

PERFORMANCE COMPARISONS OF CO-OCCURRING NATIVE AND ALIEN INVASIVE PLANTS: Implications for Conservation and Restoration

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■ **Abstract** In the search to identify factors that make some plant species troublesome invaders, many studies have compared various measures of native and alien invasive plant performance. These comparative studies provide insights into the more general question “Do alien invasive plants usually outperform co-occurring native species, and to what degree does the answer depend on growing conditions?” Based on 79 independent native-invasive plant comparisons, the alien invaders were not statistically more likely to have higher growth rates, competitive ability, or fecundity. Rather, the relative performance of invaders and co-occurring natives often depended on growing conditions. In 94% of 55 comparisons involving more than one growing condition, the native’s performance was equal or superior to that of the invader, at least for some key performance measures in some growing conditions. Most commonly, these conditions involved reduced resources (nutrients, light, water) and/or specific disturbance regimes. Independently of growing conditions, invaders were more likely to have higher leaf area and lower tissue construction costs (advantageous under high light and nutrient conditions) and greater phenotypic plasticity (particularly advantageous in disturbed environments where conditions are in frequent flux). There appear to be few “super invaders” that have universal performance advantages over co-occurring natives; rather, increased resource availability and altered disturbance regimes associated with human activities often differentially increase the performance of invaders over that of natives.

INTRODUCTION

Invasive plants are nonnative species that have successfully spread outside their native range (Richardson et al. 2000, Williamson 1996). Most invasions over the past several centuries have involved species transported directly or indirectly by humans (McKinney & Lockwood 1999, Pyšek et al. 2002). Invasive plants have attracted

much attention because of their economic costs as weeds (Pimentel 2002) and because they may reduce native biodiversity (Daehler & Strong 1994, Wilcove et al. 1998) or alter ecosystem functions (D'Antonio & Vitousek 1992, Vitousek 1990). Because only a small fraction of introduced species become invasive (Williamson 1996), and many invasive species can be considered pests (Daehler 2001), much effort has been focused on understanding what makes some species invasive (Kolar & Lodge 2001, Rejmánek et al. 2003).

A comparative approach has often been useful in helping to understand what makes invasive species so successful (Grotkopp et al. 2002, Mack 1996, Rejmánek 1995). The comparative approach involves pairing invasive species with native species or noninvasive congeners. If a consistent difference can be identified between invader and native, that difference might help explain why an invader has become so successful. Rather than summarizing attributes that might make a species invasive (e.g., Crawley et al. 1996, Pyšek et al. 1995, Williamson & Fitter 1996), this review makes use of published native-invader comparisons to examine the general question "Do invasive plants perform substantially better than co-occurring native plants?" When I refer to "plant performance," I mean a plant's success or aptitude in terms of one or more fitness-related traits. An invader that outperforms co-occurring natives is expected to increase in relative abundance over time, and abundant invaders are expected to have significant impacts on co-occurring native populations (Daehler & Carino 1999). Plant performance can be measured by various traits ranging from competitive ability to fecundity. In any case, whether or not invasive plants substantially outperform co-occurring natives has important consequences for conservation. If most invasive plants substantially and consistently outperform co-occurring natives, then we can expect serious and widespread reductions in global biodiversity as a direct consequence of today's plant invasions; we would be left with few options for preventing this, other than persistent and direct attacks on the invaders. On the other hand, if invaders rarely outperform co-occurring natives, or if their superior performance compared with natives is marginal or dependent on specific environmental conditions, then the possibility remains that the impact of invaders will be strong only under particular environmental circumstances, and these circumstances could be minimized.

Whereas "extreme" environments have often been suggested to be highly resistant to invasion (e.g., Rejmánek 1989, Mueller-Dombois & Loope 1990), Alpert et al. (2000) proposed a specific mechanism that is applicable to a continuum of environmental conditions: The relative performance of native and invasive species could vary depending on the amount of environmental stress. Other environmental variables such as disturbance regime could also differentially increase the performance of native plants relative to co-occurring invaders (Alpert et al. 2000, Hobbs & Huenneke 1992, Mueller-Dombois & Loope 1990). Under these circumstances, land managers could potentially manipulate environmental conditions to thwart invasions or reduce the abundance of unwanted invaders to acceptable levels. Thompson et al. (1995) concluded that at least some native species have

the same attributes as invasive species, but they made no attempt to compare the performance of native and invasive plants co-occurring in the same habitats. This review summarizes studies of performance differences between co-occurring native and invasive plants and uses the compiled findings to suggest general strategies for managing invasive plants. Comparisons were not restricted to taxonomically related species pairs; however, in all of the reviewed studies, the invaders and co-occurring natives had the same life form, and/or the study authors had raised concerns that the invader was directly impacting the co-occurring native.

LITERATURE SEARCH FOR PERFORMANCE COMPARISONS

In order to identify a large sample of studies comparing the performance of native and invasive plants, I searched Biological Abstracts (SilverPlatter Information Inc, Norwood, MA) for the publication years 1985–June 2002. The following search was performed for words within the entire database record, including the Abstract: Native *and* (Invasive *or* Invad* *or* Exotic *or* Alien) *and* (Subject = plant *or* plants). For all citations identified using this search filter, the titles and abstracts were read to identify relevant studies. A few additional studies were identified through citations within papers found during the initial search. A number of studies (e.g., Gould & Gorchov 2000, Melgoza et al. 1990) examined the effect of an invader on a native plant but did not provide comparable data on how the native affected the invader; such studies could not be used for the comparative purpose of this review. Some studies compared large groups of invaders and natives (e.g., Crawley et al. 1996, Goodwin et al. 1999, Pyšek et al. 1995), but these studies were not included in this review because they mainly compared general life history traits or biogeographic characteristics, rather than plant performance.

For studies containing appropriate comparative data on one or more native-invasive species pairs, the measure of performance was recorded, and the native's performance was rated as inferior to, equal to, (no statistical difference), or better than that of the invader. In many cases, performance had been measured under more than one condition. If the relative performance of the native depended on the conditions, then the specific conditions under which the native's performance was superior or equal to that of the invader were recorded. Usually, performance assessments (inferior, superior, or equal) were based on the statistical analyses given in the original papers. However, in some cases the authors did not clearly present the statistical comparison for a specific time or condition. In such cases, overlapping standard error bars in graphs were conservatively taken to indicate nonsignificant differences in performance. In some studies, performance data were given for several native and invasive species. Unless the natives were clearly paired with invaders, performance results were recorded using the following rules: If

one native was superior to all invaders, then the study was recorded as finding superior performance of a native; if there was no clear pattern (some natives equal to invaders), then the study was recorded as finding equal performance between natives and invaders; if the invaders as a group clearly outperformed the natives as a group, then the study was recorded as finding inferior performance by natives.

