

Parasites, pathogens, and invasions by plants and animals

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Biological invasions cause billions of dollars in economic damage each year and are a serious threat to native biodiversity. Introduced animals and plants may escape 75% or more of the parasite and pathogen species from their native range. While they do accumulate novel parasite species from their new location, this number is generally only a fraction of the number lost. Individual plants and animals are also generally less frequently infected (prevalence minus percent individuals infected) in introduced compared to native conspecific populations. In conjunction with other biological and physical factors, release from parasites helps explain the increased demographic performance of invasive species, potentially accounting for much of the damage they cause.

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Biological invasions are increasing as a result of the integration of global economies (Cohen and Carlton 1998). Although the effects of some introductions are undetectable, certain species have dramatic ecological and economic impacts (Parker *et al.* 1999; Ruiz *et al.* 1999) (Figure 1). Preventing further introductions and mitigating the impacts of established introduced species are growing concerns among policy makers and environmental managers and require a scientific basis. Research effort on introduced species is increasing, as evidenced by the rise in the number of publications over the past 30 years. Yet, answers to one fundamental question – what factors determine invasion success? – remain elusive (Keane and Crawley 2002; Shea and Chesson 2002).

Invasion success is an ambiguous concept (Starfinger 1998), in part because the ultimate success of an introduced species is the integrated product of a multistage process of (1) transport, (2) establishment, and (3) demographic expansion (Kolar and Lodge 2002; Shea and Chesson 2002). Although parasites might influence the

establishment of introduced species under certain exceptional conditions (Drake 2003), this theoretical prediction will be difficult to test because the establishment phase of invasions is rarely observed. We focus on post-establishment demographic expansion because this determines the abundance and impact of an invader. Multiple biotic factors, including resources (Dobson 1988), competition (Crawley 1986; Byers 2000), and natural enemies (Darwin 1859; Elton 1958; Dobson 1988; Torchin *et al.* 2001, 2002, 2003; Mitchell and Power 2003) can all affect the demographics of an invader, either independently or interactively. Thus, when considering these hypotheses, it is critical to recognize that they are not mutually exclusive and support for one does not necessarily refute another (Torchin *et al.* 2002; Settle and Wilson 1990). This review focuses exclusively on the role of parasites and pathogens; further work is required to both compare the importance of parasites and pathogens to other biotic factors, and to examine possible interactions between them. For simplicity and because pathogens are parasitic in nature, we will often refer to “parasites” instead of “parasites and pathogens”. We define parasites here, without reference to taxonomy, as organisms that feed on a single host individual per life history stage (Lafferty and Kuris 2002).

Parasites are ubiquitous in natural plant and animal communities and their importance in their hosts’ ecology is becoming increasingly evident (Dobson and Hudson 1986; Gilbert 2002). Parasites can negatively impact host population density and growth rate (Crofton 1971; Anderson and May 1978; Hudson *et al.* 1998) both directly (metabolically reducing host growth, reproduction, and survivorship) and indirectly (interacting with predation, competition, or both) (Hudson *et al.* 1992; Gilbert 2002).

Introduced species may experience a decrease in population control by natural enemies (Darwin 1859; Elton 1958), including parasites (Lafferty and Kuris 1996;

In a nutshell:

- Parasites are ubiquitous and important components of natural communities
- Successful introduced species often invade without their native parasites and accumulate relatively few new ones
- Reduced parasitism may contribute to the post-invasion success of introduced species and could help to explain much of the damage they cause
- When parasites do infect introduced plants and animals, they may provide a valuable service to humans, by reducing the impacts of invasive species

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Courtesy of S. Crausby

Figure 1. Native to China, black bamboo (*Phyllostachys nigra*) has invaded Maui (pictured) and other Hawaiian islands in the last century. In moist areas, it can form dense thickets that exclude native species.

