Managing dominance of invasive plants in wildlands

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Invasive exotic plants threaten nature reserves and wildlands, where eradication may be neither a cost-effective nor an obtainable objective for controlling widespread weeds. In such cases, long-term management objectives should address the maintenance of desirable community and ecosystem processes through reduction in invasive plant abundance and distribution to acceptable levels. Strategic approaches to invasive plant control should include restoration of critical functional groups, mitigation of environmental stressors and reduction in exotic sources of disturbance to improve biotic resistance of the native community and reduction in invasive plant dominance. Monitoring to assess progress toward management goals is essential to identify needed changes in protocol as more is learned about drivers of community processes.

Keywords: Exotic species, invasive species, natural enemies, species management.

INVASIVE exotic plants are a growing threat to the maintenance of native species and to the ecosystem integrity of wildlands[1–3]. Invasive exotic plants (IEP) are implicated in the decline of threatened and endangered species because they alter ecosystem processes, change community structure and displace native species[4–6]. The uncontrolled expansion of IEP also can jeopardize protection status of natural reserves and preclude the protection designation of otherwise high-priority conservation areas. Invasive alien species are difficult to manage in conservation areas, because wildland reserves are often extensive and poorly accessible. High risks of collateral damage limit the tools available for control and the necessity for frequent intervention stresses available resources and the political will necessary for long-term control. In many cases management must address multiple invasive species simultaneously and correction of chronic biotic and environmental issues such as site degradation or ungulate impacts may need mitigation as a precondition for IEP control. Moreover, effective management of invasive species in wildlands is often dependent on coordinated efforts of national, regional and local governments, of private and non-profit interests and of individual landholders. Such coordination is only possible if supported by a legislated legal framework based on rigorous scientific underpinnings.

Prevention and early eradication often are seen as cost-effective means of managing invasive species[7]. Eradication measures are most effective when populations are few and small[8]. Moreover, reaching a goal of eradication presumes that high-risk species can be recognized, all individuals located and the species no longer distributed in trade. The strongest correlate of invasiveness is the behaviour of the species where they have been introduced elsewhere[9,10]. When the species is new to horticulture, reliability of the risk assessment is more variable. Search strategies for rare species and small populations which characterize the initial stages of invasions are labour-intensive and require a high level of taxonomic expertise. Potentially invasive exotic plants arrive and spread by multiple pathways which, in the absence of pre-introduction screening, are difficult to monitor[11]. Even eradication of small populations cannot be assured without consistent systematic monitoring to detect plants germinating from the seed bank. Prevention and eradication protocols are likely to be most successful when applied to high-priority circumscribed areas that can be closely monitored, such as small islands or conservation reserves. They are challenging to implement over large areas and may not be cost effective.

When the extent and duration of the invasion is such that eradication is no longer feasible, populations of invasive species must be managed strategically to reduce impacts to an acceptable level with resources available. Management protocols to reduce the abundance of exotic species are likely to differ from those designed to eradicate populations. Determination of acceptable levels of impact requires reliable information on consequences of spread as a function of abundance. While investments in the control of IEP in agriculture or rangelands can be balanced against net economic benefits, benchmarks for control of IEP in wildlands are less easily determined[12,13]. Objectives for the reduction in IEP impacts might include recovery of populations of endangered species, increases in native species diversity and restoration of ecosystem processes characteristic of native communities. Such an approach requires an understanding of the causes of population decline, failure of natural regeneration, or alteration of ecosystem processes, which is often incomplete. Here I discuss some of the patterns and processes that might be used to design an

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IEP control strategy where invasive species have spread beyond the capacity to eradicate them.

Impacts of IEP on wildlands

Invasive species are generally those non-native species that spread without human aid and have adverse economic or ecological impacts[14,15], often because they reach high densities and biomass[16]. Management protocols, disturbances such as fire and windstorm, and changes in environmental parameters, such as climate, hydrology and nutrient loading, all may bring about changes in the relative abundances of species and potentially in ecosystem processes[17]. Similarly, the change in dominance brought about by some plant invasions can have consequences for changes in ecosystem structure and processes. Changes in species dominance (relative abundance) may bring about wholesale changes in ecosystem functioning with consequences for rare species, trophic structure and ecosystem services[18].

