEW

Minireviews provides an opportunity to summarize existing knowledge of selected ecological areas, with special emphasis on current topics where rapid and significant advances are occurring. Reviews should be concise and not too wide-ranging. All key references should be cited. A summary is required.

When do herbivores affect plant invasion? Evidence for the natural enemies and biotic resistance hypotheses

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Two venerable hypotheses, widely cited as explanations for either the success or failure of introduced species in recipient communities, are the natural enemies hypothesis and the biotic resistance hypothesis. The natural enemies hypothesis posits that introduced organisms spread rapidly because they are liberated from their co-evolved predators, pathogens and herbivores. The biotic resistance hypothesis asserts that introduced species often fail to invade communities because strong biotic interactions with native species hinder their establishment and spread. We reviewed the evidence for both of these hypotheses as they relate to the importance of non-domesticated herbivores in affecting the success or failure of plant invasion.

To evaluate the natural enemies hypothesis, one must determine how commonly native herbivores have population-level impacts on native plants. If native herbivores seldom limit native plant abundance, then there is little reason to think that introduced plants benefit from escape from these enemies. Studies of native herbivore-native plant interactions reveal that plant life-history greatly mediates the strength with which specialist herbivores suppress plant abundance. Relatively short-lived plants that rely on current seed production for regeneration are most vulnerable to herbivory that reduces seed production. As such, these plants may gain the greatest advantage from escaping their specialist enemies in recipient communities. In contrast, native plants that are long lived or that possess long-lived seedbanks may not be kept “in check” by native herbivores. For these species, escape from native enemies may have little to do with their success as exotics; they are abundant both where they are native and introduced.

Evidence for native herbivores providing biotic resistance to invasion by exotics is conflicting. Our review reveals that: 1) introduced plants can attract a diverse assemblage of native herbivores and that 2) native herbivores can reduce introduced plant growth, seed set and survival. However, the generality of these impacts is unclear, and evidence that herbivory actually limits or reduces introduced plant spread is scarce. The degree to which native herbivores provide biotic resistance to either exotic plant establishment or spread may be greatly determined by their functional and numerical responses to exotic plants, which we know little about. Generalist herbivores, through their direct effects on seed dispersal and their indirect

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effects in altering the outcome of native–non-native plant competitive interactions, may have more of a facilitative than negative effect on exotic plant abundance.

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Non-native plant invasion into native communities has become a ubiquitous conservation problem. Most native communities contain at least one, and often many exotic plants (Holm et al. 1997, Pimentel et al. 2000). A growing body of work indicates that the rapid spread of some non-indigenous species can reduce native species diversity and alter ecosystem functioning (Vitousek and Walker 1989, D'Antonio and Vitousek 1992, Schmitz et al. 1997, Walker and Steffen 1997, Parker and Reichard 1998). While our understanding of the impacts of exotic plants on recipient communities has grown substantially, why non-native plants become established and dominant in the first place is often unclear.

Ecological thinking about the invasion process has been largely shaped by two prominent hypotheses proposed by a pair of ecology's founding fathers. The natural enemies hypothesis, first articulated by Darwin (1859) and later amplified by others (Williams 1954, Elton 1958, Gillett 1962), provides an explanation for why some introduced species are often rare in their native range but become superabundant in recipient communities. It posits that release from specialist natural enemies (herbivores and pathogens) enables exotics to become abundant in their new range. The biotic resistance hypothesis, first developed by Elton (1958), provides an explanation for why many exotics fail to establish or spread in recipient communities. This hypothesis states that introduced species can be kept from taking hold in some recipient communities by strongly interacting native species (competitors, pathogens or herbivores).

Since introduced plants are more likely to escape from co-evolved specialists as opposed to generalist herbivores (except in cases where plants have been introduced onto herbivore-free islands), an assumption behind both the natural enemies and biotic resistance hypotheses is that specialist enemies keep plants in check in their native range whereas generalist herbivores provide community resistance to invasion in recipient communities (Strong et al. 1984). Although these hypotheses make predictions regarding invasion success on the one hand (escape from enemies) and failure to invade on the other (due to biotic resistance), both suggest that herbivores may play an important role in affecting plant invasion. Here we review the empirical evidence for each of these hypotheses and highlight important issues related to these hypotheses that would benefit from future research.