A total of 119 published papers containing comparative performance data were identified. Among these, some involved the same species pairs; results from these studies were pooled to create a single summary comparison of that species pair. For four invaders (*Acacia saligna*, *Centaurea maculosa*, *Lythrum salicaria*, and *Tamarix ramosissima*), independent studies compared these invaders to different native species at different locations or times. These cases were considered separate comparisons for purposes of generating summary statistics. Summary statistics on performance results are based on tallies rather than meta-analysis because there was no satisfactory way of weighing context-dependent differences in performance identified within native-invader species pairs. The total number of paired, independent comparisons between native and invasive plants was 79 (Appendix 1, see the Supplemental Material link in the online version of this chapter or at <http://www.annualreviews.org/>); 13 pairs consisted of congeners and 59 (75%) of the paired comparisons involved data obtained from manipulative experiments. The comparisons included studies from all major geographic regions of the world. North America was the most common geographic region for the native species (46% of comparisons). Asia was underrepresented, with only one study where the native was from Asia (Yamashita et al. 2000). In contrast, Asia and/or Europe (Eurasia) was the origin for over half (54%) of the invaders. The comparisons involved various plant life forms, distributed as follows: 32% grasses, 23% other herbs including vines, 25% shrubs, and 20% trees. Separate analyses by geographic region or life form were not attempted owing to small sample sizes.

PERFORMANCE COMPARISONS

Measures of Performance

The most common measure of performance was growth rate (Figure 1), probably because it is simple and inexpensive to measure in pot and field experiments. Other common measures of performance can be grouped into those related to individual growth rate, at least in theory (e.g., photosynthesis, tissue construction costs, total leaf area) and those related to population spread (e.g., fecundity, dispersal rate, germination rate, survival). Finally, some common measures of performance were not easily placed in either category: competitive ability, standing biomass, and phenotypic plasticity. Specific examples of comparisons involving each of these performance measures are detailed below. Less frequently encountered comparisons of performance between native and invasive plants ($n < 5$ studies) were seed

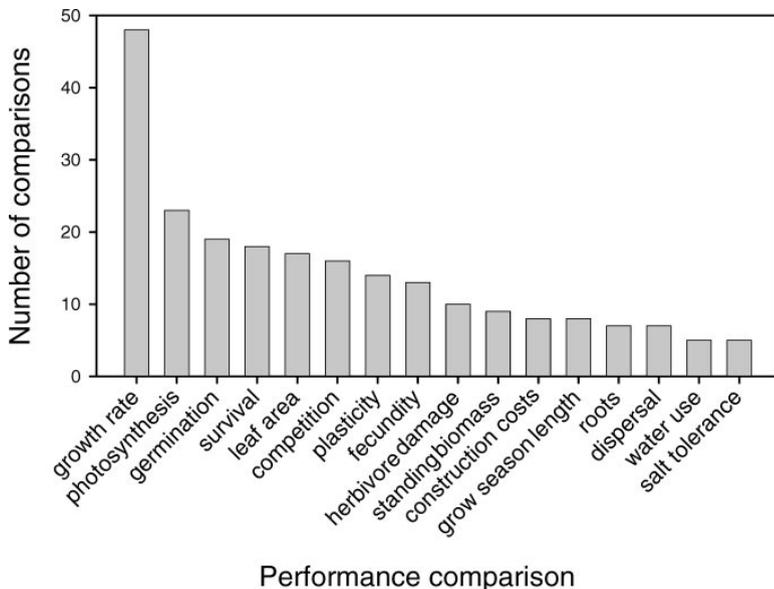


Figure 1 Performance comparisons between native and invasive plants, by frequency of occurrence. Only performance measures for which five or more comparisons were encountered are shown. The total number of comparisons exceeds the total number of studies reviewed because some studies measured multiple aspects of performance.

predation rates, seed longevity, rate of pathogen attack, allelopathic capacity, and environmental breadth.

Context-Dependence of Performance

Among the 79 independent performance comparisons between native and invasive plants, only 10 comparisons (13%) showed consistent performance advantages for the invader for all measured performance variables across all growing conditions (Figure 2). When one considers only the 55 comparisons that involved more than one growing condition, invaders had universally superior performance in only 6% of cases. The most common growing conditions favoring natives over invaders were environments with low resource availability (nutrients, water, or light; Figure 2). Some studies identified a specific disturbance regime, such as periodic flooding (Sher et al. 2000), mowing, or fire that favored the native over the invader (pooled as “special disturb” in Figure 2). On several occasions (e.g., Holmgren et al. 2000), removal of introduced grazers favored the native. Certain invaders consistently had poor performance when directly competing with natives. Presumably, these invaders have become abundant because frequent disturbances reduce the intensity of competition with natives (e.g., *Bunias orientalis*; Dietz et al. 1998).

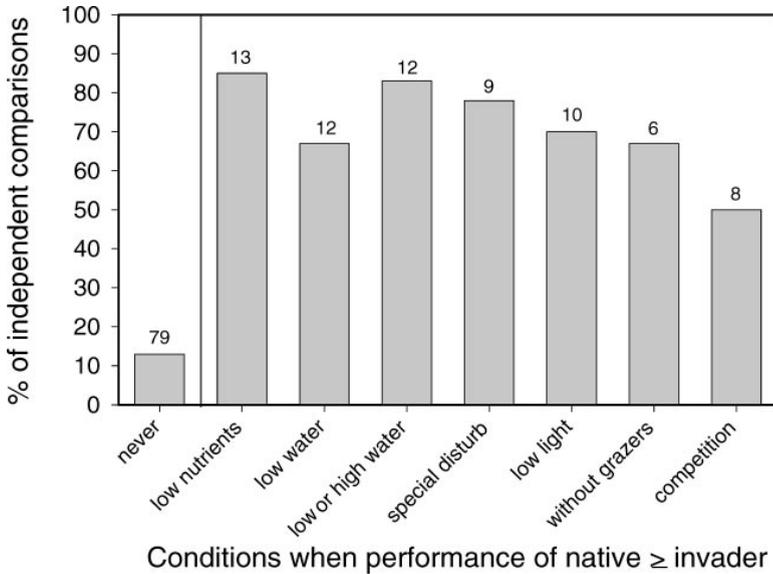


Figure 2 Conditions under which the native's performance was equal to or better than that of the invader. Only conditions favoring natives in three or more independent comparisons are shown. Percentages are based upon the total number of studies that manipulated each condition (given above each bar).

Specific examples of context-dependent performance are detailed in the summaries of individual performance measures below.