Torchin *et al.* 2002). Often, parasites do not invade with their hosts, leading to a decrease in the number of parasite species and the proportion of hosts infected in the introduced range (Cornell and Hawkins 1993; Mitchell and Power 2003; Torchin *et al.* 2003). Because parasites can reduce host population abundance, density, and spread (Crofton 1971; Anderson and May 1978; Hudson *et al.* 1998), decreased parasitism may allow species that were innocuous in their native range to become widespread, problematic invaders in their introduced range (Torchin *et al.* 2001; Mitchell and Power 2003). We review evidence for and against these hypotheses, and consider what factors control variation among host species, parasite species, and habitats. We do so for both plant and animal hosts, and seek to integrate perspectives across these taxa.

■ Escape and accumulation of parasite species

Through several mechanisms (reviewed by Torchin *et al.* 2002), the invasion process can “filter out” parasites that occur in an invading host's native range. First, invasions often result from the introduction of small subsets of native populations (and sometimes from uninfected life-history stages), which reduces the probability of introducing parasites along with a host species. Second, many parasites have complex life cycles requiring more than one host, which may not be present in the new region, thus preventing establishment of the parasite. Dobson and May (1986) suggest there may be about an order of magnitude difference in the successful establishment of directly transmitted parasites compared to those with complex life cycles. Finally, for parasites with density-dependent transmission, there is a threshold host density below which a parasite cannot persist in a host

population (Kermack and McKendrick 1927). Thus, host population bottlenecks (low host density) in the initial stages of invasion may break transmission, eliminating those parasites present in the founder population.

In analyzing all known published studies, we found that introduced plant species generally escape over half of their native parasites (Table 1). In the broadest of these studies, 473 plants introduced to the US from Europe escaped over 90% of their native fungal and viral pathogens (Mitchell and Power 2003). Studies of birds (Dobson and May 1986), insects (Cornell and Hawkins 1993), and fishes (Kennedy and Bush 1994), and of molluscs, crustaceans, fishes, birds, mammals, amphibians, and reptiles (Torchin *et al.* 2003) indicate that introduced animal species also escape the majority of their native parasites. Across diverse animal taxa, native populations

were, on average, infected with 16 parasite species (primarily helminths – flatworms and roundworms) and an average of only three of these species successfully accompanied an invader to its introduced range (Torchin *et al.* 2003).

When plants and animals invade new regions most of their parasites are left behind, yet some do manage to invade along with their hosts (Mitchell and Power 2003, Torchin *et al.* 2003). Although it is not the topic of this review, introduced parasites and pathogens can sometimes have serious impacts on native communities (Dobson and Hudson 1986; Dove 2000; Rizzo and Garbelotto 2003) and the introduction of parasites may even facilitate some invasions (Dove 2000; Tompkins *et al.* 2003).

Introduced plants and animals commonly appear to accumulate new parasite species from the introduced range, but not in sufficient numbers to replace the species that they escaped (Figure 2). On average, introduced

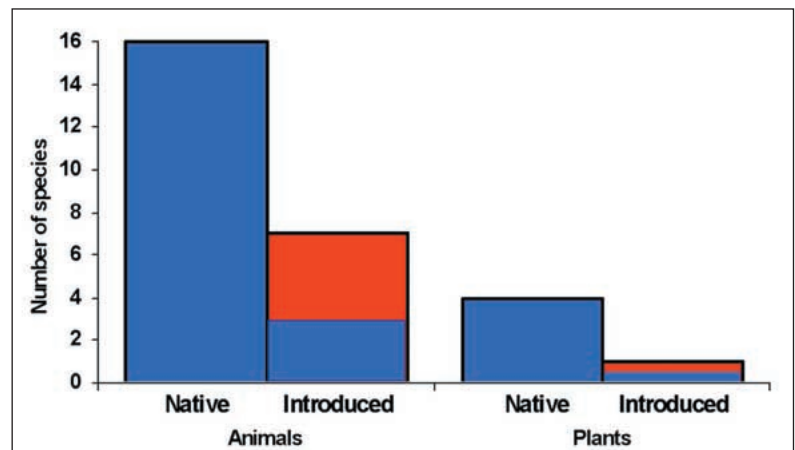


Figure 2. Release from parasites as average number of parasites in native and introduced animals and average number of pathogens on native and introduced plants. Blue bars indicate parasites/pathogens from the invader's native region and red bars indicate novel parasites/pathogens that were accumulated in the introduced region. Data are from Mitchell and Power (2003) and Torchin *et al.* (2003).