Controls on the distribution and abundance of species lie at the heart of processes structuring communities and ecosystems[16] and understanding those processes is important in designing effective management protocols. Dominant species affect growth and establishment of co-occurring species[18] through their impacts on the availability of light, nutrients and/or moisture and on trophic interactions with herbivores, pathogens, pollinators and dispersal agents. Invasive exotic grasses suppress growth and regeneration of native shrubs and trees and grass invasions are often associated with low diversity of native seedlings[19,20]. The impacts of invasive plants on natural and managed ecosystems have been reviewed elsewhere[7,21].

Vitousek[22] suggested that IEP impacts on plant communities are likely to be greatest when the invasion introduces a new growth form, functional group or ecosystem process. Compelling examples include species that alter nutrient and moisture supply, for example, through nitrogen fixation or high evapo-transpiration rates[23–25], invasive grasses, which increase fine fuel loads and fire frequency[26,27] and invasive shrubs and trees which alter the physiognomy of grasslands[28]. Such IEP alter environmental conditions for all components of the community and may leave residual or legacy effects that persist for many years after their removal. For example, frequent fires fueled by alien grasses not only reduce regeneration of fire-sensitive species, but also volatilize nitrogen and mobilize other nutrients, thereby reducing nutrient supply[26].

Nevertheless, dominant IEP do not always suppress native species, which may be limited by other factors. MacDougall and Turkington[29] suggest that IEP may be either 'passengers' or 'drivers' of ecosystem change. That is, they either may reflect the environmental conditions of the ecosystem, reaching high abundances under local circumstances, or their abundance may cause the changes in ecosystem structure and processes. If IEP reflect, rather than cause, changes in ecosystem processes, reduction in IEP dominance may not be sufficient to restore community composition. A management strategy for control of IEP should begin with a careful evaluation of the environmental context of the invasion and the impacts of the target invasive species on native species populations and ecosystem services.

Benchmarks and goals

IEP management projects should have clear goals and benchmarks by which to measure progress. On this basis managers will have the tools to evaluate effectiveness of protocols, to alter protocols when necessary and to justify expenditure of resources. Where invasive species are widespread or the wildlands under management are affected by multiple species, managers should consider goals that entail reduction of impacts rather than eradication. Such management strategies are likely to be site-specific rather than regional or species-specific. In any case, benchmarks by which to measure effectiveness of a management strategy should address goals for population, community, and ecosystem processes in addition to cover reduction of the target weeds. For example, the success of biological control agents might be measured in the facility with which the new agent establishes self-reproducing populations, in the impact of the agent on biomass of the target weed, in the impact on population growth of the target weed and/or in the impact on community and ecosystem processes in the target community[30–32]. In practice, success is commonly measured in establishment of the agent and in qualitative assessments of biomass reduction of the target weed. As a consequence, our understanding of impacts of exotic biocontrol agents on new communities and new ecosystems is scant[33].

Results of IEP control efforts may be surprisingly at odds with initial goals. It is not uncommon for managers to successfully reduce biomass of one IEP, only to be confronted with the population expansion of the same or other species into the new openings[34]. Recruitment of high-priority native species and regeneration of the target plant community may be seed- or pathogen-limited rather than inhibited by competition with the IEP and thus may not respond to IEP control[20,29]. Effects of the management protocol on target IEP as well as on the host ecosystem should be evaluated through a monitoring programme.

Different management goals may mandate strongly different approaches to invasive species control. Goals for IEP control in wildlands might include restoration of the composition, structure and ecosystem processes historically characteristic of native communities. Alternatively rehabilitation of high-priority ecosystem services may be facilitated by exotic species. Under some circumstances watershed protection and maintenance of downstream water supply may entail the removal of those IEP with high water demand[24]; under other circumstances IEP have been used to provide watershed protection[35]. High priority natural areas may mandate the removal of all non-native species in an effort to ensure ecosystem structure and processes that will support the historic suite of native species. An acceptable community structure and composition of other wildlands may be maintained by periodically reducing high density patches of target IEP.

