
Exotic Plant Species as Problems and Solutions in Ecological Restoration: A Synthesis

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Abstract

Exotic species have become increasingly significant management problems in parks and reserves and frequently complicate restoration projects. At the same time there may be circumstances in which their removal may have unforeseen negative consequences or their use in restoration is desirable. We review the types of effects exotic species may have that are important during restoration and suggest research that could increase our ability to set realistic management goals. Their control and use may be controversial; therefore we advocate consideration of exotic species in the greater context of community structure and succession and emphasize areas where ecological research could bring insight to management dilemmas surrounding exotic species and restoration. For example, an understanding of the potential transience of exotics in a site and the role particular exotics might play in changing processes that influence the course of succession is essential to setting removal priorities and realistic management goals. Likewise, a greater understanding of the ecological role of introduced species might help to reduce controversy surrounding their purposeful use in restoration. Here we link gen-

eralizations emerging from the invasion ecology literature with practical restoration concerns, including circumstances when it is practical to use exotic species in restoration.

Key words: alien species, biological invasions, community structure, disturbance, ecological resistance, invasibility, non-indigenous species, seed banks.

Introduction

Over the past two decades invasive non-native (hereafter, exotic) organisms have come to be recognized as one of the most serious ongoing causes of species declines and native habitat degradation (Vitousek et al. 1997; Wilcove et al. 1998). For managers of parks and reserves exotic species are an ongoing threat to the persistence of native assemblages because they can consume native species, infect them with diseases to which they have no resistance, outcompete them, or alter ecosystem functions, making it difficult and expensive to return the ecosystem to its prior, often more desirable, condition (Vitousek et al. 1997). A major goal of restoration practitioners is to return a habitat to a more desirable condition involving a particular species composition, community structure, and/or set of ecosystem functions (Noss 1990).

Invasive exotic species may play a role in the restoration process in the following ways. First, their presence or dominance at the site may be part of the condition leading to the assessment that restoration is needed. In the best-case scenario restoration may be as simple as removing founding individuals of an exotic species. Second, exotic species may be the first species to recolonize after disturbances associated with removal. Third, exotic species may be the first to colonize after a planned disturbance (powerline right-of-way, pipeline corridor, etc.) even if they were not present in the pre-disturbance community and may interfere with restoration efforts or alter successional processes that would otherwise lead to a native assemblage. Fourth, they may leave behind a legacy after removal that makes long-term restoration of the site difficult or challenges management goals. This legacy may be in the form of a buried seed bank or chemical or physical alteration to the habitat. Finally, exotic species may be used by managers to restore particular functions if native species are not available. This latter situation is prevalent in reclamation projects where site conditions are badly degraded and native species may not be able to survive or cannot deliver the desired functions.

Here we consider ways in which exotic species can influence ecological restoration and some of the issues surrounding their occurrence and use. A large literature

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now exists on the ecology of plant invasions, but this literature has not been well integrated into restoration and management. Thus, one of our goals is to begin to link emerging generalizations in the field of plant invasions with restoration issues. We view this as part of a broader dialogue needed to begin developing stronger principles for restoration practitioners. Rather than exhaustively reviewing the literature, we aim to raise important issues about exotic plants in restoration settings to stimulate further research and discourse. We focus on the role of plant invaders because plants are generally an important part of restoration projects even if the target goal is an animal population.

Disturbance, Succession, and Invasion

Despite our increased acceptance of disturbance and change as fundamental to all ecological systems, the practical reality of restoration and management (i.e., limited resources, short funding cycles) has required producing particular target conditions within a short time and maintaining them for long periods. How do exotic species fit into our understanding of disturbance, succession, and ultimately restoration? Are there ways in which managers can anticipate which species will respond to disturbance and how long the responding species will persist in a community? A question fundamental to restoration practitioners is this: Can aspects of planned disturbance or exotic species removal be manipulated so as to maximize the likelihood that potentially undesirable species will not be a long-term part of the vegetation? Similarly, an understanding of the potential transience of exotics in a site and the role they might play in changing processes that influence the course of succession is essential to setting priorities and realistic goals.