Table 1. Parasite escape and accumulation for introduced plants

Host species	Parasite type(s)	Sample size (plants/populations)	Parasite richness in native range*	Proportional escape*†	Proportional accumulation*‡	Proportional decreased species richness*¶	Reduced infection prevalence/intensity	Reference
<i>Ammophila arenaria</i> (European beachgrass or Marram grass)	Root-infecting fungi	192/16 native, 40/1 introduced	9	0.89	0.63	0.33	N/A	De Rooij – Van der Goes et al. 1995 (native range), Beckstead and Parker 2003 (introduced range)
<i>Ammophila arenaria</i> (European beachgrass or Marram grass)	Root-infecting nematodes	192/16 native, 40/1 introduced	10	1.0	0.10	0.90	N/A	De Rooij – Van der Goes et al. 1995 (native range), Beckstead and Parker 2003 (introduced range)
<i>Cnidium hirta</i> (soapbush, a shrub)	Sedentary foliar insects, unidentified foliar insects, and unidentified foliar fungi	1248/12	N/A	N/A	N/A	N/A	–80%**	DeWalt et al. 2004
<i>Silene latifolia</i> (bladder campion, a forb)	A floral smut fungus	>1000/86	1	0	0	0	>85%§	Wolfe 2002
13 species in Asteraceae (forbs)	Sedentary seed-infesting insects	1200/6 per spp	N/A	N/A	N/A	N/A	99.8%§	Fenner and Lee 2001
401 randomly chosen species (non crops)	Rust, smut, and powdery mildew fungi	N/A	3.1	0.98	0.07	0.90	N/A	Mitchell and Power 2003
72 randomly chosen species (crops)	Rust, smut, and powdery mildew fungi	N/A	6.1	0.85	0.25	0.64	N/A	Mitchell and Power 2003
473 randomly chosen species	Viruses	N/A	0.49	0.45	0.45	0.24	N/A	Mitchell and Power 2003

* Based on species counts summed across each geographic range.
† Number of parasite species from the host's native range that escaped divided by total number in the native range.
‡ Number of parasite species accumulated in the host's introduced range divided by number escaped from the native range.
¶ Number of parasite species in the host's introduced range divided by number in the native range.
§ Based on percent of individual plants infected.
**Based on percent of leaf area damaged.
N/A Data not available.

plant species accumulate fewer than half as many new parasites than they escaped (Table 1). For example, the 473 plant species analyzed by Mitchell and Power (2003) accumulated an average of only 13% as many new fungal and viral pathogen species as they escaped. On average, introduced animals accumulated about 25% as many parasite species as they escaped, such that introduced animal populations were, on average, infected with less than half the number of parasite species in populations within their native range (Torchin et al. 2003).

Care must be taken when undertaking comparisons of parasite species lists among native and introduced host ranges. Analyses should control for geographic range size (below) and sampling effort. Standardizing sampling area and averaging (instead of summing) species richness across areas (Torchin et al. 2003) or including range size as a variable in an analysis (Mitchell and Power 2003) can control for this potential confounding factor. Additionally, records of parasite species richness across the host's geographic range may not accurately reflect rates of parasitism and associated pathology experienced by individual hosts, which is what will impact population demographics. For example, by sampling multiple host populations within both native and introduced ranges, Wolfe (2002) showed that quantifying parasite species richness only at the geographic range scale can overlook decreases in parasite species richness experienced by local popula-

tions. While the anther smut fungus (*Microbotryum violaceum*) was present in both bladder campion's native and introduced ranges, it was found in 36% of native populations and only 8% of introduced populations. Thus, the decreases in parasite species richness reported at the geographic range scale may underestimate (or overestimate) those experienced by local populations, the scale most relevant to demographic success of the introduced species.