What is an acceptable level of impact of an IEP on an ecosystem? The answer will determine to what level (cover, biomass, density) IEP are to be reduced and will depend on our understanding of the relationship between IEP biomass or cover and the impact on community and ecosystem processes of concern. Even low population levels of an IEP known to hybridize with an endangered species may not be acceptable. On the other hand, exotic shrubs and trees invading forest understorey may register little measurable impact on native species or on ecosystem processes until high densities are reached. In the latter case, an effective impact reduction strategy might target a few high priority areas; attention to areas of lower priority might be delayed until resources become available and the target species came under control (R. Loh, pers. commun).

Progress toward management goals should be assessed through monitoring of appropriate benchmarks. Where protection of critical native species is of concern, then growth, survival and regeneration of these populations should be tracked. It will be important to know whether reductions in the impacts of IEP are sufficient to promote growth of critical populations. If other factors such as recruitment or natural enemies limit population growth, then seed supplementation or pest control may be necessary to reach goals. In addition to information on the target IEP, managers require information on non-target species. At what intervals must the population be reduced to maintain target impact levels? Have other IEP expanded to fill newly available space? Have the control operations had an impact on non-target species of concern?

A high priority may be maintenance or reestablishment of community structure and succession processes because this framework provides the context within which co-occurring or satellite species exist[18]. Thus high-priority target IEP may be those that alter physical structure of communities. For example, woody vines can impede tree regeneration in forest gaps[36]; periodic measurement of vine and liana cover would provide a gauge of the structural context of the community. Dynamic patch and succession processes are difficult to measure. Treefall gaps, important regeneration sites in many forest ecosystems[37], often occur at scales of hectares or greater so that the scale at which to assess the impacts of IEP (or of their reduction) on tree regeneration and natural succession processes should be appropriately large.

Where invasive impacts on ecosystem services are the principle concern, then those services should be monitored directly. In South Africa, invasive pines were found to have significant impacts on downstream delivery of water, their removal correspondingly restored groundwater levels[24]. In contrast, effects of removal of the invasive *Tamarix* in southwestern United States are likely to be negligible if the IEP is replaced by the native cottonwood[38]. Some species leave a residual impact on ecosystem processes following their removal[39]. Effects of allelopathic species and of species promoting high fire frequencies may be expected to persist for many years. Information on responses of ecosystem processes to IEP control will provide a basis on which to determine future management priorities in similar situations.

Toward design of an IEP management strategy

Figure 1 provides a schematic for understanding approaches to effective control strategies. It emphasizes three factors that have strong impacts on plant abundance: resource availability, pest and pathogen pressure, and propagule supply. Disturbance and habitat fragmentation affect both propagule supply and resource availability. Resource availability is influenced by site conditions, as reflected in site