The natural enemies hypothesis

The natural enemies hypothesis is predicated on the assumption that plants are suppressed in their native range by natural enemies; escape from these enemies enables alien populations to grow explosively in communities into which they are introduced. The notion that introduced species avoid population regulation by leaving specialist enemies behind is an intuitively appealing idea. Ecological textbooks often offer this as an explanation for why exotic plants can become so abundant in recipient communities (Crawley 1997). Moreover, the natural enemies hypothesis forms part of the conceptual underpinning for biological control (Debach and Rosen 1991, Van Driesche and Bellows 1996), in that specialist herbivores are introduced into a new range to control introduced plants. This perspective was encapsulated by Williams (1954) who stated, "The theory that underlies the biological control of weeds is relatively simple and is applicable only to exotic weeds. It postulates that the great increase of reproductive rate and vegetative vigor that a plant may show after its introduction into a new country is due primarily to a lack of natural enemies, implying that in its native country its comparatively innocuous status is maintained by such enemies ...". However, it should be noted that not all biocontrol practitioners have held this viewpoint. Huffaker (cited in Huffaker 1957) stated that "while aggressive and abundant exotic [weed] pests are always good prospects for biological control, it does not follow and is ecologically unsound to postulate that such aggressiveness and abundance in the new land is necessarily due to an absence of natural enemies. There are far too many other reasons why a pest may be relatively innocuous in its native land yet aggressive and troublesome in environments new to it".

What is the evidence supporting the natural enemies hypothesis? Surprisingly, the hypothesis has received little critical assessment. A rigorous empirical test would involve parallel experiments in the native and introduced range. In both ranges, experiments would exclude herbivores from plants and examine the impacts on plant abundance and population growth. If the natural enemies hypothesis is correct, experiments should show that native herbivores have strong negative impacts on plant demography, resulting in reduced plant population sizes or population growth rates. In contrast, these same plants in the introduced range should suffer little herbivore damage, and plant abun-

dance and population growth should be greater in the introduced versus the native range. We are not aware of any studies of this sort. In the literature, there is a striking dichotomy of opinion regarding the importance of escape from natural enemies. On the one hand, among those who work on invasion biology, it is commonly asserted that the lack of natural enemies explains why introduced plants spread rapidly. The implication is that strong top-down consumer control limits plant abundance in the native range. Yet, among those that work on native plant consumer interactions, the role of top-down processes in affecting native plant population dynamics has been the subject of much debate and little consensus for many years (Hairston et al. 1960, Owen and Wiegert 1981, Louda 1982, 1983, 1994, Belsky 1986, Crawley 1989, Louda and Potvin 1995).

Insight into the potential for the natural enemies hypothesis to operate can be gained by evaluating the types of plants and the overall ecological context in which native herbivores have strong suppressive impacts on native plant populations. Based primarily on their own work, Louda (1989, 1995) and Louda and Potvin (1995) provide a verbal model that predicts that plant life-history characteristics should critically affect the ability of specialist herbivores to limit the abundance of native plants. Louda and Potvin (1995) assert that short-lived perennial plants with heavy dependence of regeneration on current seed production should be most affected, at the population level, by specialist herbivores. In contrast, annuals that produce many dormant seeds may be buffered from the population impacts of consumers, particularly if seedling recruitment is always safe-site rather than seed-limited (Andersen 1989, Crawley 1989, 1992). Long-lived perennials (such as trees) that either depend on vegetative spread or that can compensate across years for periodic bad years in seed production should similarly be buffered from significant population-level effects of consumers.

Impact of specialist herbivores in the native range

Several studies support the role of specialist insects in reducing plant abundance via seed predation. Louda and her colleagues have shown that seed-feeding herbivores significantly affect the demography and population abundance of two perennial plants, golden bush (*Hazardia squarrosus*) and Platte thistle (*Cirsium canescens*). Louda has shown that herbivory results in a 39 to 61% reduction in seed production, depending on the year, location and species studied (Louda 1982, Louda and Potvin 1995). This magnitude of seed loss translates directly into reduced plant abundance in future generations (Louda 1982, Louda and Potvin 1995). The fact that the plants involved in these interactions lack a

long-lived seedbank makes them particularly vulnerable to seed predation. For Platte thistle, two other features are important. First, a relatively short growing season constrains this thistle's ability to compensate for herbivory. Second, since these thistles are monocarpic, population persistence is critically dependent on current seed production. Herbivory that decreases seed rain has direct effects on subsequent thistle recruitment and future adult plant abundance, essentially reinforcing the fugitive status of these thistles. In Europe, strong interactions with native herbivores likely have similar population-level effects on native European thistles (Sheppard et al. 1995, Sheppard 1996). Just as the natural enemies hypothesis predicts, herbivory contributes to the suppression of these thistles in their native range; escape from specialist herbivores may explain why European thistles are so abundant in portions of their introduced range in the United States.

Plants may benefit from emancipation from other guilds of herbivores besides seed feeders. For example, Scots broom (*Cytisus scoparius*) individuals in Europe live 10–12 yr (Waloff and Richards 1977, Rousseau and Loiseau 1982). However, Scotch broom that has been introduced into the United States and Australia can live 17–20 yr (Rees and Paynter 1997). In England, Waloff and Richards (1977) reported that nearly twice as many Scots broom plants survived to ten years of age in plots protected from herbivores compared to plants in plots where invertebrate herbivores were suppressed. A presumed (although untested) explanation for increased longevity of Scots broom in its introduced range is escape from herbivore attack (Rees and Paynter 1997).

