Directing Research to Reduce the Impacts of Nonindigenous Species

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Abstract: *Management of nonindigenous species is a crucial aspect of maintaining native biodiversity and normal ecosystem functions. We attempt to guide researchers in developing projects that will be of use to conservation practitioners, tangibly improving applied conservation measures. We advocate a directed approach for conservation research to aid in prioritizing nonindigenous species for intervention by resource managers. This approach includes outlining what needs to be known to make such relative judgments about the impacts of nonindigenous species and the most promising methods by which to obtain such information. We also address active measures that should be taken once priorities have been set, highlighting the roles of risk assessment and research in improving control efforts. Ultimately, a better match between research and practical conservation needs should result in more effective reduction of the effects of nonindigenous species on native species.*

Dirección de la Investigación para Reducir los Efectos de Especies Exóticas

Resumen: *El manejo de especies exóticas es un aspecto crucial para el mantenimiento de la biodiversidad nativa y de las funciones normales de un ecosistema. Intentamos guiar a los investigadores para desarrollar proyectos que serían de uso para los practicantes de la conservación, mejorando tangiblemente las medidas de conservación aplicada. Apoyamos una estrategia dirigida de investigación para la conservación para ayudar a priorizar especies exóticas para la intervención de los manejadores de recursos. Esta estrategia incluye delinear lo que se necesita saber para hacer juicios relativos sobre los impactos de especies exóticas y los métodos más promisorios para obtener dicha información. También nos abocamos a las medidas activas que deberían ser tomadas una vez que se establezcan las prioridades, subrayando los papeles de la evaluación de riesgo y la investigación para mejorar los esfuerzos de control. A fin de cuentas, la mejor conjun-*

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ción de la investigación con las necesidades de conservación práctica debe resultar en una reducción más efectiva de los efectos de las especies exóticas sobre las especies nativas.

Introduction

The effects of invasive nonindigenous species on native species and ecosystems have become one of the world's most serious conservation issues (Walker & Steffen 1997; Wilcove et al. 1998). The detrimental impacts of nonindigenous species are likely to increase as international trade in plants and animals increases and as climate and land use continue to change (Office of Technology Assessment 1993). Due to the potential for nonindigenous species to negatively affect populations, communities, and ecosystems of native species, failure to take steps to prevent new invasions and inaction or slow response to the discovery of a newly established nonindigenous species are implicit management decisions in their own right. The desire to respond effectively has prompted governments to call for improved strategies for reducing nonindigenous species impacts at national, regional, and local levels (e.g., Commonwealth of Australia 1997; U. S. Executive Office 1999). To succeed, however, these strategies require a sound base of information on the spread, ecological effects, and control of nonindigenous species. Some important theory about invasions has been developed, and there are abundant data on a growing number of individual case studies, but further research is required to satisfactorily address the need for integrated strategies. Gaps between ecological theory and the practical needs of conservationists, land managers, planners, and public policymakers have resulted in an inability to address critical problems caused by invasive nonindigenous species. For example, although several published studies existed on the ecology of the zebra mussel (*Dreissena polymorpha*) before its proliferation in North America, U.S. and Canadian conservation managers lacked the capacity to predict, much less control, the species' spread (Ricciardi et al. 1998; Strayer et al. 1999). The information that existed was either insufficient, inaccessible, or not in a digestible form for resource managers to utilize readily.

We outline and identify research questions that, if answered, would help bridge the gap between basic ecology and its application to nonindigenous species problems. We have set important research questions within a framework that aims to prioritize nonindigenous species for management or policy actions (e.g., control, removal, prevention). Because monetary resources are always limiting, managers must routinely decide which populations and species to control immediately, which to control if time and money permit, and which to leave alone (Hiebert 1997). In the first section, we address a fundamental, two-part question: what do we need to know to enable this prioritization, and how do we best obtain the needed information? In the second section, we discuss research that can continue after priorities are set. Table 1 outlines important research issues that pertain to these areas and contains suggestions on studies and data needed to address each. This paper is not a comprehensive review, but rather an outline of what would be most useful for conservationists to know and research that may most effectively yield this knowledge.