Growth-Rate-Related Traits

Invasive plants are often characterized as having unusually rapid individual growth rates, allowing them to outgrow, overgrow, or quickly crowd out natives (Cronk & Fuller 1995). Certainly, examples like "mile-a-minute weed" (*Polygonum perfoliatum*) support the idea that invaders can have very rapid growth rates (Oliver 1996). Nevertheless, among the reviewed comparisons, there was no clear evidence that invaders necessarily grow faster than co-occurring natives (Figure 3). Instead, the more rapid growth rate of invaders appears to be condition- or context-dependent. A study was far more likely to conclude that invaders had a universal growth-rate advantage if the study examined only one growing condition. Among 14 growth-rate studies conducted under only one growing condition, none showed a growth-rate advantage for the native. In contrast, among the 12 comparisons where a growth-rate advantage of the native was observed (Figure 3), all were conducted under more than one growing condition or environment. For example, the growth rate of native plains poplar (*Populus deltoides*) exceeded that of the invasive Russian olive (*Elaeagnus angustifolia*) when plants were grown with a high water table, whereas

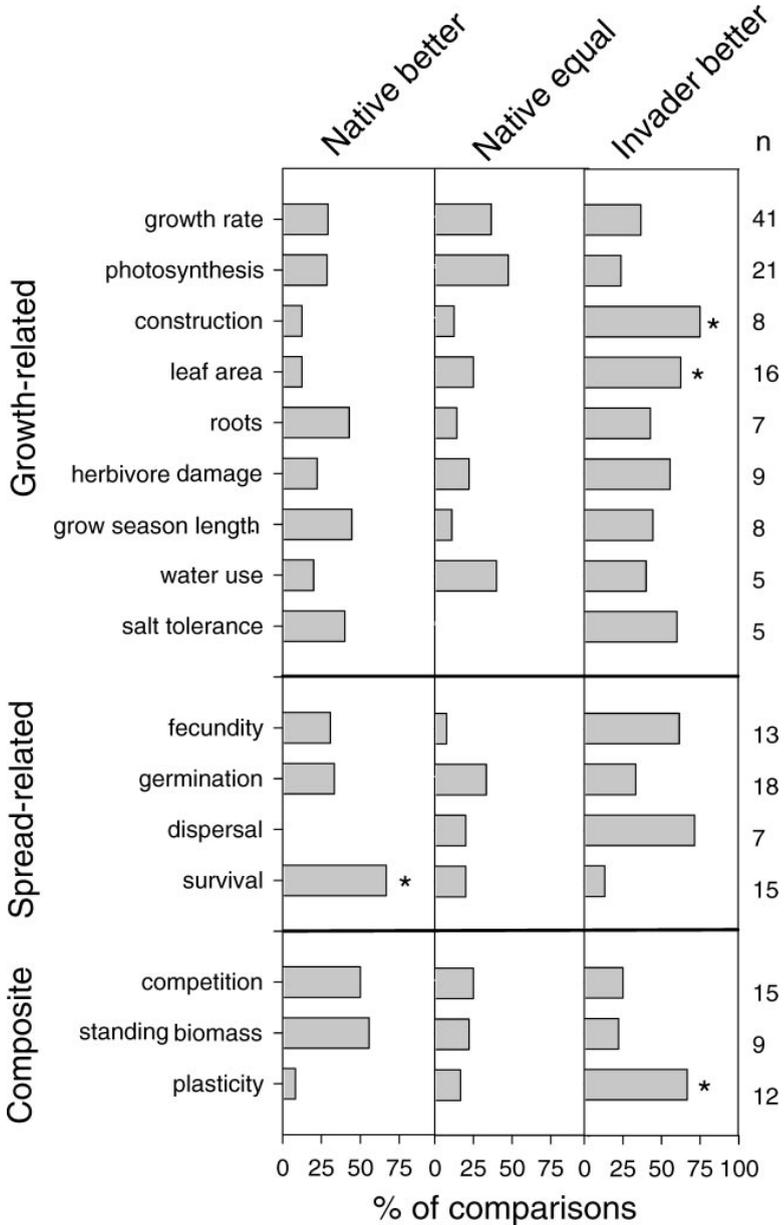


Figure 3 Summary of native versus invader performance, according to whether the native performed better than (*first column*) or as well as (*second column*) the invader under some conditions, or whether the invader always performed better (*third column*). Asterisk indicates significant difference (chi-squared exact test, exact $P < 0.05$). The column to the far right (n) indicates the number of independent comparisons for each measure of performance.

conclusions were different when the table was lower (Shafroth et al. 1995). Under conditions of reduced salinity, the growth rate of native willows (*Salix* spp.) equaled or exceeded that of invasive salt cedar (*Tamarix ramosissima*), a troublesome riverside invader in controlled river courses in the southwestern United States (Cleverly et al. 1997, Glenn et al. 1998). Reduced salinity would be expected along these river courses if the natural flood regime were restored in these areas. In salt marshes of the western United States, higher salinity favored the growth of native pickleweed (*Salicornia subterminalis*) over the invasive European annual beardgrass (*Polypogon monspeliensis*) (Kuhn & Zedler 1997). In the northwestern United States, the native perennial grass *Festuca idahoensis* had a growth advantage over invasive European grasses under lower water conditions, particularly with less winter rain (Borman et al. 1990). In Europe, native *Cystoseira nodicaulis* (a macroalga) had a substantial autumn and winter growth advantage over ecologically similar *Sargassum muticum* introduced from Asia (Arenas et al. 1995). These examples illustrate the importance of making comparisons over different times and under different growing conditions, and the findings from these studies suggest site-specific management strategies for promoting the growth of natives over the growth of invaders.

Similar cases of context-dependent performance were observed for photosynthetic capacity and root growth. Under dry conditions, a native Venezuelan bunchgrass, *Trachypogon plumosus*, had higher photosynthetic rates than invasive African molasses grass (*Melinis minutiflora*) (Baruch 1996). The native California dune grass *Elymus mollis* had higher rates of photosynthesis in the field than the invasive European dune grass, *Ammophila arenaria* (Pavlik 1983a). The same study observed higher photosynthetic rates for the invader in the laboratory, again pointing out the context-dependence of performance. Pattison et al. (1998) reported higher photosynthetic rates among forest invaders when they evaluated several native-invasive species pairs in the Hawaiian Islands. They concluded that “the invasive species appear to be better suited than native (Hawaiian) species to capturing and utilizing light, particularly in high light environments such as those characterized by relatively high levels of disturbance” (Pattison et al. 1998). As the latter statement implies, the invaders’ advantage was substantially less or nonexistent under lower light condition (as would be more typical of an undisturbed forest environment). It should also be noted that Pattison et al. (1998) grew all plants in a nutrient-enriched commercial potting medium. It would be interesting to know how photosynthetic rates would compare between invaders and natives growing in a nutrient-poor environment, more similar to soil conditions in most undisturbed Hawaiian rainforest.