Despite these examples, there are many cases in which pest pressure does not keep successful invaders "in check" in their native communities. Many successful exotics are actually quite abundant where they are native. Examples of relatively abundant native European plants that have also become abundant weeds in North America include *Ulex europaeus*, *Stellaria media*, *Carduus tenuifolius*, *Carduus pycnocephalus*, *Sonchus oleraceus*, *Pycris echioides* and *Senecio vulgaris*, to name just a few (Vilà pers. obs.). In some cases, plants may be abundant in their native range because they do not receive much herbivore damage. Yet, many native perennials are both widespread and dominant despite harboring diverse and plentiful pest populations. These species support persistent pest populations because of their predictable availability in space and time. They remain persistent community members because they have life-history attributes – long life spans (in some cases due to clonal growth) or long-lived seedbanks – that enable them to compensate at the population level for herbivore damage (Harper 1977, Crawley 1992, 1997). Because they remain abundant in the face of herbivory, it is unlikely that escape from natural enemies is the sole explanation for why these species become abundant in recipient communities. A case in

point may be goldenrod, *Solidago altissima*. In its native range, goldenrod supports a very diverse and occasionally abundant suite of herbivores (Maddox and Root 1990). Long-term insect exclusion studies have shown that periodic defoliation by two outbreaking species of chrysomelid beetles, *Microrhopala vittata* and *Trirhabda virgata*, reduces the density of goldenrod ramets (Root 1996, Carson and Root 2000). Although this can have important implications for plant community structure (Carson and Root 2000), despite heavy herbivory, goldenrod still remains a community dominant in many old fields in the eastern United States. Defoliation reduces ramet growth and density, but it does not destroy genets (as is the case with the monocarpic thistle). Clonal growth (via rhizomes) undoubtedly buffers goldenrod populations from the effects of periodic bouts of defoliation. In Europe, *S. altissima* was introduced from North America in the 18th century (Voser-Huber 1983 as cited in Meyer and Schmid 1999), and it has become a noxious weed (Zwölfer 1976). Plants support a much reduced phytophage community in Europe than they do in the United States (Jobin et al. 1996). While escape from herbivory may partly explain high goldenrod density in Europe, it is clear from work in the native range that the plant is capable of being a community dominant even when exposed to high herbivore loads. As such, plant life-history characteristics are as important as escape from herbivores in enabling *S. altissima* to be abundant in Europe.

The fact that some native plants remain abundant despite heavy herbivory has important implications for biological control. The likely success of biocontrol may have as much to do with particular plant life-history attributes and environmental conditions as it does with the ability of the biocontrol agents to establish and attain high density. A good case in point concerns interactions between ragwort (*Senecio jacobaea*) and cinnabar moth (*Tyria jacobaeae*). Ragwort is abundant and has a widespread distribution in its native range in Europe (Harper and Wood 1957). While cinnabar moth herbivory can result in extensive defoliation, it does not appear to limit ragwort abundance in most native populations (Van der Meijden 1979, Crawley and Gillman 1989). Defoliation reduces seed production but this usually does not translate into lowered abundance because recruitment in many cases may be microsite rather than seed limited (Crawley and Gillman 1989). For identical reasons, cinnabar moth does not appear to be the most effective biocontrol agent on ragwort (Myers 1980, McEvoy et al. 1993); control by cinnabar moth is only effective in disturbed sites, where recruitment may be seed limited (McEvoy et al. 1993). The most successful control strategy for ragwort involves exposure to a single biocontrol agent – the flea beetle (*Longitarsus jacobaeae*), which kills plants outright – along with promotion of plant competition (McEvoy and Coombs 1999).

Impact of generalist herbivores in the native range

Some of the best examples of native consumers reducing the abundance of native plants come from studies of generalist consumers. For example, in grassland and dune systems, intense mouse granivory on large-seeded plants can dramatically reduce the abundance of these species (Davidson et al. 1984, Brown et al. 1986, Brown and Heske 1990, Hulme 1996, Howe and Brown 2000, Maron and Simms 2001). Rodent herbivores can also severely limit plant establishment and productivity (Summerhayes 1941, Batzli and Pitelka 1971, Mills 1986, Ostfeld et al. 1997, Virtanen et al. 1997, Sirotnak and Huntly 2000). Yet, since rodent granivores/herbivores are often generalists and occur in most communities, it is unclear whether plants that are affected by these consumers in their native range truly escape them in their introduced range (see evidence for biotic resistance below). Whether seeds from introduced plants escape granivores may be primarily dictated by their size and palatability in relation to seeds produced by natives (Blaney and Kotanen 2001). If an introduced species produces particularly large and palatable seeds in relation to those present in the recipient community, selective seed consumption by granivores (sensu Price and Jenkins 1986, Hulme 1998) may inhibit exotic plant establishment. Alternatively, selective foraging by native granivores on large-seeded natives may favor the establishment of small-seeded exotic species. A key question here, and one that deserves more attention, concerns whether specialists or generalists are more likely to influence plant abundance in the native range. If generalist herbivores have a greater overall role in suppressing native plant abundance than do specialists, then introduced plants may not actually escape from herbivore pressure at all.