Both "natural" and direct human disturbances are known to promote invasive exotic species (Hobbs & Huenneke 1992; Lozon & MacIsaac 1997; D'Antonio et al. 1999). Natural disturbances that promote invasion include small-scale ones such as rodent activity (e.g., Peart 1989; D'Antonio 1993; Schiffman 1994) and larger scale ones such as fire (e.g., Richardson 1988; Richardson et al. 1990), floods, and insect outbreaks (e.g., Peart 1989; Maron & Connors 1996). In some situations exotic species are short-lived and successional to native species (see examples in D'Antonio et al. 1999). If this can be anticipated, then little money needs to be spent on their removal in the post-disturbance environment. By contrast, many exotic species are long-lived plants or persistent annuals that set up feedbacks that perpetuate their own persistence (e.g., cheatgrass/fire cycles in the Great Basin deserts; Whisenant 1990). Their invasion represents a long-term alteration in the successional trajectory of a site. Many of these exotic species defy sim-

ple life history classification because they are both good colonizers after disturbance and persistent community members (see Cronk & Fuller 1995). Their control should be a top management priority, as should research aimed at understanding the system attributes that promote their invasion or are altered by them as they establish.

There are several reasons why disturbances will promote invasive exotic species in plant communities, and an understanding of these may provide insight into management options. Physical disruption of the soil surface and exposure of soil to light and greater temperature fluctuation can increase nitrogen mineralization. Elevated resource levels should favor fast-growing species and can lead to their invasion or increased dominance (e.g., Huenneke et al. 1990; Maron & Connors 1996). Several exotic species that take advantage of resource-rich post-disturbance environments are capable of excluding native species for many years (e.g., Hughes & Vitousek 1993; Busch 1995; Maron & Connors 1996). Disturbance often results in high soil nitrate pools (e.g., Christensen 1973; Dahlgren & Driscoll 1994; Tardiff & Stanford 1998), which can directly increase the germination of weed seeds (Baskin & Baskin 1998). Invasive non-native species often have very large persistent seed banks (Newsome & Noble 1986; Lonsdale et al. 1988; Baskin & Baskin 1998). Indeed they often maintain a much larger seed bank in their new home than where they are native (Noble 1989). Hence, even if they were uncommon in the pre-disturbance vegetation, their seeds may have accumulated in the soil over time. For example, Drake (1998) found that exotic species made up 67% of the soil seed bank in an undisturbed Hawaiian woodland even though they comprised less than 12% of the aboveground cover and less than 5% of the annual seed rain. Altered environmental conditions associated with disturbance, including elevated soil nitrate, and increased light and temperature fluctuations should promote seed germination for many species, including exotics (Baskin & Baskin 1998). Several investigators have shown that species composition after disturbance is somewhat predictable from the pre-disturbance seed bank (e.g., Smith & Kadlec 1985; van der Valk & Pederson 1989). Hence, in the case of planned disturbance, sampling of the pre-disturbance seed bank can provide insight into whether exotics might become abundant at a site. Manipulation of factors that stimulate germination may be a means of discouraging exotic species.

Aspects of the disturbance regime can be manipulated to try to promote native over exotic species. For example, if it is necessary to disturb an area of vegetation where most of the native species are fire tolerant, piling and burning the removed plant material on site may stimulate regeneration of native species from the soil seed bank while decreasing the seed bank of fire in-

tolerant exotics. Fire has been successfully used to reduce the seed bank of the exotic forb *Centaurea solstitialis* (yellow star thistle) in California (Hastings & DiTomaso 1996). However, even within fire-tolerant vegetation fire can promote exotic species. For example, on Vandenberg Air Force Base in central California controlled burning of maritime chaparral was conducted to encourage regeneration of declining endemic shrub species. One site with a listed rare plant became heavily invaded by the South African succulent *Carpobrotus edulis* (Hottentot fig) after burning (Zedler & Scheid 1988). It is now known that seeds of *C. edulis* are abundant in soils throughout this region, and although they do not survive fire well, discontinuities in fuel distribution create microsites where they do not experience killing temperatures during controlled burns (D'Antonio et al. 1993). In addition, locally abundant deer transport viable *C. edulis* seed to burned areas, and soil conditions after fire are highly conducive to growth of *C. edulis* seedlings (D'Antonio et al. 1993). These problems were not recognized until well after fire had been used to manage chaparral on the Base and *C. edulis* became abundant in all burns conducted during the 1980s (Hickson 1988). Although it can be an aggressive competitor against native species (D'Antonio & Mahall 1991), *C. edulis* is relatively easy to control if plants are removed when young. In addition, manipulation of the distribution of fuel before fire could help eliminate those microsites where seeds are otherwise not experiencing lethal temperatures. An important lesson from this is that managers must be broad thinking when considering possible responses to their planned activities and must respond quickly to surprises.