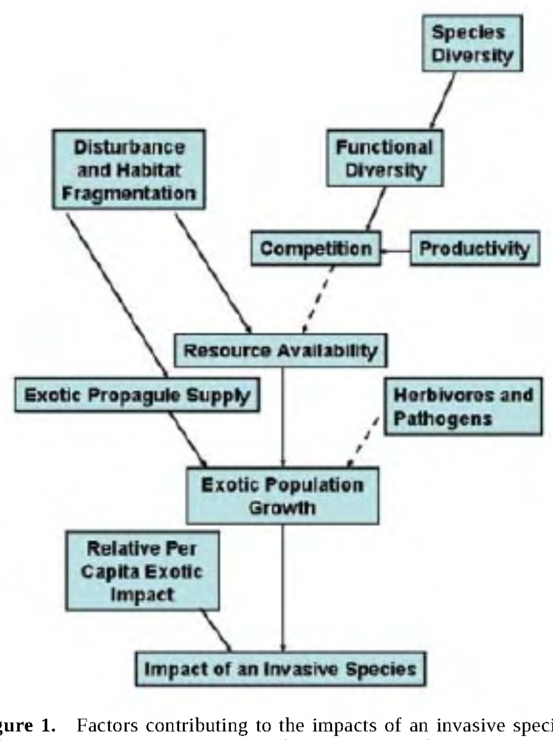

Figure 1. Factors contributing to the impacts of an invasive species. Relative *per capita* exotic impact refers to impacts of IEP species relative to those of resident species. Exotic species introducing new growth forms, functional groups or ecosystem processes are expected to have a more substantial impact than those similar to native species. Impacts of an IEP are expected to be a function of its abundance which in will be affected by resource availability, propagule supply, and natural enemies (Reprinted from Denslow and DeWalt[48]).

Table 1. Management guidelines for control of invasive exotic plants (IEP) in conservation areas

1. Vegetation and environmental surveys will help to identify priority areas for management and for monitoring IEP spread.
2. Define goals and establish benchmarks as guidance for developing IEP management strategies.
3. Identify IEP that alter ecosystem processes or change community structure; these species are high priorities as targets for control.
4. Monitor progress toward goals and periodically evaluate effectiveness of protocols.
5. Manage vegetation to promote competition with IEP and increase biotic resistance.
6. Assess the role of competition from IEP in suppressing native species to develop targets for acceptable IEP abundance.
7. Facilitate populations of native or non-invasive pioneer species to reduce dominance of IEP following disturbance.
8. Minimize impacts of novel disturbances such as trails and fence lines to reduce establishment of IEP within managed areas.
9. In forest ecosystems, promote development of native understorey vegetation to improve biotic resistance to shade-tolerant invaders.
10. Carefully evaluate exotic species used in rehabilitation and restoration projects to avoid introducing or facilitating the spread of IEP.
11. Minimize sources of seed rain on reserve margins, from large trees, and from other sources of large numbers of propagules.
12. Couple biological control with vegetation management to maximize impacts on IEP.
13. Promote healthy native herbivorous insect communities to improve biotic resistance of wildlands.

productivity, and by competition for those resources by resident species. The local diversity of species and functional groups can affect the biotic resistance of the ecosystem through competition for resources. Table 1 summarizes recommendations for managers of wildland ecosystems.

Resource availability

Resource supply is broadly controlled by local environmental conditions, such as climate, soil and substrate characteristics, vegetation cover and land forms. However, resource availability to plants is modified by competition from existing vegetation, by changes in resource supply due to biotic, abiotic and anthropogenic factors and by disturbances that reduce vegetation biomass and alter site characteristics. Fluctuations in resource availability, such as those associated with disturbance or management actions, have also been tied to ecosystem invasibility[40]. An assessment of the spatial patterns of resource availability should help managers develop strategies to regulate or modify patterns.

Resource supply is an important component of ecosystem invasibility. Sites with high resource availability and favourable environmental conditions are likely to be hot spots of exotic species establishment. Both native and exotic species are seen to respond similarly to ecological gradients in the landscape, suggesting that species-rich assemblages in resource-rich environments may be particularly vulnerable to exotic invasions[41–44]. Vegetation surveys[45,46] will help managers recognize species-rich ecosystems, areas of high resource supply and hot spots of endemicity that may be high priorities for IEP management.

Both experimental and observational studies provide examples in which the biotic resistance of native communities appears to be high[47,48]. Competition can reduce seedling establishment, growth rates and biomass of invading species; thus improvement in cover of established vegetation may be an effective deterrent to invasive plants, especially when used in combination with other methods of control. A review of biological control projects suggests that biocontrol agents are most effective when their introduction is coupled with vegetation management to increase competition from desirable species[30,31]. In grassland ecosystems this may take the form of reduced grazing pressure to allow more complete vegetation development, which, when coupled with increased herbivory pressure from biocontrol agents, effectively suppresses the target exotic species.