Natural enemies – concluding thoughts

At one end of the plant life-history continuum, it is clear that plants lacking a seedbank that are entirely dependent on current seed rain for regeneration will be adversely affected by specialist consumers that reduce seed production. Less obvious, perhaps, is the impact of herbivores on plants with alternative life-histories, for example annual or perennial plants that have seedbanks of moderate density. Simulations suggest that these plants can be significantly affected at the population level by herbivory (Maron and Gardner 2000). To determine the range of conditions under which the natural enemies hypothesis might apply, we need a better understanding of both the suites of plants most likely to be suppressed by native herbivores, and the types of herbivores (generalists versus specialists) most likely to have a suppressive impact. Comparative

studies aimed at determining the ecological conditions and life-history attributes of plants that best predict whether herbivores will influence population abundance would do much to advance our understanding of plant–herbivore relations and the applicability of the natural enemies hypothesis. Progress in this direction has been slow, in part because the lion’s share of plant–herbivore studies has focused on plant defense or herbivore dynamics on one hand, or community effects of herbivory on the other. Despite over forty years of intensive research on plant–consumer interactions, we still possess only a rudimentary ability to predict the conditions under which herbivores might affect plant abundance, distribution or population dynamics.

The biotic resistance hypothesis

While the success of non-native species is often attributed to the lack of enemies in recipient communities, the failure of some exotics to either establish or spread is often explained by negative impacts of interactions between native biota and introduced species. Cases of plants that fail to invade due to herbivory are suspected; however, the fundamental issue concerns how generally native herbivores impose substantial biotic resistance to invasion.

One interesting but untested possibility is that native generalist herbivores can only effectively limit introduced plant spread when plant density is below some threshold. If exotic plants are relatively rare in relation to herbivore abundance, heavy herbivore pressure may effectively limit an increase in plant population size. However, once exotic plant abundance rises above some lower threshold (perhaps due to propagule pressure), native herbivore numbers may not show a numerical response to this increase in plant abundance if they themselves are predator-limited. Consumption of the same absolute number of propagules would result in a lower percentage of seed consumed as the exotic population increases. If this were the case, native herbivores might be ineffective at limiting the spread of exotics after they cross a density threshold. Limited evidence for such a threshold effect comes from studies of post-dispersal seed predation on two South African *Acacia* species. Seed predation by rodents was negatively correlated with *Acacia* cover (Holmes 1990). Possibly seed predation decreased at increasing *Acacia* cover because the predators became satiated or because there was a reduction of rodent density (i.e. reduction of suitable nesting habitat). Whether this is a common feature of native herbivore–exotic plant interactions is unknown.

Even if herbivores do exhibit a numerical response to increasing exotic plant density, they may still be ineffective at suppressing exotic plants once they have become

superabundant. In Australia, the adults and larvae of the lepidopteran *Etiella behrii* breed and feed on *Ulex europaeus* seed pods; yet, despite the moth attack, gorse is still increasing in abundance (Faithfull 1997).

Within the context of weed biocontrol, researchers have attempted to estimate what level of damage by biocontrol herbivores might result in efficacious control of their weedy hosts. Noble and Weiss (1989) predicted that predispersal seed predation of the shrub *Chrysanthemoides monilifera* would have to reduce more than 95% of seed production to provide satisfactory control. Hoffmann and Moran (1998) found that a 98% seed destruction in *Sesbania punicea* in South Africa by the introduced weevil *Trichapion lativens* was unable to reduce the density of the host plant. These studies indicate that once exotics become extremely common and seedbank density becomes large, the ability of seed predators to suppress exotic plant population growth may be limited. Parker (2000) has shown that even in the absence of a seedbank, a biocontrol weevil would have to consume between 70 and 99.9% of Scots broom seeds in order to halt the population growth of the plant. It would be interesting to know whether specialist biocontrol agents might be more effective at controlling the initial expansion of exotics, during the period when plants are fairly abundant but the seedbank size is small. Careful demographic modeling (sensu Parker 2000) would shed more light on this issue.

The ability of generalist herbivores to limit the establishment of an exotic hinges upon the steepness of the herbivore functional response curve. To limit plant establishment, generalists must consume plants while they are at very low density (or biomass). This may be fairly unlikely given herbivore foraging behavior. A more probable scenario is that generalist herbivores only exhibit a functional or numerical response to exotics once they become common. To fully appreciate the potential for biotic resistance due to herbivory to operate, both the functional and numerical response of native herbivores to changes in exotic plant abundance must be understood. This is an area that is ripe for investigation.