Removal of Exotics in Nature Reserves as a Restoration Practice

Managers of many reserves estimate they spend an enormous amount of their annual operating budget on control of non-indigenous species. For example, at Hawaii Volcanoes National Park, Resources Management director Tim Tunison estimates that 80% of their annual budget is spent controlling exotic species. Likewise, at Golden Gate National Recreation Area and Point Reyes National Seashore, two California parks within a Mediterranean climate region, over 60% of the Resources Management budget is spent controlling exotic species (S. Farrell, GGNRA, 1999, personal communication). More broadly, exotics pose a serious threat in at least 194 of the 368 National Park Units in the United States (NPS 1997). System-wide management plans called for more than 535 species to be managed between 1996 and 2000 at a cost of more than \$80 million dollars, but actual funding for that period allowed less than 10% of

the projects to be conducted (\$8 million available) (NPS 1997). In 1998 for those plants and animals listed under the Endangered Species Act, management costs ranged from \$32 to \$42 million annually, 90% of which was due to invasive species (Wilcove & Chen 1998).

Because funding for invasive species management efforts is typically limited, it is essential to prioritize those species and populations that are most important to control. Prioritization should be based on potential impacts of invaders and potential for control. Yet determining the potential or real impact of an exotic species is difficult, particularly if the species is new to a region and has not been well studied in similar environments. Also, pre-invasion baseline data describing the ecosystem may be unavailable (Parker et al. 1999). Lag times associated with population explosions of invasive species (Hobbs & Humphries 1995; Kowarik 1995; Crooks & Soule 1999) also complicate assessment. *Melaleuca quinquenervia* (melaleuca) and *Schinus terebinthifolius* (Brazilian pepper) were introduced to Florida in the late 1800s (Ewel 1986), but their populations did not begin to "explode" until the 1950s. Under these types of scenarios exotic species currently colonizing a natural area could potentially be disregarded until populations have exploded and removal has become more difficult. This is especially likely to occur during the early stages of an invasion in vast natural areas that are not heavily monitored (Crooks & Soule 1999). Hence, it seems vital that managers of reserves are alert for potential threats within their region and that vigilant monitoring and rapid response teams are a part of management plans.

Management plans that include removal of harmful exotic organisms are often not linked to a post-removal revegetation plan. Yet the two should go hand in hand because removal frequently results in soil disturbance and subsequent regeneration by the same or other unwanted exotic species. For example, Luken and Matimiro (1991) found that removal of *Lonicera maackii* (Amur honeysuckle) from temperate forest understory environments stimulated resprouting from basal stems and honeysuckle reestablishment from seed. The extent to which post-removal revegetation is needed depends on the biology of the invader, the spatial extent of the invasion, and the length of time the invader has been present. The longer the time the invader has been present, the more it might have contributed to the seed bank, disrupted the input of natives to the seed bank, and affected the soil so that restoration might not be easy (see Legacies under Removing Exotics: Approaches, Concerns, and Legacies, below). For example, Holmes and Cowling (1997a,b) found a stronger decline in native species richness, diversity, and abundance and an increase in the abundance of exotics in the seed bank of historically invaded compared with recently invaded fynbos vegetation in the Cape region of South Africa.

An important consideration when planning a restoration project is the condition of the surrounding region. In many countries fast-growing human populations at the edges of reserves and natural areas, in "buffer zones," and inside reserves themselves put increasing pressures on the reserve's biological resources (e.g., Meyerson 1998). Pressures include human traffic through the reserve, which increases the likelihood of exotic propagules coming in and the amount of disturbed land for their establishment; human harvesting of species within reserve boundaries; increasing isolation of the reserve from other "intact habitats"; and increasing fragmentation of the reserve itself. Sites with a history of human impact and/or sites adjacent to long-impacted areas have been shown to have a high representation of exotic species in their soil seed banks (reviewed in Luken 1997). Even natural areas without adjacent population pressures are subject to introduction of invasive "hitchhikers" both on animals that cross park boundaries and by human visitors (e.g., Chaloupka & Domm 1986; Hobbs & Huenneke 1992; Lonsdale & Lane 1994). All these pressures will affect the success of restoration. Nonetheless, it may be useful to set restoration goals based on where reserves fall on an urban to rural gradient because reserves adjacent to urban areas are likely to be heavily affected by exotic species and control or eradication of exotics may not be a financially viable option.