Not many studies specifically examined root growth, but among the available studies, there was no consensus advantage for invaders (Figure 3). In New Zealand, the native grass *Festuca novae-zelandiae* had root growth advantages over invasive hawkweeds (*Hieracium* spp.) in certain low-fertility soils (Fan & Harris 1996). Marler et al. (1999) found no difference in fine-root densities of invasive spotted knapweed (*Centaurea maculosa*) and the native bluebunch wheatgrass (*Agropyron*

spicatum) when averaged across depths. The invader tended to have deeper roots but the native had denser fine roots at shallower depths. Either rooting strategy could be advantageous, depending on environmental conditions. In comparing invasive ice plant (*Carpobrotus edulis*) with native *Haplopappus* spp., D'Antonio & Mahall (1991) observed the opposite rooting pattern: The invader had denser fine roots near the surface, whereas the natives had deeper roots.

For total leaf area and tissue construction costs, there was a statistically significant trend toward invaders having higher leaf area and lower construction costs than natives (Figure 3). Invaders tended to have greater leaf area, whether measured as absolute area or leaf area ratio (leaf area per total plant mass) and when combined with lower construction costs (Baruch & Goldstein 1999), this increased area might be expected to give the invaders a growth advantage. The number of studies examining construction costs remains small, and further studies would be useful to determine if a statistical trend toward lower construction costs among invaders is generalizable. One recent study on invasive purple loosestrife (*Lythrum salicaria*) found that the invader did not have lower construction costs relative to some ecologically similar native species in North America (Nagel & Griffin 2001). Furthermore, although low tissue construction costs and higher leaf area might appear to provide a universal growth-rate advantage (but see Poorter & Bergkotte 1992), there are likely to be trade-offs in the form of reduced leaf longevity (Reich et al. 1997). Native plants with lower leaf area ratio and higher construction costs are likely to have longer leaf life spans, which can result in comparable overall above-ground production efficiency per unit foliar biomass, compared with (invasive) plants with larger leaf area ratios and lower construction costs (Reich et al. 1992). In low-nitrogen environments, having a longer leaf life span (with the cost of slower growth) may actually be superior in the long run because plants with longer tissue life spans are more efficient at holding scarce nutrients (Aerts & van der Peijl 1993). If a native plant community is adapted to low-nutrient conditions, then increased nutrient levels are likely to promote the success of invaders adapted to take advantage of these high nutrient levels. Experiments have demonstrated increased success of invaders following nutrient additions alone (Huenneke et al. 1990), although more often nutrient additions interact with physical disturbance to promote invasion (Burke & Grime 1996, Duggin & Gentle 1998, Li & Norland 2001, Weiss 1999). Human-related eutrophication and physical disturbance of the environment can probably explain the success of many invaders (e.g., Allan 1936, D'Antonio et al. 1999, Hobbs & Huenneke 1992).

Competition

Competitive ability or performance can be measured in various ways (Goldberg & Landa 1991). Most of the reviewed studies pitted invaders against ecologically comparable, similar-sized native species. Conclusions about competitive performance were generally based on the final biomass of the invader relative to the native species when grown in competition. As with most other fitness-related traits, the

relative competitive performance of native versus invasive species often depended on environmental conditions. Among the 16 studies that experimentally assessed competitive performance, only five (31%) seemed to show universally superior competitive performance by the invader. These five invaders were *Bromus inermis* (Nernberg & Dale 1997), *Dipsacus sylvestris* (Huenneke & Thomson 1995), *Lythrum salicaria* (Mal et al. 1997) *Pennisetum setaceum* (Carino & Daehler 2002), and *Spartina alterniflora* (Callaway & Josselyn 1992). For one of these species (*Dipsacus*), the situation was not clear. This invader seemed to outcompete the native in a greenhouse study, but an accompanying field study was inconclusive (Huenneke & Thomson 1995). The case of *Lythrum* also requires a caveat; the native (*Typha angustifolia*) was clearly the superior competitor in the first year, but by the end of the experiment (fourth year), *Lythrum* appeared to have the competitive advantage (Mal et al. 1997).

Among the remaining 11 comparisons of competitive performance, the native was equivalent or superior to the invader, at least under certain growing conditions. In South Africa, the native woody legume *Virgilia orboides* had superior performance when grown in competition with ecologically similar Australian invaders (*Acacia longifolia* and *Albizia lophantha*) under both high- and low-nutrient conditions (McDowell & Moll 1981). In several comparisons, competitive performance depended on nutrient availability. Under high- and moderate-nutrient conditions, invasive *Acacia saligna* significantly outperformed native *Protea repens*, but when the two were grown together in competition under low-nutrient conditions (native Clovelly soil with acid-washed sand), the performance of the native was comparable to that of the invader (Witkowski 1991). Likewise, when the California native grass *Elymus glaucus* was grown in competition with the European invader *Bromus mollis*, the invader performed better at high soil nitrogen levels, but the outcome was reversed under lower-nitrogen conditions (Claassen & Marler 1998). Similar results were obtained in a comparison of competitive ability between invasive spotted knapweed (*Centaurea maculosa*) and the native perennial grass *Pseudoroegneria* (*Agropyron spicatum*) (Herron et al. 2001). In New Zealand, the native grass *Festuca novae-zelandiae* appeared able to suppress an invasive herb (*Hieracium pilosella*) in low-fertility soils if a single clipping treatment was applied, but the native was less successful under higher-nutrient conditions (Fan & Harris 1996). In a study of competitive hierarchies among 20 wetland plants in three environments, Keddy et al. (1994) concluded that invasive purple loosestrife (*Lythrum salicaria*) had strong competitive effects on the phytometer species across all environments; however, it is interesting to note that the phytometer species had strong effects on purple loosestrife in the low-nutrient environment, reducing its biomass by nearly 50%. About half of the native species tested showed lesser reductions in biomass in the low-nutrient environment (Keddy et al. 1994), indicating that many natives tolerated competition better than purple loosestrife did under low-nutrient conditions. Whereas low-nutrient conditions often increased the relative competitive performance of natives, no native species had an increased competitive advantage under high-nutrient conditions.

Another example of an environmental condition that increased the relative competitive performance of a native species was decreased water availability (Smith & Brock 1996). A performance advantage for natives under reduced water conditions was also observed in several other species pairs and for other performance measures (Figure 2). Mesleard et al. (1993) observed superior competitive ability of a native halophytic grass, *Aeluropus litoralis*, over invasive *Paspalum paspalodes* under conditions of increased soil salinity. This pattern has also been reported for other native halophytes in competition with invaders (Kuhn & Zedler 1997, Zedler et al. 1990).