The above conceptual issues notwithstanding, observational studies indicate that native herbivores have great potential to limit exotic plant spread. For example, there are many instances of herbivore attack limiting the establishment of introduced agricultural plants. Mack (1996a) describes several tree species planted for forestry in the tropics that have not naturalized due to heavy native insect attack. Similarly, native microbial pathogens, such as viruses and protozoans, are the cause of the destruction of introduced crops. Yet, while pests can destroy large plantations or intensive cultivations of deliberately introduced species, this does not necessarily imply that biotic barriers are effective at limiting the naturalization and invasion of other (non-

cultivated) species. Many exotic species that are accidentally introduced may initially have small populations, and these probably go extinct due to low propagule pressure and/or physical factors rather than due to attack by native herbivores and pathogens.

Herbivore diversity on introduced plants

Biotic resistance is suggested because introduced plants are not always herbivore-free. Although plants arriving from a long distance may initially escape from herbivore and pathogen attack (Westman 1990), these plants are often rapidly discovered by native herbivores (Strong 1974, Strong et al. 1977, Tabashnik 1983, Thomas et al. 1987, Auerbach and Simberloff 1988). The phytophagous fauna of introduced species can be as diverse as that of native species. In Florida, in less than 20 yr two species of introduced oaks, *Quercus acutissima* and *Castanea crenata*, have recruited as many leaf-miners as native oaks (Auerbach and Simberloff 1988). In Australia, a total of 114 species of phytophagous insects representing 5 orders, 50 families and 101 genera can be found on the exotic *Mimosa pigra*. The diversity of herbivores on *M. pigra* in its introduced range is similar to that in the native range (Wilson et al. 1990). The introduced thistle *Cirsium arvense* is attacked by over 80 insect species (24 families) in Canada (Maw 1976). In California, the introduced thistles *Cirsium vulgare*, *Carduus pycnocephalus* and *Silybum marianum* support 30, 40 and 47 species of phytophagous insects, respectively (Goeden 1971, 1974, Goeden and Ricker 1986). Although the number of different herbivores found on these thistles may be high when sampled across a large distributional area, in any given population herbivore diversity is likely quite low. This underscores the fact that while introduced species can accumulate a great diversity of enemies, this does not necessarily lead to greater biotic resistance to invasion. For example, 44 phytophagous species occur on the European blackberry (*Rubus fruticosus*), yet herbivory appears to have little effect in suppressing populations of this species (Bruzese 1980). Similarly, although introduced *Mimosa pigra* is attacked by 114 species of insects, the plant suffers only minimal damage because insect presence and abundance is spatially and temporally quite variable (Wilson et al. 1990). Even in experimental terrestrial mesocosms, increasing herbivore diversity does not dramatically decrease autotroph biomass (Naem et al. 1996).

Guilds of herbivores on exotic plants

Most studies documenting herbivory on exotic plants examine the impacts of only two functional groups of native herbivores: grazers and seed feeders. The inten-

sity of herbivory imposed by these two guilds of consumers appears quite different. Native seed predators generally have significantly greater impacts on exotic plants than do folivores. Averaged across all studies, seed predators reduced the abundance of exotic plant seed by 32%. However, levels of seed predation can often be much higher. Ants, for example, can reduce exotic plant seed abundance by 90% (Holmes 1990). It is usually unknown how reductions in seed abundance affect exotic plant density. An exception is the weed *Abutilon theophrastri* (Malvaceae). The hemipteran *Neisthrea louisianica* kills 21% of *A. theophrastri* seeds, and causes a reduction in seed weight, seed viability and seedling emergence (Kremer 1995).

There are few examples of either native stem borers or sap-feeders attacking exotic plants. This probably reflects the fact that researchers simply have not looked for these herbivores on exotic plants. The only case where stem borer herbivory on an exotic species has been studied indicates that these herbivores can be quite damaging. The stem burrower *Euhrychiopsis lecontei* (Coleoptera) reduces more than half of the root and shoot biomass of the Eurasian watermillfoil *Myriophyllum spicatum* (Holaragaceae) in US lakes (Creed and Sheldon 1995, Sheldon and Creed 1995). In San Francisco Bay, the native sap-feeder *Prokelisia marginata* (Homoptera) can reduce 51% of the above-ground biomass and 73% of the seed set of the introduced cordgrass, *Spartina alterniflora*. This herbivory, however, appears to have little effect on *Spartina* spread and population abundance at this site (Daehler and Strong 1994, 1997).