Management of Exotics after Planned Disturbance

Predicting species responses to disturbance has been a major focus of ecological research. Thus there is a basic literature that should be useful for predicting how both native and exotic species should respond to planned disturbances. Planned disturbances typically are different from historic disturbances. Perhaps the most significant difference is that planned disturbances often disrupt the soil profile over a large scale. Examples of disturbances that have been left to "revegetate" naturally are abundant on our landscape. In some cases, such as the eastern deciduous forests of the United States, natural regeneration after farmland abandonment has led to the widespread occurrence of forests that are largely similar (although younger) in structure to pre-disturbance forests. By contrast, in other settings anthropogenic disturbance has led to persistent weedy communities that in no way resemble those native to a region (e.g., Conn et al. 1984; Brandt & Rickard 1994; Styliniski & Allen 1999). The problem seems particularly severe in arid and semiarid habitats or highly enriched farmlands. Managers in Everglades National Park found that to restore native plant communities on a former farmland park in-holding, the highly altered enriched agricultural soils had to be removed (J. Ewel, 1999, per-

sonal communication). The environmental conditions under which severe anthropogenic disturbances revegetate readily with native species need to be explored systematically.

Planned disturbances are now often accompanied by revegetation plans that include minimizing disturbance to the soil profile and reconstruction of the soil profile after disturbance. Topsoil is frequently collected and stored, to be replaced at the surface during revegetation. Although this practice is important for restoring the native seed bank and soil microbial community, there have been few studies of storage duration. It is known that the seed bank of native species declines over time when new seed input is disrupted (e.g., Holmes & Cowling 1997a,b; van der Valk & Pederson 1989). Hence, the longer the time topsoil is stockpiled, the more likely it is that viable seeds of native species will decline. Because many harmful exotic species have persistent seed banks (e.g., Holmes 1988; Lunt 1990; Baskin & Baskin 1998; Drake 1998), it is likely that the proportional representation of exotics in the seed bank will increase with time in storage.

Can planned disturbances be designed to have negative effects on exotic species? Because disturbances typically increase resource levels and stimulate germination, it seems unlikely they can be planned to eliminate all exotics. Yet in circumstances where native and exotic species at a site are adapted to different types of disturbance, it may be possible to select against particular exotic species during restoration. The success of such approaches will be site specific, and practitioners should gather detailed information on conditions associated with their disturbances (e.g., fire temperature, moisture condition of the fuel bed) to gain a mechanistic understanding of successes and failures.

Removing Exotics: Approaches, Concerns, and Legacies

A variety of techniques can be used to remove exotic species from reserves or restoration sites. These most commonly include hand removal, mechanical removal, herbicides, fire, or some combination of the above (e.g., Masters & Nissen 1998). Biological control is practiced primarily in rangeland or agricultural settings and has not been used greatly in habitat restoration, perhaps with the exception of *Lythrum salicaria* (purple loosestrife). The technique used in a given site depends on both the biology of the species and socioeconomic, political, and cultural factors. For example, fire is used to control *Genista monspessulana* (french broom) in areas of Golden Gate National Recreation Area (California) that are distant from houses. In other sectors of the same park closer to urban lands, *Genista* is controlled using hand or mechanical removal. Herbicides are not used because of the scale of the invasions, proximity to hous-

ing, and environmental considerations (S. Farrell 1999, personal communication).

Selective manipulation of soil fertility might allow for control of some undesired species. Although application to natural areas may be difficult, this approach is potentially useful in a restoration project where the particular nutrient requirements of an invader are known. Where high N-demanding exotic species are present, several investigators have suggested the addition of sawdust or a carbon "cocktail" to decrease soil-available N (Wilson & Gerry 1995; Arthur & Wang 1999; Reeve-Morghen & Seastedt 1999). The underlying reasoning behind this idea is that labile C will stimulate microbial population growth and that increased microbial populations will then immobilize soil N. The resulting lower soil N will differentially affect the faster growing more N-demanding plant species, decreasing their competitive advantage over native species for at least a brief window of time. Wilson and Gerry (1995) and Reeve-Morghen and Seastedt (1999) demonstrated that adding carbon to soil can decrease standing mineral N pools, but neither study was able to demonstrate that this affected interactions among native and exotic species. The efficacy of this approach is currently questionable (Corbin et al. in press).

Biological control is currently being explored for several exotic plant species that affect wildland habitat value (for a review see DeLoach 1997). To date, there are very few examples of its use in wildland management except for control of rangeland and aquatic weeds. Sometimes reserves benefit from biocontrol agents released on weeds in nearby agricultural settings. For example, biocontrol agents were shown to decrease the abundance of the noxious weed *Senecio jacobaea* (tansy ragwort) in Redwoods National Park, but the agents had been released in the region for control of *S. jacobaea* on rangelands and not in the Park. Release of biocontrol agents in U.S. Parks and reserves has been controversial. Advocates of weed biological control contend there is little evidence that control agents cause unexpected damage. However, Simberloff and Stiling (1996) pointed out that only a small percentage of all biocontrol releases have been carefully studied. Rather than arguing to abandon biological control, they insist that control agents not be pronounced safe until research supports this conclusion (Simberloff & Stiling 1996). We advocate greater research in this area.