Standing Biomass/Cover Abundance

Several field-based studies measured changes or differences in standing biomass/cover of native versus invasive species under different environmental conditions (Figure 3). Such changes are probably due to a combination of factors, including competition. Working in upland prairies of the western United States, Wilson & Clark (2001) found that a specific mowing regime reduced cover of the invasive Eurasian grass *Arrhenatherum elatius* while increasing cover of native prairie grasses. In the Chilean matorral, Holmgren et al. (2000) observed increased cover of native species, particularly the native grass *Bromus berterianus*, in plots that had been fenced to keep out alien grazers. Stromberg & Griffin (1996) analyzed the vegetation of California grasslands and found that native grasses remained dominant or codominant on lands that had not been historically cultivated. Cultivation presumably altered soil texture and nutrients, favoring invasion by Eurasian grasses. Furthermore, current high levels of gopher disturbance, even on lands no longer in cultivation, seem to favor dominance by the alien grasses (Stromberg & Griffin 1996). Other studies involving seed additions of either natives or aliens (but not both) followed by environmental manipulations (e.g., Hobbs & Atkins 1988) have likewise identified conditions favoring increased cover/biomass of natives, but these studies are not considered here because their differential treatment of natives and invaders precluded direct performance comparisons.

Four studies in the standing biomass category (Figure 3) tested whether invasive species tend to attain higher biomass/productivity than ecologically similar native species. Two of these studies found that the invader attained higher biomass than an ecologically similar native (Pavlik 1983b, Callaway & Josselyn 1992), while the other two studies found no difference in standing biomass between invader and native (Horn & Prach 1994, Smith & Knapp 2001a).

Reproduction and Spread-Related Traits

Some studies examining reproductive ecology have identified spectacular advantages for the invader. For example, invasive smooth cordgrass (*Spartina alterniflora*) in San Francisco Bay had a sevenfold advantage in seed production over native California cordgrass (*Spartina foliosa*), and the germination rate was also higher for the invader (Callaway & Josselyn 1992). Similarly, in the South African

fynbos, introduced *Banksia ericifolia* had twofold higher seed production per canopy area compared with native *Leucadendron laureolum* (Honig et al. 1992). The alien also had advantages in germination speed and germination rate (Honig et al. 1992). Despite examples like these, other studies found no clear advantage for the invader. For example, in a glacier foreland, native *Poa kerguelensis* produced nearly three times more seeds per plant than invasive *Poa annua*; percent germination of seeds was similar (80–90%) for both species (Frenot & Gloaguen 1994). The native required a cold pretreatment for germination, but this would not seem to be a disadvantage in a glacial environment. Among 31 comparisons of fecundity and/or germination, the invader had a consistent reproductive advantage in only 14 (45%) of the cases (Figure 3). In the remainder of cases examining fecundity and/or germination, either the invader did not have a clear reproductive advantage (as in *Poa annua* versus *Poa kerguelensis*), or the invader's advantage was context-dependent. For example, although invasive fountain grass (*Pennisetum setaceum*) in Hawai'i had higher seed production per plant than native pili grass (*Heteropogon contortus*) under higher water conditions, the native had the fecundity advantage under drought conditions (Goergen & Daehler 2001b). Likewise, under conditions of low water availability, invasive fountain grass had lower seedling survival compared with the native grass (Goergen & Daehler 2002). An analogous situation was reported from Australia: over 80% of individuals of the native grass *Danthonia richardsonii* flowered and produced seeds under dry field conditions. In comparison, among three co-occurring alien grasses fewer than 5% of individuals flowered under these conditions (Virgona & Bowcher 2000). Survival of the native was also higher in the low water environment (Virgona & Bowcher 2000).

In some cases, fire seemed to give natives a reproductive advantage. Seeds of a native Australian grass (*Austrostipa compressa*) had higher germination rates than an invasive African grass (*Ehrharta calycina*) after exposure to high heat (Smith et al. 1999). The native also had higher densities of germinable seeds in the field after fire (Smith et al. 1999), although germinable seed densities were not compared in unburned areas. Similarly, in Hawai'i, fire caused high seed (and adult) mortality in invasive natal redbud (*Melinis repens*), resulting in low seedling recruitment and cover abundance after fire, compared with the co-occurring fire-tolerant native grass *Heteropogon contortus* (Tunison et al. 1994).

Although most comparisons of fecundity were based on seed production, Aptekar & Rejmánek (2000) compared potential for vegetative reproduction between American beach grass (*Leymus mollis*) and the invasive European beach grass (*Ammophila arenaria*) on U.S. Pacific coasts. They found that the native produced significantly more nodes (potential propagules) per rhizome length than the invader. Rhizome fragments of the native also remained viable in seawater for a longer time (Aptekar & Rejmánek 2000), suggesting a dispersal advantage for the native.

Overall, there was a trend toward a seed dispersal advantage for invaders ($P = 0.06$, Figure 3), but statistical power was limited by the small number

of studies. Richardson et al. (1987) concluded that the winged, wind-dispersed seeds of introduced Protaceae (*Hakea* spp.) have a dispersal distance advantage over native South African Protaceae, which are often gravity or ant-dispersed. Also in South Africa, introduced *Banksia ericifolia* was found to have lighter seeds with larger wings compared with native *Leucadendron lauroleum*, providing the alien with a dispersal distance advantage (Honig et al. 1992). In California, scats of jackrabbit and deer contained more seeds of invasive *Carpobrotus edulis* than seeds of the presumed native *C. chilensis*, implying a dispersal advantage for the invader (Vila & D'Antonio 1998a). Rejmánek (1996) has proposed that the presence of an efficient bird-disperser may be a key predictor of invasion success among fleshy-fruited plant species, so it is surprising that few studies have compared bird dispersal preferences between native and invasive plants. In a subtropical forest, Montaldo (2000) examined fruit removal rates by birds for two invasive plants (*Rubus ulmifolius* and *Ligustrum lucidum*) and three native plants. There was no clear difference in fruit removal rate between invaders and natives, but the invaders had higher fecundity. Similar findings were reported in a comparison of invasive Oriental bittersweet (*Celastrus orbiculatus*) and native holly (*Ilex opaca*) in a North American temperate forest; fruit removal rates did not differ significantly between the native and invader, although there was a trend toward a higher removal rate for the native (Greenberg et al. 2001). In contrast, fruits of the invasive European hawthorn (*Crataegus monogyna*) were more attractive to American robins than fruits of a native American hawthorn (*C. douglasii*) (Sallabanks 1993). This study was particularly interesting because it showed preference by native birds for fruits of an invasive plant, but so far this situation appears to be the exception rather than the rule (Montaldo 2000).

Among the reproduction and spread-related traits, there was one statistically significant trend: natives tended to have a survival advantage over invaders at some life stage, under at least some environmental conditions (Figure 3). Some of these cases have already been mentioned (e.g., higher relative survival of native *Populus*, *Heteropogon*, and *Danthonia* as well as *Leymus* rhizomes under specific environmental conditions). In Argentinean montane forests, a native tree, *Lithraea ternifolia*, was estimated to have higher seedling and juvenile survival at sites with shallow, rocky soils, compared with an invasive North American competitor, *Gleditsia triacanthos* (Marco & Paez 2000). In New Zealand, although the native vine *Parsonsia heterophylla* had a slow growth rate, it was capable of surviving at lower light levels compared with invasive vines (Baars & Kelly 1996). In woodlands of Ireland, reduced grazing pressure would likely result in higher seedling and juvenile survival of the native understory shrub *Ilex aquifolium* compared with invasive *Rhododendron ponticum*, particularly on sites with an accumulation of leaf litter (Cross 1981). Vila & D'Antonio (1998b) reported a survival advantage for the invader, *Carpobrotus edulis*, over native *C. chilensis* in one environment, but not in another environment. It is surprising that so few demographic studies have compared the survival of native and invasive plants across life stages and

environments (e.g., Marco & Paez 2000) as such studies can provide clear insights into management strategies that could differentially promote natives.