Effects of native herbivores on exotic plant performance and population abundance

What is the evidence that generalist herbivores can limit exotic plant performance and spread? To answer this question, we reviewed all studies ($n = 18$) from 1986 to 1998 listed in the Life Science Collection (Appendix I) that focused on the impacts of native herbivores on exotic plants in the broadest sense – all animals that feed on living plant material (e.g. fruit and seed predators, folivores, root feeders, etc). Our review does not include grazing or browsing by livestock (reviewed by Popay and Field 1996) or studies that simulated herbivory by clipping plants. The survey includes both natural and human-managed ecosystems (i.e. agroecosystems, rangelands). Although post-dispersal seed predation was sometimes evaluated by placing seed depots on the soil (Appendix I), the majority of studies compared performance between plants exposed to and those protected from herbivores. A summary of some of these studies indicates that on average, native herbivores reduce the performance of early life-history stages of exotic plants (i.e. seed set, seed viability, seedling

recruitment, survival and growth) by a third. Herbivores reduce the performance of adult exotic plants (i.e. adult plant size and growth) by almost one half. On average, attack by herbivores caused 62% of the exotic plant mortality. Mortality was extremely high in some cases, especially as it affected seedlings. In coastal California, for example, 90% of the South African *Carpobrotus edulis* seedlings and almost 40% of experimentally transplanted cuttings were completely consumed by native mammals (Vilà and D'Antonio 1998a, b). However, exotic species that are attacked by native herbivores sometimes have greater compensatory abilities than do native plants. For example, the Asian evergreen shrub, *Lonicera japonica*, that has invaded mixed forests of the coastal plains of South Carolina (USA) appears quite tolerant to grazing. In contrast, its native congener *L. sempervirens* allocates less biomass to leaves and stems than *L. japonica* and thus recovers more slowly when grazed (Schierenbeck et al. 1994).

Mack (1996b) has advocated the approach of comparing traits between exotic and native congeners in the same range to determine the unique traits possessed by exotics that enable them to establish and spread. There is great potential for taking this approach with respect to herbivore resistance or tolerance traits. For example, Richards (1984) has shown that the exotic grass *Agropyron desertorum* is more tolerant of heavy livestock grazing in the intermountain west of the United States than is its native congener *A. spicatum*.

Although native herbivores can clearly reduce exotic plant performance, it is usually unknown how these impacts alter exotic plant abundance. Perhaps the best case involves the native stem borer *Euhrychiopsis lecontei* (Coleoptera), which reduces plant size of the Eurasian watermillfoil, *Myriophyllum spicatum* (Holaragaceae), and has been implicated in the destruction of watermillfoil in some US lakes (Creed and Sheldon 1995). Rabbit grazing on the introduced plant *Conyza sumatrensis* in Great Britain reduces recruitment and can suppress the number of adult plants (Case and Crawley 2000). Yet, while native herbivores can kill exotic plants, it is usually unknown whether strong interactions of this sort are widespread and common enough to significantly affect invasion rate or the distribution of exotics in recipient communities. This is a critical question, and experimental studies that quantify the impact of native herbivores on both individual performance and the rate of population spread are sorely needed.

Specialist native herbivores attacking introduced plants

Some evidence indicates that native enemies prefer introduced plants over their native congeners (Thomas et al. 1987, Solarz and Newman 1996, Soldaat and Auge

1998). These cases represent a net diet range expansion by specialist phytophagous insects. For example, in the Sierra Nevada of California, the native butterfly *Euphydryas editha* has historically fed upon the native plant *Collinsia parviflora*. Recently, however, the butterfly has incorporated the forb *Plantago lanceolata* into its diet. Preference trials have shown that some females prefer *P. lanceolata* for oviposition. *P. lanceolata* grows in sympatry with *C. parviflora*, and was introduced into California over a century ago (Thomas et al. 1987). *Abutilon theophrasti* is a noxious weed of irrigated crops of temperate regions. Seed predation by the native hemipteran *Niesthrea lousianica* reduces seed viability and thereby limits the abundance of *A. theophrasti* (Kremer and Spencer 1989). *Niesthrea lousianica* also utilizes other malvaceous species as hosts but development of the insect on these plants is incomplete or slower than on *A. theophrasti* (Kremer and Spencer 1989). In Florida, the soapberry bug, *Jadera haematoloma*, has recently colonized the exotic goldenrain tree, *Koelreuteria elegans*, that was introduced from Southeast Asia in the 1950s (Carroll and Boyd 1992). These bugs have rapidly evolved mouthparts that enable them to perform better on introduced versus native hosts (Carroll et al. 1997).

Louda and Rand (in press) have shown that a subset of insects specialized to feed on reproductive tissue of native thistles also show great propensity to expand their diets and attack a synchronously flowering introduced bull (or spear) thistle, *Cirsium vulgare*, in localities where native and introduced thistles co-occur. Likewise, "specialist" insects introduced to control weedy thistles have been found feeding on, and severely damaging, native thistles (Louda et al. 1997, Louda and Rand in press). Louda and Rand (in press) found that native insects destroyed 71–88% of the potential seed production of the introduced bull thistle, depending on the year plants were sampled. Although the effects of this herbivory on bull thistle abundance are not known, the population impact may be substantial based on the fact that these same insects play a major role in decreasing the fecundity, growth and survival of the native thistle that flowers at the same time (Guretzky and Louda 1997, Jackson 1998, Louda and Rand in press).