Monitoring and maintenance after invasive species removal efforts and subsequent restoration is essential but is often overlooked. Species with buried seed banks, such as *Alliaria petiolata* (garlic mustard) or *Genista monspessulana* and *Cytissus scoparius* (scotch broom), or extensive and persistent rhizomatous networks, such as *Phragmites australis* (common reed), require repeated follow-up treatment, sometimes for several years. Al-

though notoriously difficult to fund, continued maintenance may save time and resources over the long term. For example, the cost of initial treatment on a site invaded by *Tamarix* or retreatment of an invaded site not maintained can run \$675 an acre in the first year (1997 constant dollars, Lake Mead National Recreation Area, cited in Wilcove & Chen 1998). However, these costs drop to \$10 an acre in the second year and to less than \$10 an acre every 2 to 3 years thereafter (Wilcove & Chen 1998). In other cases it may be that regular maintenance of a restored site does not make financial sense. Long-term management costs should be considered on a case by case basis.

Legacies

Restoration of a site colonized by an invasive species can present a unique challenge because some species can continue to affect a system after their removal, preventing attainment of the desired restoration outcome (Cronk & Fuller 1995). Several researchers have found that exotic plant species are capable of controlling particular aspects of ecosystem biogeochemistry. For example, the invading actinorrhizal N fixer *Myrica faya* (Canary Islands faya tree) has colonized young volcanic soils in Hawaii (Vitousek et al. 1987; Vitousek & Walker 1989) where it can fix N at a rate four times as high as all other sources of fixation combined. Currently, it is being killed by an introduced leafhopper (*Sophonia rufofascia*), leaving behind a legacy of high soil N. Introduced perennial grasses that pose high fuel danger appear to be benefiting from this die-off, complicating efforts at restoration (Adler et al. 1998). Similarly, *Acacia* spp. in South Africa have been shown to fix large amounts of N, and soil N has increased significantly after their invasion (Witkowski 1991; Stock et al. 1995). Kourtev et al. (1999) reported a higher density of European earthworms in the northeastern United States beneath the exotic species *Microstegium vimineum* (Japanese stiltgrass) and *Berberis thunbergii* (Japanese barberry) and an associated increase in N-mineralization and nitrification, as well as decreased litter thickness. These factors combine to create very different soil conditions than would occur if only native species were present. The reversibility of these conditions and their impacts on restoration warrant further study.

In addition to altering N availability, exotic species can alter soil salinity (Vivrette & Muller 1977). These effects can persist long after the species have been removed and can make it difficult for native species to recolonize an area. For example, Vivrette and Muller (1977) found that the annual South African species *Mesembryanthemum crystallinum* (crystalline iceplant) concentrates salt from throughout the soil profile into trichomes on the leaf surface. Each summer after the

plants die the salt is deposited in a thick layer on the soil surface where it inhibits germination of most species. Soil salinity remains elevated long after *M. crystallinum* removal, and areas formerly dominated by this species have proven difficult to restore (D'Antonio et al. 1992).

Invasive species have also been implicated in increasing rates of soil erosion. For example, in South Africa riverbank erosion has been accelerated by several species, including *Acacia mearnsii*, *A. longifolia*, *A. saligna*, *Sesbania punicea*, and *Pinus pinaster*. These exotic species are ill adapted to the flooding regimes in the fynbos biome and so are easily ripped out by rushing waters and take mats of native vegetation with them, exposing mineral soil and increasing rates of erosion. Erosion may also be increased under introduced stands of *Pinus* spp. in South Africa that have characteristically sparse ground cover (Macdonald & Richardson 1986). In simulations of conditions in parts of the United States *Centaurea maculosa* (spotted knapweed) stands are associated with increased surface run-off and sediment yield when compared with bunchgrass-dominated sites (Lacey et al. 1989).

Restoration of sites degraded by exotic species and soil erosion pose a particular challenge. After invasion the topography may no longer resemble the pre-invasion conditions, and removal of the exotic may cause further erosion, especially if there is a lag between removal and native plant establishment. Highly degraded sites may no longer be able to support the desired species assemblages. Under these circumstances it may be necessary to take a piecemeal approach and stabilize the soil using synthetic or biodegradable materials or establish native vegetation before exotic removal. This planting could resemble the species assemblage desired when the restoration is complete or it could be an interim fallow planting that can improve site quality.