Phenotypic Plasticity

Among 12 comparisons of phenotypic plasticity, most concluded that the invader was more plastic than the native (Figure 3). Most observations of greater phenotypic plasticity in invaders involved changes in biomass allocation patterns in response to different environmental conditions (Baruch & Bilbao 1999, Black et al. 1994, Fan & Harris 1996, Luken et al. 1997, Maillet & Lopez 2000, Simoes & Baruch 1991, Yamashita et al. 2000). Other studies reported greater plasticity for the invader in terms of physiological responses (Pattison et al. 1998, Williams & Black 1994), circumnutation (Larson 2000), or germination in response to temperature (Frenot & Gloaguen 1994). It seems that invaders often do have higher phenotypic plasticity than natives, and this plasticity probably allows invaders to succeed in a wider range of environments, but it does not a priori indicate a performance advantage over natives within any single, defined environment. Furthermore, natives probably often have higher genetic variation in comparison with co-occurring invader populations that were established from a small group of founders. It would be interesting to know if the range of phenotypes expressed in an invading population exceeds the range of phenotypes expressed in a native population, since it is this total phenotype range (genetic and plastic) that determines a species' ability to respond to environmental changes over time or space. Kitayama & Mueller-Dombois (1995) found that native species generally had greater overall environmental breadth compared with invaders, and this wide breadth was related to high genetic variation within the natives (Kitayama et al. 1997, Daehler et al. 1999).

Effects of Natural Enemies

If an invader is significantly affected by natural enemies in its native range, then release from natural enemies could give it a fitness advantage in its introduced range. Nine studies were found comparing the effects of herbivory on native and invasive species. In six of these cases, herbivores had a larger impact on the native plants (Figure 3). One of these cases involved introduced grazers (Caldwell et al. 1981) and four involved cases where native vertebrate herbivores likely occurred at unusually high abundances owing to human elimination of their natural predators (Cross 1981, Lesica & Miles 1999, Pyke 1986, Schierenbeck et al. 1994). The one remaining study was largely anecdotal, reporting "heavy nocturnal leaf feeding by crickets" on a native species; the invasive species were "unaffected" by crickets (McDowell & Moll 1981). One of the nine herbivory comparisons found no consistent differences in level of herbivory on native and exotic eucalypts in Australia (Radho et al. 2001). Two studies (22%) found greater herbivore damage on the invasive species than on the native, but in both cases the herbivore was introduced (Bellingham 1998, Gross et al. 2001). Keane & Crawley (2002) summarized eight additional studies examining herbivory on native and invasive plants; five of these

showed greater damage among native plants. Based on the studies to date, we cannot generally assume that native plants are more heavily damaged by herbivores than invaders. Successful biocontrol efforts cannot be used as evidence that an invader's advantage was due to release from herbivory because biocontrol agents themselves have been released from their natural predators, pathogens and competitors (Keane & Crawley 2002). There also appears to be no general trend toward greater seed predation rates for natives versus invaders (Blaney & Kotanen 2001b), although individual exceptions have been reported (e.g., Richardson et al. 1987). Likewise, there appears to be no general trend toward greater rates of attack by fungal pathogens among native species than among invaders (Blaney & Kotanen 2001a), although again, exceptions are known (e.g., Goergen & Daehler 2001a). Interestingly, Mitchell & Power (2003) found that native plants had greater absolute numbers of pathogens than invasive pest plants, but unlike Blaney & Kotanen (2001a), they did not make comparisons for co-occurring species and no estimates of pathogen damage were available.

General Conclusions from Performance Comparisons

In the majority of reviewed cases, native plants were equivalent to or had performance advantages over invasive plants under at least some growing conditions (Figure 2). Because the published literature on invasive species is likely to be biased toward studies of the most troublesome invasive pests (Simberloff 1981), it seems safe to conclude that invaders with universal performance advantages over ecologically comparable native species (i.e., super invaders) are quite rare, even among aggressive invaders (Rosenzweig 2001). Trade-offs in physiology and life history (Sinervo & Svensson 1998) are likely important in constraining invaders, but the rare "super invaders" may circumvent some trade-offs (Holway 1999). Assuming sufficient habitat heterogeneity, the performance data imply that most native species should be able to maintain natural populations even as invading plants spread, but the native populations might persist within a narrower range of environmental conditions (narrower realized niche) than before the invaders arrived. Conditions where invaders had the largest performance advantage (high resource availability, high physical disturbance, or departures from the natural disturbance regime; Figure 2) are generally associated with human activities.

STRATEGIES FOR MAXIMIZING PERFORMANCE BY NATIVES

Preserve "Intact" Natural Systems

Preserving "intact" natural systems is an obvious priority for many conservation biologists. From the perspective of invasion biology, natural areas that have experienced minimal human disturbance have long been noted to be less invaded than areas that have been directly disturbed by humans (Allan 1936, Rejmánek

1989). Although this pattern may be partly explained by fewer alien propagules having been introduced to intact natural systems, the studies reviewed here also suggest that the relative performance of most invaders would be reduced in many intact natural systems where key resources are likely to be scarce. Such systems may generally favor the survival, growth, or recruitment of natives. Physical protection of representative samples of intact natural systems also can provide us with invaluable reference information about conditions that are likely to favor local native species over most invaders. Key data that could be obtained from preserved natural systems include measures of nutrient, water, and light availability, assessment of natural disturbance regimes/environmental heterogeneity, and identification of factors associated with crucial population processes such as recruitment.

Focus on the Most Promising Restoration Sites

If data are available from an intact natural system, then promising restoration sites would ideally be identified based on matching resource availabilities and conditions (Critchley et al. 2002). Depending on the system of interest, key resources that maximize native:invader performance ratios will differ, but an obvious strategy for reducing invasive species problems is to avoid restoration sites with unusually high resource availability. For example, in northern California, a former cultivated field is likely to be rich in nutrients from past fertilization and have deeper and richer soil than a sloping, rocky site that has not been cultivated (Stromberg & Griffin 1996). Restoration of the former old field site with native perennial bunch grasses is likely to require substantially more effort and long-term maintenance because of more severe invasive plant problems (Stromberg & Griffin 1996).