Exotic plants subsidizing native herbivore populations

If native herbivores respond numerically to increased exotic plant abundance, exotics have great potential to subsidize native herbivore populations. Grains introduced for agriculture have had a tremendous subsidizing effect on herbivorous geese populations (Jefferies et al. 1995, Bazely and Jefferies 1997). Whether exotics embedded in native communities have pervasive subsidizing effects on native consumer populations is un-

clear. The broader effects of exotic plants on food web interactions are only beginning to be studied. However, a fascinating recent example illustrates how the presence of exotics can ripple through food webs. In Montana, the native deer mouse, *Peromyscus maniculatus*, voraciously eats biocontrol gallflies (*Urophora affinis* and *U. quadrifasciata*) that overwinter within the senesced seedheads of the exotic spotted knapweed, *Centaurea maculosa*. In this case, an invasive plant supports an abundant biocontrol herbivore that provides a novel winter food source for mice. The net result is movement of mice into sites that support high knapweed density (Pearson et al. 2000). Whether the long term effect of this subsidy will be to increase *P. maniculatus* overwinter survival remains to be seen.

Habitat-specific patterns of herbivory on exotics

How habitat-specific patterns in invasive plant spread are determined by interactions with native herbivores is unclear. The best example of an herbivore affecting exotic plant distribution comes from the biological control of St. John's wort, *Hypericum perforatum*. In the western United States, St. John's wort undergoes periodic bouts of suppression by the biocontrol beetle *Chrysolina quadrigemina* (Holloway and Huffaker 1951, Holloway 1957). However, plants gain a refuge from biocontrol when growing in the shade because beetles perform more poorly in the shade (Holloway 1957, Huffaker 1957). Similar habitat-specific differences in the impacts of herbivory have been documented for native plant-herbivore interactions as well (Louda 1982, 1983, Collinge and Louda 1988, Louda and Rodman 1996).

Herbivore facilitation of exotic plant spread

It is generally thought that communities that are more heavily disturbed are more prone to invasion (Crawley 1987, Hobbs and Huenneke 1992, Lodge 1993, Burke and Grime 1996, Lonsdale 1999). What might be the interaction between disturbance and biotic resistance due to herbivory? Although exotic plant colonization should be facilitated by disturbance, some evidence indicates that it also may enhance herbivory on plants that establish in disturbed sites. For example, Pierson and Mack (1990) found that the exotic grass *Bromus tectorum* suffered greater defoliation and higher mortality in experimentally created openings than in intact conifer forests in California. In the Redwood National Park (USA), Bossard (1991) found that quail and grouse herbivory on introduced Scotch broom, *Cytisus scoparius*, seedlings was greater within disturbed plots than in intact ones. However, native herbivores can themselves act as agents of disturbance, thereby faci-

tating the establishment or spread of exotic plants (Mack 1989, Hobbs and Huenneke 1992). In Californian grasslands, periodic soil disturbance by gophers enhances germination of two introduced annual forbs, *Erodium brachycarpum* and *E. botrys* (Rice 1985). In this case, however, subsequent heavy herbivory on *Erodium* by California voles (*Microtus californicus*) reduces net reproduction and survival (Rice 1987).

Native herbivores may indirectly facilitate exotic plant spread in other ways besides creating disturbance. Recently Davis et al. (2000) proposed that plant communities become more susceptible to invasion when there is an increase in the amount of unused resources. This predicts that selective herbivory on native species can facilitate invasion indirectly, by decreasing resource demand by natives and increasing the amount of unused resources available to colonizing exotics. Although this has not been directly tested, it bears investigation.

Herbivores might directly facilitate exotic plant spread by consuming and subsequently dispersing exotic seeds (Zedler and Black 1992). Native giant kangaroo rats, *Dipodomys ingens*, carry seeds of exotics to burrow sites; burrowing creates a disturbance that facilitates exotic seedling establishment (Schiffman 1994). In coastal California, deer consume fruits of introduced iceplant, *Carpobrotus edulis*, and effectively disperse iceplant seeds through their scat (D'Antonio 1990, Vilà and D'Antonio 1998b). Whether the net impact of native herbivores positively or negatively influences the spread of exotic plants remains an open question. It may be that by dispersing seeds, changing competitive interactions and creating soil disturbance, some native herbivores have more of a facilitating than inhibiting effect on exotic plant invasion (Schiffman 1997).