Can We Create Communities That Are Not Invasible?

Many land managers and restoration practitioners desire to create communities of native species that are resistant to further invasion by exotic species. But can they do so? Solving this problem has taken on a new urgency because recent studies suggest native species diversity and exotic species diversity are positively correlated (Planty-Tabacchi et al. 1996; Wisser et al. 1998; Levine & D'Antonio 1999; Stohlgren et al. 1999; Symstad 2000). This is in contrast to earlier theory that argued that species-poor communities are more invasible because they have less "biotic resistance" (see Levine & D'Antonio 1999). Small-scale experimental studies suggest that high native diversity can decrease vulnerability to invasion, but larger scale investigations suggest these local effects are swamped out by regional factors influencing diversity (Levine & D'Antonio 1999; Levine 2000). This

suggests that natural areas prized for high species diversity may be especially vulnerable to invasion and warrant extra vigilance against harmful invaders.

To create local-scale communities that are less prone to invasion, we need to understand which aspects of communities confer resistance to invasion and how these local-scale mechanisms translate to larger-scale management. Hobbs and Humphries (1995) referred to this as needing to understand system attributes. Despite this seemingly obvious need there have been few experimental studies of mechanisms responsible for resistance to invasion. Most arguments regarding resistance have been based on the assumption that competition is the major force determining plant community membership and that the creation of highly competitive plant assemblages should prevent further invasion (e.g., Tilman 1997). Yet native animals can facilitate invasion by their burrowing or dispersal activities (e.g., Peart 1989; D'Antonio 1993; Schiffman 1994; Simberloff & von Holle 1999; Richardson et al. 2000), suggesting that the goal of creating invasion-resistant communities at a scale above the square meter may not be realistic. In addition, abiotic factors influencing invasion success change within and among years (e.g., Myers 1983). Indeed, invasibility is a probabilistic process whereby communities exist on a dynamic continuum from more to less resistant (D'Antonio et al. 2001). Activities of native animals, natural disturbance agents, the competitive abilities of the native species, and environmental variability will influence the location of a given site along this invasibility continuum within and among years. Understanding system attributes, their contribution to invasion success or failure, and human impacts on them are an essential part of management designed to reduce invasion success.

Positive interactions among community members could also be manipulated to affect resistance. The importance of positive interactions tends to increase as abiotic conditions become more severe because neighbors can serve to buffer one another from stresses, such as desiccation, anoxic substrates caused by waterlogged soils, and high soil salinity (Bertness 1991; Callaway 1997; Pennings & Bertness 2001). The application of this knowledge in restoring severely degraded sites is readily apparent, but little work has been done manipulating positive interactions among species as a way to deter the establishment of unwanted exotic species.

Living with Exotics

Using or Accepting Exotics in Restoration

In some degraded sites it may be necessary to introduce an exotic species to assist with the restoration process.

For example, where soil erosion or the potential for it is severe many practitioners use fast-growing but sterile exotic grasses to quickly establish cover (e.g., NRC 1993). These grasses do not set seed and presumably give way to native species. However, in some circumstances it appears that seeded exotic grasses may reduce the growth of native seedlings in the critical first years after disturbance (e.g., Regelbrugge & Conrad 1990; Beyers et al. 1993). In other places where land uses such as mining or severe overgrazing have resulted in loss of soil fertility, fast-growing exotic N-fixing trees have been used to ameliorate harsh site conditions. For example, Parrotta (1992) found that an Asian N-fixing tree could grow well in degraded pastures in Puerto Rico and eventually accelerated regeneration of native rainforest. Likewise, Lugo (1988) provided observational evidence that non-indigenous trees can ameliorate harsh environmental conditions on barren sites, eventually facilitating the establishment of native tree species.

Kuusipalo et al. (1995) suggested using a fast-growing exotic species as a "sacrifice fallow" to aid in restoring degraded forest lands invaded by the large fire-enhancing native grass *Imperata cylindrica* (cogongrass) in the humid tropics of southeast Asia. Farmers prefer slash and burn cultivation of primary or secondary forests to reclaiming land invaded by *I. cylindrica*. *Imperata* creates conditions of soil compaction, nutrient deficiency, and hydrologic instability, and the susceptibility of the grass to fire prevents natural succession by destroying propagules and root symbionts. To prevent further cutting of rainforest, Kuusipalo et al. suggested planting introduced *Acacia* spp. into *Imperata* stands. The rationale behind this is that topsoil can be improved and desired woody vegetation will then be favored at the expense of more light-demanding grasses and a more heterogeneous light environment is created, favoring a higher degree of biodiversity.