In other cases, small differences in rainfall between potential restoration sites may be an important consideration. In the Hawaiian Islands, the native grass *Heteropogon contortus* formerly inhabited large portions of low elevation leeward sides of islands, but in recent years it has nearly disappeared, largely replaced by African grasses like *Pennisetum setaceum* (Daehler & Carino 1998). Under most conditions, invasive *Pennisetum* outcompetes *Heteropogon* (Carino & Daehler 2002); however, under very dry, nutrient poor conditions, *Heteropogon* performs substantially better than the invader (Goergen & Daehler 2002). It is these extremely dry and rocky (poor soil) sites that are the focus of current *Heteropogon* restoration efforts. Although alien grass seedlings are occasionally observed at these sites, they rarely survive owing to inadequate water (C. Daehler, unpublished data). In cases where the native vegetation targeted for restoration is adapted to specific environmental stresses (e.g., halophytes), even a small decrease in environmental stress (salinity) can lead to large increases in the performance of invaders (Mesleard et al. 1993). In such cases, choosing a site with more stressful conditions is likely to minimize invasive plant problems; for halophytic vegetation, salt additions may even be useful means of controlling invaders (Kuhn & Zedler 1997).

Actively Manage Resource Availability and Disturbance—Nutrient Reductions

Reductions in available nitrogen can potentially be achieved either by reducing anthropogenic inputs or by adding a carbon supplement to the soil, which can increase microbial nitrogen uptake (McLendon & Redente 1992, Paschke et al. 2000, Torok et al. 2000). By experimentally manipulating nitrogen inputs to wetlands with controlled hydrology, Green & Galatowitsch (2002) found that increased nitrogen inputs favored dominance of invasive reed canary grass (*Phalaris arundinacea*) over the native plant community. They concluded that reducing nitrate loads to wetland reserves is essential for minimizing declines in native community diversity.

In other systems, such as abandoned agricultural fields, reductions in available nitrogen to natural levels could take decades even without further anthropogenic inputs (Barton et al. 1999, Maron & Jeffries 1999). One strategy for rapidly reducing soil nutrients after anthropogenic disturbance is to remove topsoil. In an effort to restore an abandoned agricultural field to a native fen meadow, Tallowin & Smith (2001) found that removing 15–20 cm of top soil was the most effective strategy. Not only did the lower soil layer contain 85% less available phosphorus and lower nitrogen, it also had a higher calcium content, similar to that of soils in natural fen meadows (Tallowin & Smith 2001).

As a less extreme method of reducing nutrients, available soil nitrogen can be reduced by adding sawdust or sucrose to the soil. Paschke et al. (2000) used sucrose additions to reduce available soil nitrogen on abandoned crop land in Colorado. Over four years, plots that had been dominated by invasive *Bromus tectorum* were converted to a community that closely resembled the natural late seral shortgrass steppe vegetation. There was also less overall recruitment by a variety of weedy species in the reduced-nitrogen plots, even in wet years (Paschke et al. 2000). Interestingly, Evans et al. (2001) found that fires promoted by *Bromus tectorum* decrease nitrogen in the system through volatilization. Over the long run, this change could promote a shift away from dominance by *Bromus* back toward a late seral native community. Zink & Allen (1998) found that available nitrogen was reduced after adding organic mulch to a restoration site, and they suggested that this reduction gave native California sagebrush (*Artemisia californica*) a competitive edge over exotic annuals. Likewise, Alpert & Maron (2000) observed decreased biomass of invaders into nitrogen-rich soil patches after the addition of sawdust, while the sawdust did not reduce the abundance of native species. In contrast, Morghan & Seastedt (1999) did not observe an increase in dominance by natives following addition of sucrose and sawdust to a high elevation Colorado grassland. In that study, the treated plots were small in size (1.5 × 3 m), and these plots may have been swamped by alien seeds originating from outside the plots, allowing the aliens to remain abundant (Morghan & Seastedt 1999). In a mixed prairie grassland, plots receiving sawdust had higher bare ground, but native species responded most strongly to tilling, which presumably created more neighbor-free establishment sites for natives (Wilson & Gerry 1995). The latter two examples point out that

additional factors besides nutrient reduction may affect the relative success of natives and invaders.

Other nutrients besides nitrogen could also be profitably manipulated in specific circumstances. For example, the common dandelion, *Taraxicum officinale*, seems to be an unusually poor competitor for potassium, suggesting that simple soil manipulations could be used to control this weed (Tilman et al. 1999). Increases in phosphorus associated with soil disturbance have also been suggested to promote alien invasion in some grasslands (Hobbs & Huenneke 1992), and some specific methods have been proposed for reducing soil phosphorus (Gough & Marrs 1990). Although most nutrient reduction studies to date have involved monitoring herbaceous species in grasslands, the reviewed performance comparisons of native and invasive plants suggest that nutrient reductions would also be beneficial for restorations involving native woody plants. Soil pollution with anthropogenic nitrates is likely to increase as the human population grows to demand higher production agricultural systems (Kawashima et al. 1997, Van Der Voet et al. 1996). Identifying long-term strategies for keeping excess nitrogen and other nutrients out of specific natural or restored native systems will be crucial for maintaining these systems over the long term (Bobbink & Roelofs 1995).

Other resources like light and water could be manipulated locally to promote native species over invasives, but these manipulations may be costly or impractical on a large scale. At the very least, if excesses of certain resources such as water occur at discrete times (e.g., following an unusually heavy rain), then reconnaissance efforts aimed at preventing the establishment and spread of invaders could be focused on these specific times. For example, Burgess et al. (1991) noted that introduced buffel grass (*Cenchrus ciliaris*) failed to spread significantly for many years; however, during two unusually wet years many seedlings became established and later grew to form dense stands. Other studies have also identified the role of brief, discrete periods of increased resource availability in facilitating invasions (Davis & Pelsor 2001).

Manipulate Disturbance

One strategy for promoting natives is to attempt to mimic natural disturbance regimes. For example, restoration of the historic flood regime along rivers in the southwestern United States would probably favor the re-establishment of native vegetation over the currently established invasive *Tamarix ramosissima* (Sher et al. 2000). A similar situation seems to occur with invasive *Elaeagnus angustifolia* along river banks in the western United States; restoration of the historic flood regime would probably favor re-establishment of natives (Shafroth et al. 1995). Maintaining the historic fire regime often favors the growth of native species over invaders (Schultz & Crone 1998, Tveten & Fonda 1999). For example, in California grasslands, warm season burning seems to favor native plants over invasive annual grasses (Meyer & Schiffman 1999). Restoration of historic grazing regimes can also help promote native species diversity (Collins et al. 1998). In other cases, disturbances that do not necessarily match the historic disturbance regime may still

favor natives over invaders. For example, early spring mowing alone converted a grassland dominated by an invasive perennial grass (*Arrhenatherum elatius*) to a native perennial grassland (Wilson & Clark 2001). The growth pattern and phenology differed between the invader and natives such that mowing in early spring differentially removed biomass and developing inflorescences of the invader, resulting in increased flowering and growth of the native perennial grass (Wilson & Clark 2001). This example again illustrates how comparative demographic studies of invaders and co-occurring natives could be used to identify restoration strategies.