IEP also may preempt resources, especially light, nutrients and water, suppressing growth and regeneration of native species[5]. However, it has been difficult to document the direct impact of competition from IEP in species extinctions. For example, Sax *et al.*[49] show that IEP have doubled the floras of oceanic islands without corresponding extinctions of native species and meta-analysis by Gurevitch and Padilla[50] suggests that endangered species are more likely to be stressed by grazing from domestic livestock and from habitat alteration than from competition from IEP. In their review, Fridley *et al.*[11] conclude that this apparent paradox of the competitive impact of IEP reflects the variety of processes involved in invasive establishment and spread, the relative importance of biotic and environmental controls on species distributions and the role of spatial heterogeneity in community structure. Managers will need to understand effects of competition at the stand level to set target levels of IEP abundance.

Invasive plant species may themselves affect resource supply. The N–fixing trees, *Falcataria moluccana* and *Morella faya*, increase nitrogen supply in nutrient-poor substrates in Hawai'i, facilitating establishment of a suite of exotic understorey species[23,25]. Species with high water demand may reduce water availability to other species as well as affect groundwater levels[24]. Control of these keystone species will be a high priority for re-establishing ecosystem processes that form the environmental context for the rest of the community.

Disturbances from a variety of sources are strongly associated with ecosystem invasibility[21]. However, disturbances at a variety of scales and frequencies are characteristic of native plant communities and create opportunities for establishment for both native and exotic plants[51]. Animal burrows, river meanders, flooding, ice scouring, fire and windstorm all produce areas of reduced competition which facilitate the spread of IEP as well as the regeneration of native species. Agriculture and forestry activities and road and trail construction are frequently associated with the spread of IEP[52,53].

Whether newly available resources are pre-empted by native or invasive exotics likely depends on characteristics of plants in the seed and seedling pool. In Jamaica and Florida, for example, hurricanes facilitate the spread of exotic shrubs, vines and trees[54,55], whereas in Tonga and Puerto Rico regrowth of native vegetation dominates following typhoons[56,57]. In some forests, invasive exotic species are common in treefall clearings as in the case of *Clematis vitalba* in New Zealand[58] and *Ailanthus altissima*[59] and *Acer platanoides*[60] in northeastern US where they suppress regeneration of other species. In Singapore[61] and Hong Kong[62], canopy openings are colonized by native pioneers and exotic species do not become established easily. These patterns suggest that native pioneers may provide a degree of resilience to disturbance and resistance to the establishment of exotic species. Management and restoration of native ecosystems should promote the availability of seed and seedling stocks of native pioneer species to impede establishment of IEP in native ecosystems. Novel disturbances such as trails and fence lines should be minimized, but the importance of suitable regeneration sites for native species of management concern should be taken into account when designing management protocols.

Community restoration can play a central role in the reduction of exotic species pressures in native ecosystems especially if effective competition is increased. Historical circumstance, exploitation and habitat degradation may result in loss of functional groups. For example, forests that have been grazed for many years may lack a well-developed understorey, which provides a measure of biotic resistance to IEP. Understorey shrubs, ferns, palms and herbs strongly reduce light at ground levels, suppressing seedling establishment[63,64].

Where sites are severely degraded, or where the native flora does not provide species with appropriate traits for establishing desired ecosystem services, alien species are commonly substituted[65] . Plantations of exotic trees may provide suitable conditions for the natural reestablishment of native trees and shrubs[66] and suppress undesirable exotic species such as those fueling frequent fires. Such restoration efforts can themselves become a source of invasive species[35] and may so effectively capture the site as to exclude establishment of more desirable species. Careful consideration should be given to the functional roles played by species, their impacts on ecosystem processes, their longevity, and their ability to spread beyond the project area to avoid multiplying management needs[67].