■ Influencing factors

Introduced plants and animals should be more completely released from specialist than generalist natural enemies (Cornell and Hawkins 1993). In an invaded habitat, generalist natural enemies should have greater potential than specialists to attack a newly introduced species; generalists from the invader's native range may also have more opportunities to be transported to its introduced range on other host species and may be better able to utilize other host species in the new region. Introduced herbivorous insects are infected with a higher proportion of generalist parasitoids compared to native populations (Cornell and Hawkins 1993). However, introduced populations appear to accumulate specialists and generalists at the same rate (Cornell and Hawkins 1993). Kennedy and Bush (1994) also showed that introduced fishes escape from specialist parasites more readily

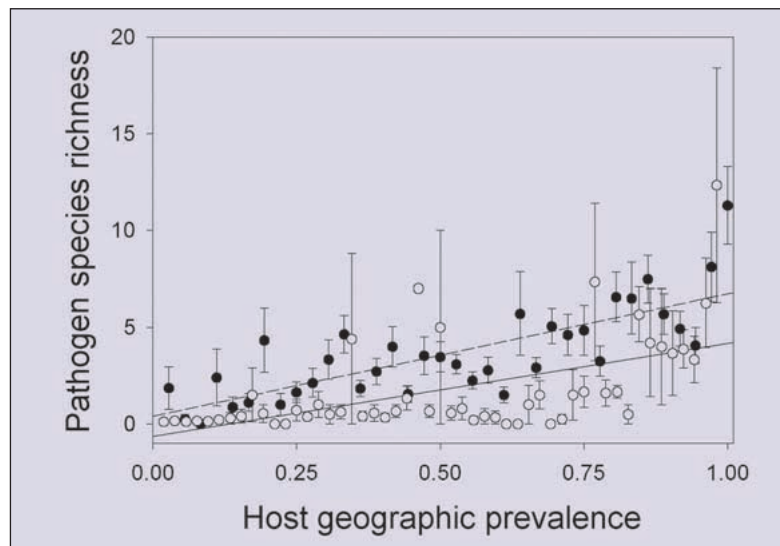


Figure 3. Pathogen species richness increases with size of host geographic range in both hosts' native (dashed line and filled circles) and introduced (solid line and open circles) ranges. Geographic range size was estimated by prevalence among states or provinces. Both slope and intercept were significantly greater for the native range than for the introduced range (Mitchell and Power 2003).

than generalists. The available studies of plants did not analyze the role of parasite specificity as directly as the animal studies did, but greater host specificity may explain why introduced plants were more released from rust, smut, and powdery mildew fungi than from viruses (Mitchell and Power 2003).

The longer an invader is established in its introduced range (and the wider its range expands), the more new enemies it should accumulate (Blaustein *et al.* 1983; Strong *et al.* 1984). Cornell and Hawkins (1993) demonstrated that parasitoid richness on introduced populations of herbivorous insects increased over time. Our analysis of data from a study on parasites of the European green crab (*Carcinus maenas*; Torchin *et al.* 2001) indicates that time since introduction accounted for over 80% of the variance in the number of parasite species present in several introduced crab populations ($R^2 = 0.83$, $P = 0.03$, $N = 5$). Geographically widespread host species generally have a greater species richness of associated parasites (Blaustein *et al.* 1983; Strong *et al.* 1984; Clay 1995). However, this effect might be expected to be weaker in the introduced range of a species, because the pool of parasite species with the potential to infect the new host is generally smaller compared to that in the hosts' native range (Blaustein *et al.* 1983). Supporting this hypothesis, Mitchell and Power (2003) reported that pathogen species richness was positively correlated with plant geographic extent in both native and introduced ranges, and the slope was greater in the hosts' native range. Moreover, introduced plant species had fewer fungal and viral pathogens in their introduced range than in their native range, even after controlling for geographic range size (Figure 3; Mitchell and Power 2003), indicating that

changes in range size are not sufficient to explain plants' release from pathogens. While this initial analysis assumes that the effects of introduced species' spatial spread and time since introduction are separate, they are in fact frequently intertwined. Future analyses should simultaneously control for range size and time since introduction, to disentangle the influences of space and time.

Repeated introductions of host species should provide more opportunities for parasites from their native range to follow them. Furthermore, parasites arriving as part of secondary introductions should be more likely to establish and spread because the introduced host population should be larger (Torchin *et al.* 2002). Repeated introductions of the black rat (*Rattus rattus*) may explain why introduced populations harbored a higher than average percentage (38%) of its native parasites (Torchin *et al.* 2003).