Further Challenges

Although particular disturbance regimes may tend to favor natives over invaders, maintaining primarily native communities may become increasingly difficult as the pool of introduced species located near a remnant native community increases (Smith & Knapp 2001b). The larger the pool of introduced species nearby, the greater the chance that at least some aliens will be able to tolerate the historic disturbance regime. More generally, the larger the species pool of potential invaders, the greater the chance that some aliens will possess traits that contradict statistical trends among invaders. For example, in a seed addition experiment testing the effects of disturbance and nutrient addition on invasion, Buckland et al. (2001) found that most successful invaders matched the predicted pattern—they became established and abundant in the physical disturbance and/or nutrient addition treatments. But one invasive grass, *Brachypodium pinnatum*, was most successful in the low fertility plots (Buckland et al. 2001). Controlling such exceptional species might require more direct, focused attacks, although the example of *B. pinnatum* is not so clear because in similar grasslands, Bobbink & Willems (1987) concluded that higher nutrients (especially nitrogen) were important in facilitating *B. pinnatum* invasion, matching the predicted general pattern for invaders.

Another problem that becomes apparent as the pool of invaders grows and the size of native habitats decreases is the proportionally greater influx of alien plant seeds into smaller patches of native vegetation (e.g., D'Antonio et al. 2001). A “seed swamping” effect could increase the net establishment of invaders, even if they are unable to develop self-sustaining populations within native habitats. This effect may be partly countered by establishing dense native vegetation around the edges of remnant native habitats (Cadenasso & Pickett 2001).

Perhaps the greatest long-term challenge to maintaining native communities is global climate change associated with urbanization and anthropogenic greenhouse gasses (Walther et al. 2002, White et al. 2002). Increases in global temperature allow warm-climate species to succeed at higher latitudes and elevations while also potentially decreasing the performance of certain native species. Such changes have already been clearly documented (Walther et al. 2002). If anthropogenic climate changes turn out to be large enough to affect vegetation patterns on a global scale, then conservation biologists may need to adopt entirely new objectives and strategies for conserving native biodiversity.

SYNTHESIS

Many conceptual and mathematical models have suggested that increases in resource availability (including space, created by physical disturbance) can increase community susceptibility to invasion (Davis et al. 2000, Fox & Fox 1986, Hobbs 1989, Shea & Chesson 2002, Sher & Hyatt 1999, Tilman 1999). Overall, these models assume that the free resources provide invaders with an opportunity to enter an established community, perhaps by reducing the intensity of competition for a limiting resource (Davis & Pelsor 2001). This idea has been generally supported by studies that manipulate resources (Brooks 1999, Duggin & Gentle 1998, Li & Norland 2001, Weiss 1999, White et al. 1997). However, the performance comparisons reviewed here suggest an additional factor that can help explain these empirical results: the relative performance of invaders versus native species may shift under higher resource conditions. Such shifts in relative performance may then allow invaders to dominate over natives as long as resource availability remains high (increased light, nutrients, or water, usually associated with anthropogenic disturbance). Because resource availability is unlikely to be uniform in any given habitat, patches of natives may be expected to persist in lower resource areas (e.g., on lower quality soil patches, under marginal growing conditions). Theoretically, a return to original (or predisturbance) resource levels would again favor native species over most invaders, but several factors may prevent their re-establishment, including

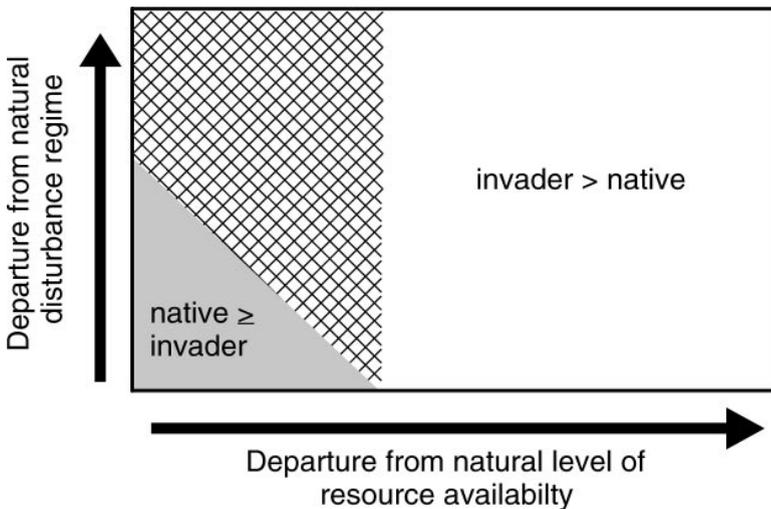


Figure 4 Conceptual model predicting relative performance of native species versus most invaders. The checkerboard region represents possible unnatural disturbance regimes (must be discovered) that might favor the native if resource availability is not extraordinarily high.

inadequate seed input by natives, a priority effect by established invaders, and overwhelming seed inputs by invaders growing in surrounding areas. Furthermore, if invaders are long-lived, then they could potentially prevent significant recruitment of native species for decades without additional intervention to remove the invaders.

Specific disturbance regimes can also favor natives over invaders (Figure 4). In most cases, the natural disturbance regime seems to favor natives (Alpert et al. 2000, Hobbs & Huenneke 1992, Mueller-Dombois & Loope 1990), but other disturbance regimes may also favor natives over specific invaders (Figure 4). Life history and demographic comparisons of co-occurring native and invasive species could aid in identifying artificial disturbance regimes that decrease the performance of invaders relative to that of natives. Manipulation of disturbance, nutrient and hydrological regimes can be considered within the general framework of "ecosystem management" (Christensen et al. 1996, Grumbine 1994), although these strategies for attaining "ecological control" of invaders may also be effective on local scales that do not necessarily extend across an entire ecosystem.

For any given habitat, there are probably a small number of "super invaders" capable of outperforming most co-occurring natives even at natural resource levels and in the presence of natural disturbance regimes. These invaders will require special attention. However, the ability of most invaders to outperform co-occurring natives appears to be context-dependent. Most environments can probably be managed to favor native species by altering resource levels and disturbance regimes so that native species performance is maximized, relative to that of most invaders. This form of "ecological control" is unlikely to eliminate all troublesome invaders from habitats where they already occur; rather, some invaders would probably coexist with natives at lower (acceptable) densities. For most habitats, we have only cursory knowledge, at best, of how environmental manipulations can be used to reduce invasive plant problems and simultaneously to promote natives. The increasing integration of well-planned environmental manipulations into restoration projects promises to provide new insights into managing invasive species problems.

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