We recognize that each invasion will have a certain degree of specificity, but generalities are emerging (Reichard & Hamilton 1997; Lonsdale 1999; Stohlgren et al. 1999), yielding encouraging insight into how invasions operate and how they may be best addressed by conservation managers and policymakers. Although complicated by economic, social, and political concerns, nonindigenous species policy decisions must also be based on clear, scientific reasoning.

What to Know to Enable Prioritization

Quantification of Nonindigenous Species Impact

Although immense ecological problems result from the introduction of some invasive species, as many as 80–90% of established nonindigenous species may actually have minimal detectable effects (Williamson 1996). Many natural areas already contain far more nonindigenous species than their managers can control, so managers must set priorities for the control, prevention, or containment of only a fraction of the non-native species they face. Distinguishing nonindigenous species with negligible effects from those that cause significant damage to native biodiversity would allow conservation workers to direct attention and resources to the most important concerns, thereby maximizing protection of native systems. Unfortunately, there is little published quantitative information on the effects of most nonindigenous species on native biota and ecosystem functioning, so priorities often have to be based on anecdotal information or subjective assessments (Parker et al. 1999). Furthermore, because positive results are more likely to be submitted and published, the invasion literature may be biased toward demonstrating that nonindigenous species have large ecological impacts (Simberloff 1981, 1986). Earlier studies of invasive species acknowledged

Table 1. Key research questions posed to effectively prioritize and manage nonindigenous species and the data required to address each.

Research question or issue	*Types of studies or data required*
Why do many invasions fail or have minimal effects? Is timing important? Is success of some invasions contingent on historical factors?	analysis of total numbers of propagules introduced (e.g., volume of ballast water or number of biocontrol agents released at a site vs. successful establishment)
	quantification of propagule transport via various vectors; pathway analyses
	mechanistic field experiments on established nonindigenous species that are decreasing or not increasing in spatial extent or density
	publishing negative results (e.g., Hairston et al. 1999; Otto et al. 1999; Treberg & Husband 1999)
Indirect effects of nonindigenous species that alter ecosystem properties	measurements of abiotic properties of carefully paired uninvaded and invaded sites
	euclidean distance and similar multivariate analyses (e.g., principal components analysis, multiple regression, multidimensional scaling) of changes to community composition and structure following invasion
	manipulative experiments to measure effects on processes or system properties such as fire frequency and intensity, nutrient cycling, and soil chemistry
Characterization of areas experiencing greatest impact of an invasive plant or animal	study of changes in landscapes, ecosystems, and communities, including details of geography, climate, geology, soil, site stability, fire history, and competitors or predators in areas of greatest and least impact
Assessing the impact of a particular invasive plant or animal	determination of possible ways the invasive species interact with native species, including competition for nutrients, water or light (plants); competition for food, shelter or nesting sites (animals); predator-prey relationships, parasite-host relationships, etc.
	empirical data to assess the importance of each of these linkages or pathways; where appropriate, use of time-lapse photography
	population/demographic studies to assess effects of nonindigenous species on abundance, reproduction, etc., of native species
	time-series data for many species within recipient community to determine whether any may be used as a bioindicator of impending impact from an established nonindigenous species
What follows invasion by nonindigenous plants or animals?	time-series data on the abundance of each resident species, especially those most suspected to interact with the nonindigenous species following its establishment
	experiments to separate direct and indirect effects
	more long-term ecological research data
	development and incorporation of remote-sensing techniques
What limits the spread of nonindigenous species? (or smaller-scale question of why invasions fail)	landscape-level evaluation of geography, climate, geology, soil, site stability, fire history, and competitors or predators at stable and moving boundaries of the invasive species
	experiments at habitat boundaries and edges of distributions
What occurs between establishment and recognition of invasive status? change in genotypes biotic alteration of the environment	analysis of average time between nonindigenous species establishment and spread
	sampling of herbarium and museum specimens for rate or occurrence of genetic changes in populations of nonindigenous species, especially those long established
	sampling along cline in native and introduced range to look for genetic changes in populations (Huey et al. 2000)
	modeling of the population dynamics of nonindigenous species, including climate data to determine whether climatic shifts, extremes, or catastrophes have favored particular groups of invasive species
What determines vulnerability to invasion in particular habitats?	quantitative description and multivariate analysis of biological and physical characteristics of habitat vs. abundance or impact of nonindigenous species
Which characteristics of a species reflect its ability to invade and damage native biodiversity?	discriminant analyses and post hoc tests of successful and unsuccessful nonindigenous species to identify traits of successful invaders
	post-release research on biological control agents: which ones become established, which ones fail, which have an impact and which do not
How can rapid assessment of potential harm for newly detected species be improved?	better information systems to allow evaluation of species and control possibilities
	assessment of harmful species not currently in the country
	protocols for monitoring and adaptive management of new invasions and control efforts

continued

Table 1. (continued)