If restoration of a fully functioning native assemblage is the goal of a project, then non-persistence of the exotic is also generally desirable. The extent to which this occurs in situations where exotics have been used to restore ecosystem function has not been carefully examined. In addition, the exotic species used for such restoration should themselves not be invasive or they can become problematic in surrounding areas. For example, *Robinia pseudoacacia* (black locust) has been used to establish cover and restore site fertility on mined lands (Ashby 1987; Soni et al. 1989). Yet it has also become a pest in several areas (Ashby 1987).

Although it is common to use exotic species during the revegetation of degraded lands, Ewel et al. (1999) argued that the growth potential of native species has not been fully explored enough in many such situations and research is needed in this area. For example, Skeel and Gibson (1996) demonstrated that any one of several

native grasses grow well on strip mine soils in Colorado and should be considered as viable or preferred alternatives to the non-native species that are typically planted in these sites.

In many situations it is extremely difficult to eradicate exotic species, and managers might choose instead to make the most of a bad situation. For example, fire-enhancing grasses have invaded dry forest and shrubland habitats throughout the world (D'Antonio & Vitousek 1992). In many areas they have caused an increase in fire frequency, which in turn has caused the decline of native species. These grasses are notoriously difficult to control and once established they do not readily give way to native species. In Hawaii Volcanoes National Park, more than 50% of seasonally dry habitats that support introduced grasses have been degraded by fire. Because of the enormous spatial extent of the invasion, the Resources Management Division is not trying to eradicate the grasses. Rather, they are trying to enhance the seed bank and population size of native species that can tolerate both competition from the grasses and recurrent fire. This ultimately will result in a different community than existed before fire, but one that at least supports native species (T. Tunison, personal communication, 1998).

When Removal of Exotics Threatens Native Species

In many settings exotic species have come to replace the functions formerly served by native species. Chen (2001) pointed out that control or eradication of exotic species could have undesirable effects on native species when an exotic species provides food or habitat for an imperiled or declining native. For example, because *Tamarix* spp. (salt cedar) have replaced native riparian tree species that endangered willow flycatchers use for nesting in the southwestern United States, the bird is now nesting in *Tamarix* in some areas, although its reproductive success in these areas is lower than in native riparian woodland (Dudley et al. 2000). *Tamarix* is an extremely water consumptive species that has a negative effect on native riparian diversity (Busch & Smith 1995). Weighing the benefit of *Tamarix* removal against the harm to flycatchers thus pits single species management against the larger scale issue of habitat decline associated with *Tamarix* invasion (Dudley et al. 2000).

Another example occurs in the Everglades where *Melaleuca quinquinervia* (melaleuca) is providing habitat for the imperiled snail kite (*Rostrhamus sociabilis plumbeus*). The situation is further confounded because *Melaleuca* is also rapidly invading and drying up the open marsh habitat that supports the primary food source of the snail kite, *Pomacea paladusa* (apple snail). In this case tension lies between the immediate removal of the harmful exotic *Melaleuca*, which could have immediate and di-

rect consequences for the snail kite, and not removing *Melaleuca*, which eventually will degrade the snail kite's habitat (Chen 2001). Somewhat ironically, the open water habitat of the snail kite is also threatened by introduced *Eichornia crassipes* (water hyacinth), which forms such dense infestations the bird cannot see its prey.

In some areas exotic species used in restoration have become important habitat for otherwise uncommon or declining native species. For example, Bajema et al. (2001) demonstrated that reclaimed mine grasslands dominated entirely by exotic species provide important habitat for the otherwise rare Henslow's sparrow (*Ammodramus henslowii*) in southwestern Indiana.

In other cases exotic plants are being actively encouraged to preserve native species. Chen (2001) described the case of *Leucaena leucocephala* (haole koa) in Saipan, in the northern Mariana Islands. This plant was introduced for erosion control but later encouraged as habitat for the endangered Nightingale reed-warbler (*Acrocephala lusciniia lusciniia*) because it mimicked the ephemeral wetland habitat commonly used by the nightingales. On Saipan it is considered especially desirable to maintain "artificially" high populations of the reed warbler because other islands in the Commonwealth are infested with the exotic Brown tree snake (*Boiga irregularis*), which has caused local extirpation of most native birds. The negative impacts of *Leucaena* on this island were not described.