Seed and propagule supply

High rates of seed rain can overwhelm biotic resistance even in healthy intact native ecosystems[68]. Opportunity, as measured by the length of time since a species was introduced, the frequency of introductions, and the area over which it was planted, is correlated with invasiveness in some groups such as pines[12]. In temperate forests, seed inputs from native species are shown to be critical for the capture of establishment sites[69]; similar processes are likely to be important for site capture by IEP as well. Traits associated with high rates of seed production (small seeds, short juvenile period, short intervals between large seed crops, effective dispersal syndromes) often are associated with invasiveness[12] and used to evaluate risk associated with species introductions[9,10]. Furthermore long distance dispersal is strongly associated with the speed of plant migrations and invasions[70]. Studies of the contributions of seed rain to plant population demography[71–73] suggest that IEP seed sources on forest margins, along trails, from large trees and in gaps could contribute to the spread of exotics into other forest habitats[53]. Controlling these sources of propagules will slow the advance of the invasion front and minimize the numbers of new invasion foci.

The presence of animal dispersal agents may be an important factor in the distribution of seeds in tropical forest communities. For example, Bleher and Böhning-Gaese[74] found that in South Africa, where the avian disperser community was species-rich, more *Commiphora* seeds were dispersed and for larger distances than in Madagascar where there were fewer avian dispersers. Native and exotic birds disperse seeds from both IEP and native species, contributing significantly both to the health of native plant communities and to the spread of IEP[75]. The conservation conflict is particularly acute where the native community of avian dispersers has been reduced as on some tropical oceanic islands[76] and exotic birds assume roles as significant dispersal agents for both native and exotic species. Humans, also, may be important vectors of seed and other plant propagules, for example through disposal of garden waste, feed for pack animals, introduction of invasive species on reserve boundaries and use of invasive species in restoration efforts. Identification of human-mediated pathways is often a significant step in the reduction of propagule pressure from exotic plants on wildland ecosystems.

Natural enemies

Escape from natural enemies is a frequently cited cause of invasiveness in plants[21,77,78]. Species dispersed beyond their native range escape the suite of pests and pathogens that check population growth. This observation forms the rationale behind classical biological control in which introduction of specialist herbivores and pathogens provide a measure of control for alien plant species in their introduced ranges[79]. The science and regulation of insect and pathogen introductions for release to control invasive plants has progressed substantially from the days of unfettered trial and error by ranchers and agriculturalists[79]. While the tool is not without risk of direct and indirect unintended consequences[33,80], direct non-target impacts are likely to be greatest among closely related species and are thus largely predictable and avoidable[79]. However, our ability to predict effectiveness of a new biological control agent is still rudimentary and there is much to learn about the use of biological control agents to control plants invasive in native ecosystems. Nevertheless, biological control is a promising tool for control of widespread invasive weeds in natural ecosystems. The specificity of impact avoids much of the collateral damage caused by chemical and mechanical control methods and the natural dispersal of the biocontrol agent can effect control in large, poorly accessible areas characteristic of parks and preserves. Assessments of long-term impacts of biological control releases suggest that they are most effective when coupled with vegetation management such as reduction of grazing pressure[30,31]. Our ability to manage vegetation in forested ecosystems is less straightforward than in grasslands, but in these ecosystems as well, reduction in disturbance and facilitation of growth of desirable species should be part of an integrated approach to pest management.

While biological control emphasizes the introduction of specialist pests and pathogens, the biotic resistance of ecosystems to the establishment and spread of invasive species may be a function of the health and diversity of its community of generalist herbivores[81]. The seeming resistance of many tropical forests to invasive species may be due in part to the large number of generalist herbivores, such as leaf cutter ants and orthopterans[48]. Management of native ecosystems for the health of the consumer trophic levels may improve the biotic resistance of these communities.

Conclusions

Where management is called on to control widespread invasive exotic species, eradication may not be a cost-effective objective. Rather, goals should address long-term objectives for community and ecosystem processes that reduce abundance and distribution of invasive exotic plants to acceptable levels. This is likely to involve ecosystem management and restoration in addition to IEP control. Restoration of critical functional groups, mitigation of environmental stressors where necessary, reduction in exotic sources of disturbance and elimination of propagule pressure are likely to improve biotic resistance of the native community. A monitoring programme that assesses benchmarks reflecting management goals will highlight needs for adjustments in protocol as more is learned about limits and controls to community processes.

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