Research question or issue	*Types of studies or data required*
What control strategies are most effective?	life-history and demographic models and key factor analyses to identify the most influential aspects of a species' population increase field trials of prevention and control techniques testing of site designs and placement that most reduce invasibility
What events follow the control or eradication of an invasive species?	identification of major species colonizing sites after invasive species have been eliminated mechanistic studies to determine when post-invasion restoration does or doesn't work, and why monitor responses of species, community, system processes, and biodiversity after application of control measures quantification of effects of biocontrol agents on the targeted pest and on nontarget species, especially for releases to control insects and arthropods

that better data on failed introductions were required to distinguish these from successful invasions (Simberloff 1989; Mack 1996). Similarly, better information on low-impact invasive species will help identify characteristics that set high-impact nonindigenous species apart, giving us greater understanding of the relative harm a new introduction may cause.

Just as not all nonindigenous species have large effects, one invader may have large effects in some areas and negligible ones in others. For example, rats can be devastating to native birds on oceanic islands, but have far less effect on islands with indigenous rats or land crabs, presumably because of selection to avoid predation (Atkinson 1985). Because managers often lack the resources to control a nonindigenous species everywhere it has invaded, they must often determine which sites, or portions of sites, are most threatened or of highest value. Studies are needed that contribute to a general understanding of what controls variation in the impact of a single nonindigenous species.

Some non-native species are capable of altering the normal functioning of ecosystems or the interactions of organisms even in relatively small numbers. Species that affect system-level processes may in turn facilitate the invasion of additional species (Simberloff & Von Holle 1999). Some known examples of such "ecosystem engineers" include *Tamarix ramossissima* (saltcedar), which reduces water available to other species that grow in the same southwestern ecosystems (Sala et al. 1996), and *Myrica faya*, a nitrogen-fixing tree that alters succession on lava flows by sharply increasing available nitrogen (Vitousek et al. 1987). Although some case studies exist, it is of the highest priority to identify ecosystem engineers and expose the mechanisms through which they alter the normal functioning of natural systems and disproportionately affect native biota.

Spread

Successful nonindigenous species frequently exhibit a lag phase, during which the population persists in low numbers in a fixed area before rapidly increasing its population growth rate and invading nearby areas (Miller & Lonsdale 1987; Kowarik 1995; Shigesada & Kawasaki 1997; Crooks & Soulé 1999). Typically the best opportunity for control or reduction of impact of a nonindigenous species is during the lag or early spread before it occupies a large area or achieves large densities. Managers, however, do not want to waste time controlling species that are never likely to expand or become troublesome. There are many fertile areas for research on the dynamics of invasion lag phases. Most fundamentally, it is not clear whether lag phases are real or simply the perceived result of our failure to note the beginnings of exponential increase (Cousens & Mortimer 1995). More-frequent monitoring would help distinguish lag phases from the null models of exponential population growth or squared areal expansion. Do lag phases of nonindigenous species vary between ecosystems; if so, how and why? Are there general early indicators that could signal when a particular species is a latent pest? Are lag phases found equally across taxonomic or functional groups, or are some more likely to demonstrate lags?

Conservation managers often use information about current and anticipated distributions to set priorities for control. Species whose ranges are increasing rapidly are of greater concern than those whose ranges are stable (Forcella 1985). If a species is increasing rapidly, early attempts to control it will likely result in lower ultimate costs than if control is delayed (Higgins et al. 2000; Zavaleta 2000). What biotic and abiotic conditions promote rapid spread? Examples in which the agent of spread is known include the rooting activity of introduced pigs, which can be an important dispersal vector for nonindigenous plants (Vitousek 1986) and pollinators that increase the reproductive success and population growth rates of *Cytisus scoparius* (Parker 1996). Similarly, some land-use and management actions may increase the rate of spread of nonindigenous species. For example, *Acacia nilotica* was a fairly benign shade and forage tree in northern Australia under sheep grazing, but became a major invasive weed following a change to cattle grazing, probably because of enhanced dispersal of seeds by cattle (Parsons & Cuthbertson 1992). If managers are aware of such side effects, they can seek alternative actions or at least, in anticipation, develop ways to mitigate the effects of actions that cannot be avoided.