Introduced species invading a habitat of close relatives should be susceptible to a broader suite of natural enemies and thus

accumulate natural enemies faster than if related hosts were not present (Strong *et al.* 1984; Mack 1996). Several studies are consistent with this hypothesis, but each has quantified parasite species richness for only one or a few host species (Mack 1996; DeWalt *et al.* 2004; Fenner and Lee 2001). So far, evidence for this hypothesis remains intriguing, but limited.

■ Release from parasites and host demographics

The growing evidence that introduced populations have fewer parasites raises the issue of whether decreased parasite richness translates into increased demographic expansion (ie increased population size or biomass) or release. This demographic release will be a function of the number of parasite species, their abundance, and their virulence. Thus, demographic release, R , can be described by

$$R = \sum_{n=1}^N (M_n * V_n) - \sum_{i=1}^I (M_i * V_i)$$

where N is the total number of parasite species in the host's native range, M is parasite mean abundance (per parasite species), V is virulence (per parasite species), n is the native range, i is the introduced range and I is the total number of parasite species in the host's introduced range. While we have formulated this model very simply, the equation could be extended to incorporate further levels of complexity such as the distribution of parasites among host individuals. However, there are no known studies for which all the terms in even this very simple model have been quantified.

In addition to harboring fewer parasite species, individual animals and plants are less infected by parasites in their introduced range than in their native range. Cornell and Hawkins (1993) showed that parasitoid prevalence (% individuals infected) is lower in introduced populations of herbivorous insects compared to their native populations. Torchin *et al.* (2003) found that, on average, parasite prevalence in introduced animal populations is less than half that in native populations and this was driven primarily by a reduction in the total number of parasite species (escape) rather than a reduction in the prevalence of individual parasite species in the introduced populations. Similarly, individuals of introduced plant species are 80–99% less infected by parasites in their introduced range than in their native range, in terms of either prevalence or severity (intensity) (Table 1). However, no studies of introduced plants have evaluated changes in parasite prevalence or severity (intensity) relative to changes in parasite species richness. Implicit in the above model is that demographic release is a function of the number of parasite species, their abundance, and perhaps most importantly, their virulence, which is difficult to quantify.

Among harmful plant invaders introduced to the US from Europe, species that were more completely released from fungal and viral pathogens in terms of species richness were also more widely listed as highly damaging (Mitchell and Power 2003). This suggests that parasites can help mitigate the negative effects of invasive species (Figure 4). For plants listed as noxious weeds in the US, both escape from old pathogens and limited accumulation of new ones contributed to this effect. These results suggest that introduced plant populations commonly experience demographic release from parasites relative to native conspecific populations. However, these analyses were entirely correlative, so experiments that manipulate parasites in both the host's native range and its introduced range are needed to clarify whether this correlation represents causation.

The first such experiments are beginning to be published, and generally support a role for parasite release in plant invasions. DeWalt *et al.* (2004) excluded fungal pathogens and foliar insects (three of four identified insects were parasites) of soapbush (*Clidemia hirta*) in both understory and open habitats in Costa Rica (native range) and Hawaii (introduced range). Parasites suppressed plant growth and survivorship only in understory habitats of the host's native range. Release from parasites may therefore explain why soapbush is invading both understory and open habitat in its introduced range, but is limited to open habitat in its native range. This contingency of parasite release on habitat reinforces the importance of sampling multiple populations within a geographic range (Wolfe



Courtesy of A Agrawal

Figure 4. To the extent that introduced populations are infected by parasites, those parasites may reduce the impacts of the introduced populations. For example, quackgrass (*Elymus repens*) is infected by crown rust (*Puccinia coronata*) throughout North America, where quackgrass is introduced, as well as in its native range in Eurasia.