Often exotic plant species have both positive and negative effects on native species. For example, *Mimosa pigra* is a leguminous shrub native to Central America introduced to Thailand and northern Australia (Braithwaite et al. 1989; Groves & Willis 1999). This species displaced native sedgeland that was the preferred habitat of many animal species such as the native Magpie goose (*Anseranas semipalmata*). Thickets of *M. pigra* also were found to have lower abundances of native birds and lizards, native herbaceous vegetation, and native tree seedlings. However, native frog populations were similar in invaded and uninvaded areas and the abundance of a rare marsupial "mouse" increased in *M. pigra*-dominated sites. Likewise, invasive *Tamarix*, introduced to the woodlands bordering the Finke River system in central Australia, negatively affects regeneration of *Eucalyptus camaldulensis* (river red gum) and understory vegetation and is associated with local declines of several reptiles and birds. But these same *Tamarix* stands support higher populations of insectivorous birds. These examples demonstrate the difficulty in evaluating the impacts of exotic species on native biodiversity (Groves & Willis 1999) and in prioritizing species for removal and control.

Additional difficulties regarding deciding when to remove a species center on knowing if a species or subspecies is truly not native to the site. The abundant marsh

grass *Phragmites australis* has provided a confounding situation for managers in the United States. The cause of *Phragmites* rapid spread on the Atlantic and Gulf coasts beyond its historical range has still not been determined (Chambers et al. 1999). Whether an exotic genotype of *Phragmites* has been introduced to the United States and has resulted in *Phragmites* becoming a significant invasive species in both fresh and brackish marsh systems or whether the massive increase in abundance of *Phragmites* over the past century is due to pollution and other habitat changes is still under investigation (Chambers et al. 1999; Meyerson et al. 2000; K. Saltonstall 1999, personal communication). The lack of knowledge of origin has led to debate regarding *Phragmites* eradication and the development of potential *Phragmites* biocontrol methods. Second, although researchers have found that *Phragmites* negatively impacts plant diversity in most systems (Farnsworth & Meyerson 1999; Meyerson et al. 2000), others have found that *Phragmites* has positive, negative, or benign effects on faunal species (Benoit & Askins 1999; Meyerson et al. 2000).

Will Removal of the Exotic Species Unwittingly Lead to Something Worse?

Many land managers are strongly focused on removal of seemingly harmful exotic species. After local eradication, however, there is little money left to monitor what replaces the exotic and virtually no money for follow-up seeding with native species. Alexander and D'Antonio (in press) surveyed species composition after broom control efforts in Marin County, California. Results suggest that broom removal is resulting in widespread dominance by the European grasses, many of which are persistent perennials associated with low diversity of native species. Numerous other investigators have observed that removal of exotic species can stimulate establishment of other exotics (Luken 1997), although the extent to which habitat values are worse than before management action is unclear. Managers should conduct research into this issue or collaborate with students in academic institutions to help gain insight into this potential problem.

Concluding Remarks

Preservation of native biological diversity is one of the major challenges of this century. Invasive non-indigenous species are a part of this challenge because a small but significant fraction of them contribute to the demise of native species. Even as land managers shift their focus to accommodate knowledge showing that change is fundamental to all ecological systems, modifying or accepting changes brought about by non-indigenous organisms is difficult.

The examples described here and elsewhere can contribute to the building of a framework for the consideration of invasive species in ecological restoration. For example, because we know that planned disturbance will alter resource availability in ways that can favor invasive species, managers should identify likely plant invaders and devise strategies to minimize their impacts after a management action. All planned disturbances and restoration projects should consider the surrounding landscape matrix and recognize that biotic exchange will occur with the management site. Projects need to be monitored for several years or longer to determine whether a desirable outcome has been achieved or whether further intervention is necessary. A greater understanding of how system attributes affect the likelihood of future invasions is needed so that these attributes can be manipulated to increase ecological resistance.

Researchers and practitioners must continue to integrate the knowledge gained from the various fields of ecology and related sciences with lessons learned from both successful and unsuccessful restoration efforts. In many cases it will not be possible to eradicate exotic species, and sites will require continuous management to reduce their impacts. In other cases conflicts will arise between invasive species management and protection of imperiled species, and these warrant careful scientific investigation. Although examples of these circumstances are currently limited, incidences are likely to increase. Systematic analyses that include an examination of the values upon which we base priorities for management, coupled with the probability of achieving desired goals, may help to make restoration efforts involving exotic species more practical and successful.

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