In addition to determining the factors that influence the abundance, biomass, or impact of nonindigenous species within their introduced ranges, special attention should be granted to the role of these factors at the edge of species' ranges (i.e., the front of the invasion). Knowing what factors limit the persistence of a nonindigenous species outside a particular range could enable mangers to simulate the conditions that control the species' range. Differences in climate or local abiotic and biotic factors may be responsible for impeding the range extension of a particular invasive species. The importance of range-setting factors can be tested experimentally or by carefully planned comparisons between sites where the invasive-species boundary is moving rapidly and those where the species is stable or spreading slowly. Simple habitat matching to predict the potential ranges of species that are already present or proposed for introduction can provide a useful starting point (Patterson 1996; Baker et al. 2000; Walther 2000; Kriticos & Randall 2001). Kriticos and Randall (2001) found that climate data for an nonindigenous species in its non-native habitat provides better information on its ultimate distribution in a second invaded area than does climate data from its native habitat. They hypothesize that native predators and dispersal barriers may limit species' distributions in the native range and that the species' true potential range is better expressed in a region that also lacks those factors.

Patterns of Abundance

Some species exhibit complex population dynamics during the invasion process, initially climbing to high densities and then settling into a lower equilibrium (Freeland 1986; Mutlu et al. 1994; Williamson 1996). It would be useful to know whether some species are more likely to show such an abundance trajectory, what causes the slowing or decrease in numbers, and what limits the final abundance of the invasive species. For example, does the nonindigenous species simply overshoot its carrying capacity and exhaust its resources, does it come under control of a pathogen due to a host shift, or do predators switch as the nonindigenous species reaches high density, thereby reducing its numbers? Invasions in which large effects are short-lived might be given lower priority than those with serious long-term consequences. For example, an early successional nonindigenous species that does not alter the ultimate course of succession is less of a threat. Long-term studies of invasions, particularly in areas where control is not possible, will boost our understanding of the dynamics and ultimate effects of nonindigenous species in this context. Epidemiology may provide useful theory and models applicable to the patterns and rates of spread of macroscopic nonindigenous species (Mack et al. 2000).

System Invasibility

One of the key summations of the SCOPE program (Drake et al. 1989) was that site characteristics within a habitat, region, or ecological system may aid or hinder invasion. Large-scale patterns of "invasibility" of natural areas have helped identify emergent properties of nonindigenous species and commonly invaded habitat types (Crawley 1987; Lonsdale 1999; Stohlgren et al. 1999), which in turn can sharpen early detection efforts. Studies should investigate more than simply the number of invading species, because substantial impacts can arise from a single non-indigenous species. The overall and relative abundance of nonindigenous species should be used as additional measures to account for the pervasiveness of nonindigenous species (e.g., Stohlgren et al. 1999). Of course, the predictive power of these approaches depends on there being little or no change in the physical or biotic environment. The accuracy of predictions for areas that are undergoing rapid and major changes, such as habitat destruction, global warming, or high-impact biological invasions, may drop quickly with time. The effects of natural and anthropogenic disturbance, native-species composition, extreme climatic events, and resource availability on the invasibility of the ecosystem or community are key research issues (Vitousek 1990; Crawley et al. 1999; Simberloff & Von Holle 1999; Smith & Knapp 1999; Stachowicz et al. 1999; Stohlgren et al. 1999). Knowledge of factors that fortify the resistance of communities to invasion could lead to effective management techniques.