2002; Torchin 2003). Soil microbes from the native range of plants have more negative effects on host growth than microbes from the plants' introduced range in the cases of both black cherry (*Prunus serotina*; Reinhart *et al.* 2003) and spotted knapweed (*Centaurea maculosa*; Callaway *et al.* 2004). These studies suggest that release from pathogenic soil microbes contributes to these species' spread as invaders, although interactions with mutualists as well as parasites probably contribute to these effects. A similar approach was applied to European beachgrass (*Ammophila arenaria*), but this species did not experience demographic release from parasites (Beckstead and Parker 2003), even though it was infected by 33% fewer fungal pathogen species and 90% fewer pathogenic nematode species in California (its introduced range) than in the Netherlands (its native range) (Table 1). As a whole, these studies suggest that demographic release of introduced plants from parasites is a common, but not universal, consequence of reduced parasite species richness.

For introduced animals, studies of species that have invaded several different regions suggest that certain introduced populations do particularly well demographically as a result of release from parasites. The European green crab (*Carcinus maenas*) has invaded several regions around the world, and so provides the opportunity to compare geographically independent invasions. Prevalence of parasitic castrators (which block reproduction and growth) of the green crab was negatively associated with demographic success (biomass and body size) in Europe. While several factors could interact with parasitism and influence this result, Torchin *et al.* (2001) found that factors such as latitude, environmental quality, limb loss (a proxy for predation), and other types of parasites had no

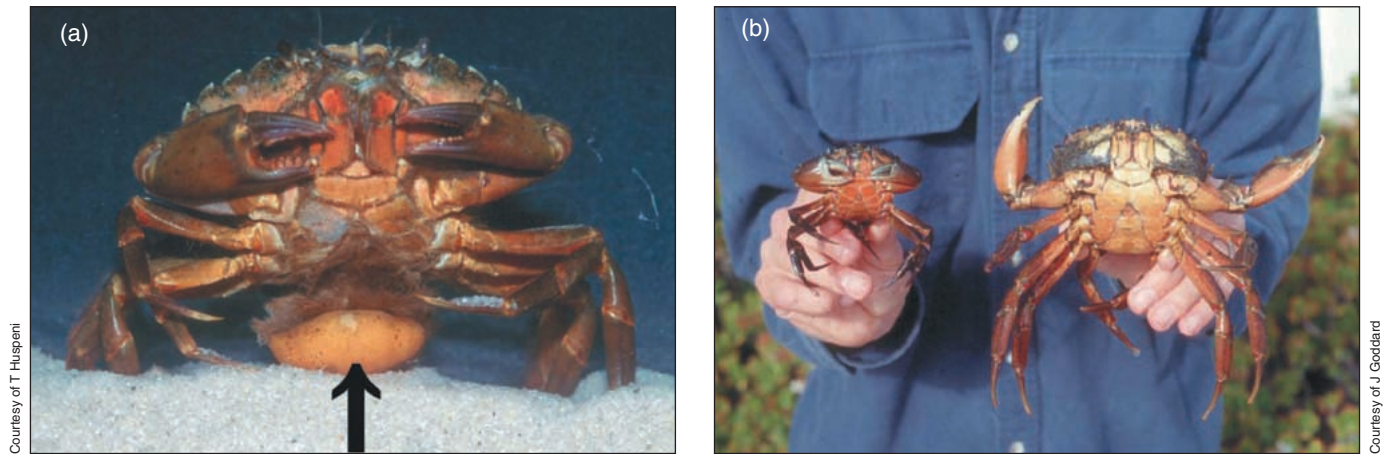


Figure 5. (a) Parasitic castrator (*Sacculina carcini*) under the abdomen of a European green crab (*Carcinus maenas*). (b) Size comparison of largest green crabs caught from a parasitized population in the crab's native range (left) and unparasitized population in the crabs introduced range (right).

significant effect in their analysis. Furthermore, introduced populations of green crabs were not infected with parasitic castrators, were significantly larger and had a greater biomass compared to European populations (Torchin *et al.* 2001; Figure 5). Similarly, in Australia, introduced cane toads (*Bufo marinus*) experience a release from parasites, with 59 helminth species reported in their native range compared to 16 species reported in Australia and 28 species reported across all introduced regions (Barton 1997). Interestingly, most of the helminths reported from Australia are parasites which transferred from native anurans (Barton 1997). Also, introduced toads in Australia are not infected by ectoparasites, whereas in their native range, ectoparasite infestations are negatively associated with toad condition index and may control their densities (Lampo and Bayliss 1996). The extent to which this translates into demographic success of introduced toad populations requires further investigation.