Conclusions and future directions

Based on what is known about the effects of native herbivores on native plant abundance, it is unlikely that escape from specialist herbivores provides a general explanation for why introduced plants spread explosively within recipient communities. Instead, the natural enemies hypothesis probably applies to the limited subset of plants that possess life-history features that limit their ability to compensate for herbivore damage. For these species, herbivore-driven reductions in demographic performance translates directly to lowered population size. Emancipation from these native herbivores in recipient communities can be expected to contribute to rapid population growth.

Whether herbivores provide meaningful biotic resistance to invasion is uncertain. While there is abundant evidence that native herbivores can be damaging to exotics, whether these effects are of sufficient consistency and intensity to hinder the spread of exotics is not

well understood. Much progress could be made in this area by placing native herbivore–exotic plant interactions in a broader demographic context. Only by examining how herbivores affect stage-specific demographic transitions of introduced plants, and viewing herbivore damage in the context of the entire plant life cycle (sensu Harper 1977) can we determine how commonly herbivory by native herbivores actually reduces the population size or rate of spread of introduced plants. Especially valuable would be studies that quantify effects of native herbivores on introduced plants over a range of introduced plant densities. Experiments of this sort would broaden our understanding of how both the functional and numerical responses of herbivores change with increasing exotic plant density, and provide greater insight into whether native herbivores actually provide resistance to the initial establishment of introduced plants. Finally, studies should be conducted that examine the constancy of herbivore–plant interactions across a large geographic area so that the herbivore–exotic plant interaction could be placed in a broader context. Whether negative impacts are generally outweighed by indirect facilitative effects of native herbivores on introduced plants awaits additional data and analysis.

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Appendix I: Studies on the effect of generalist native herbivores on alien plant species.

Alien plant ¹ /origin ²	Country	Native herbivore/guild	Study type	Reference
<i>Abutilon theophrasti</i> (Malvaceae) H/NA	USA	<i>Niesthrea lousianica</i> (Hemiptera)/ pre-disp seed pr.	exclosure exclosure + insect release	Kremer 1995 Kremer and Spencer 1989
	USA	artrop. + small vert/ post-disp seed pred.	exclosure + seed depot	Cardina et al. 1996
<i>Acacia saligna</i> <i>A. cyclops</i> (Papilionaceae) S/Aus	SAf	ants + <i>Rhabdomys pumilio</i> (rodent)/ post-disp seed predator	seed depot	Holmes 1990
<i>Asparagus asparagoides</i> (Iridaceae) H/E	Aus	<i>Macropus eugenii</i> (Macropodidae)/ grazer	exclosure	Bell et al. 1987
<i>Asphodelus fistulosus</i> (Iridaceae) H/E	Aus	<i>Macropus eugenii</i> (Macropodidae)/ grazer	exclosure	Bell et al. 1987
<i>Bromus tectorum</i> (Poaceae) G/E	USA	small vertebrates/grazer		Pierson and Mack 1990
<i>Carpobrotus edulis</i> (Aizoaceae) PS/SAf	"	mammals/grazer	exclosure exclosure exclosure	D'Antonio 1993 D'Antonio et al. 1993 Vilà and D'Antonio 1998a, b
<i>Conyza sumatrensis</i> + <i>C. canadensis</i> (Asteraceae) A/NA	France	invert. + vert. herbivor/grazer	exclosure + pesticide	Thébaud et al. 1996
<i>Cytisus scoparius</i> (Papilionaceae) S/E	USA	<i>Lophortyx pictus</i> (quail) <i>Reithrodontomys megalotis</i> (mice) post-disp. seed pred.	seed depot exclosure	Bossard 1991 Bossard and Rejmanek 1994
<i>Hakea sericea</i> (Proteaceae) S/Aus	SAf	insects + small vert./ pre-disp. fruit pred.	observational	Kluge and Siebert 1985
<i>Lonicera japonica</i> (Caprifoliaceae) S/A	USA	mammals + moths/grazer	exclosure	Schierenbeck et al. 1994
<i>Mahonia aquifolium</i> (Berberidaceae) S/NA	Germany	<i>Aphrophora alnii</i> (Homoptera)/ grazer	observational	Auge et al. 1997
		<i>Rhagoletis meigenii</i> (Diptera)/ p-disp. seed pred.	observational observational	Auge et al. 1997 Soldaat and Auge 1998
<i>Opuntia maxima</i> + <i>O. stricta</i> (Cactaceae) PS/CA	Spain	small vertebrates post-disp. seed pred	exclosure	Vilà and Gimeno (unpubl.)
<i>Spartina alternifolia</i>	USA	<i>Prokelisia marginata</i> /sap-feeder	exclosure + pesticide	Daehler and Strong 1997

1. Life form: A = annual, G = grass, H = herb, M = macrophyte, PS = perennial succulent, S = shrub.

2. A = Asia, Aus = Australia, CA = Central America, E = Europe, NA = North America, SAf = South Africa.