■ Parasitism and competition

So far we have focused on introduced species and their parasites without reference to the rest of the community, but a full understanding of the role of parasites in biological invasions requires consideration of how parasites affect interactions between introduced species and native competitors (Figure 6). Parasites which differentially impact competitors (whether or not they infect both species) can shift competitive dominance from one species to another (Park 1948; Holt and Lawton 1994; see Tompkins *et al.* 2003 for an example of an introduced parasite mediating competition). For instance, in South Africa, the introduced European mussel (*Mytilus galloprovincialis*) is not infected by parasites, while its competitor, the native mussel (*Perna perna*), is infected with two trematode species – one castrates it and the other reduces its competitive ability (against the invader) and its growth (Calvo-Ugarteburu and McQuaid 1998). In the same way, introduced live-bearing fishes had a substan-

tially lower number of parasite species in Australia, as compared to ecologically similar native fish, which may give them a competitive advantage (Dove 2000). Settle and Wilson (1996) and Aliabadi and Juliano (2002) showed that introduced insects benefit when parasites shift the competitive advantage from competing natives to favor the introduced species.

Among introduced plants, patterns of reduced parasitism relative to native competitors are not as evident compared to animals (for insect herbivores, see Keane and Crawley 2002; Agrawal and Kotanen 2003; Siemann and Rogers 2003). Cross-species comparisons appear to detect release from parasites less frequently than do cross-regional comparisons. Fungal pathogen species richness does not differ among native and introduced grasses in the US, and may even be lower on the native plants (Clay 1995). Perhaps because of this, several experimental manipulations of fungal pathogen abundance have not detected demographic release of introduced plant species relative to native species (Blaney and Kotanen 2001; Siemann and Rogers 2003). However, in an experiment in Canadian grassland, host-specific, root-infecting fungal pathogens strongly decreased the performance of rare native plants and had little detectable impact on five highly invasive species (Klironomos 2002). The degree of negative feedback from soil-borne pathogens to plant growth in a pot experiment explained over half the variation in relative plant abundance in the field, suggesting that release from fungal pathogens was a key factor in allowing invasive species to dominate this community.

Given the multiple scenarios for interactions between parasites, introduced species, and native species, it is important to evaluate all possible outcomes in these interactions. An analytical framework combining a comparison of differential parasitism in populations of a single species both in its native and introduced region (cross-regional comparison) and a comparison of native versus introduced species (generally competitors) in the same region (cross-species comparison) in the context of the



Courtesy of D. Larson

Figure 6. Leafy spurge (*Eurphorbia esula*; on left with yellow flowers) was introduced from Eurasia to the US, where it is now a major threat to native plant communities and rangelands of the Great Plains. It displaces native species such as the sego lily (*Calochortus nuttallii*; on right with white flower), perhaps because few parasites infect it in the US.

model provided above will help to fully evaluate enemy release and the role of parasites in biological invasions. For example, an introduced population may be released from parasites either relative to native conspecific populations, or relative to native species competing with the invader, both, or neither, depending on how strongly parasites impact each population. When used in combination, testing these hypotheses will reveal the extent to which parasites and pathogens keep their host populations in check and the consequences of release from these natural enemies on the demography of introduced species. To our knowledge, this joint approach has not yet been employed.

■ Conclusions

Parasites are common and important components of natural communities. When introduced to a new region, plants and animals generally escape most of their native parasites. Over time, they accumulate new parasites in their novel region, but on timescales observed thus far,

this generally amounts to only a fraction of those they have escaped. The resulting decrease in parasitism helps explain why some introduced species proliferate in their new environment and become destructive invaders. By breaking the bonds of old host–parasite associations, and occasionally forming new ones, species introductions provide “natural experiments” that can be used to reveal the extent to which parasites control host populations and structure ecological communities. Parasites can provide a valuable service of pest control. However, more research is needed to investigate the extent to which reduced parasitism controls the impacts of introduced species relative to other factors. A better understanding of this relationship, in both ecological and economic terms, will provide useful information for resource managers developing strategies to control invasive species.

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