Such research could also help conservation planners design and locate reserves more likely to resist invasion. Current theory predicts, for example, that reserves having a high ratio of perimeter to interior are highly vulnerable to invasion (Timmins & Williams 1991; Harrison 1997; Rose 1997). In the Coast Ranges of California, small patches of serpentine soil have a higher diversity of nonindigenous plant species than do large, continuous serpentine areas, a pattern ostensibly caused by higher rates of dispersal into small patches (Harrison 1997). Similarly, uses of adjacent land could influence the proximity of source populations for invasive species. Spatial factors such as proximity to towns, streams, roads, and trails on the site increase invasion incidence (Timmins & Williams 1991; Pyšek & Prach 1994; Thompson 1999). Perhaps, however, preserves that are isolated from other natural or seminatural areas by urban or agricultural development may be better protected from certain nonindigenous species, especially invasive diseases, simply because these nonindigenous species are unable to cross the developed areas (Hess 1994). These ideas about invasibility have yet to be rigorously tested in the context of reserve design and siting.

Impact Thresholds

Conservation workers are particularly interested in uncovering thresholds of abundance of particular nonindigenous species beyond which control of the nonindigenous species or recovery of native biota is not practical. Conversely, we need to know the level at which a nonindigenous species should be maintained to minimize its impact on the native community. It is sometimes assumed that the impacts of a given nonindigenous species correlate closely with its abundance in an area, but this may not be true for all species, especially below some threshold abundance. Characterization of the relationship between impact and abundance for a wide array of nonindigenous species and systems would help conservation managers rank nonindigenous species for control and prioritize specific areas for management.

Obtaining Knowledge for Prioritization

Experimental Studies of Interactions between Nonindigenous Species and Native Communities

Developing rigorous approaches for predicting the effects of nonindigenous species requires a more quantitative and experimental assessment of the impacts of established nonindigenous species (Settle & Wilson 1990; Petren & Case 1996; Juliano 1998; Byers 2000). Knowledge gained from assessment of current invasions can also be synthesized to derive testable generalizations about how to predict and mitigate the effects of new nonindigenous species. Ultimately, we need to predict these effects at multiple scales, including the site, region, nation, and continent because management planning and implementation occur at all levels and the impacts of species vary between sites and among regions. Data on the effects of nonindigenous species may be effectively shared and communicated through an internet registry and search engine (Ricciardi et al. 2000).

The effects of invasive species include those on individuals (e.g., reduced growth or reproduction); population size, structure, or genetic composition (e.g., extinction); community composition and structure; and ecosystem processes (e.g., nutrient cycling). Unfortunately, much of the research reporting detrimental effects is based on observational and/or correlative methods and does not clearly demonstrate that the nonindigenous species was responsible for the observed effects (Parker & Reichard 1998). Some of the logical and statistical difficulties of comparative studies can be circumvented with techniques such as modified Before-After-Control-Impact (BACI) designs (e.g., Underwood 1994). The accumulation of nonindigenous species data may eventually allow formal meta-analyses of invasion impacts, which could help with prioritization of problematic taxa. Given that nonindigenous species come from all taxa and trophic levels, quantification of effects should allow comparison between different taxa and trophic levels to aid the process of prioritization.

Another way to evaluate the effects of nonindigenous species within different systems is to develop consistent bioindicators of ecosystem health. Bioindicator species are presently used to measure the impacts of pollution, fire, and mining (e.g., Andersen & Sparling 1997) and perhaps could also be used to gauge the effects of invasive species. Carefully selected bioindicators have an intuitive appeal because they can integrate responses to stress of members of the invaded community at different trophic levels.

Study of Nonindigenous Species History and Related Species

In addition to studies that examine a nonindigenous species in its present context, studies of the past dynamics of a nonindigenous species or studies of a related species in the present may be useful alternatives (Thebaud et al. 1996; Pyšek 1998; Radford & Cousens 2000). Although each invasion is at least somewhat idiosyncratic, the behavior of an introduced species is often similar in multiple invasions (Reichard & Hamilton 1997). In addition, the inherent ability of a species to invade may correlate with phylogeny or phenotypic traits, and the search for trends is an important post hoc analysis of previous invasions. To predict which nonindigenous species are likely to have an impact, research that seeks to identify characteristic traits of successful and damaging nonindigenous species is a top priority (Rejmánek & Richardson 1996; Reichard & Hamilton 1997). As an example of how difficult this can be, however, biological control workers have been trying for approximately a century to predict (and intentionally produce) the effects of nonindigenous species on a target species, yet have managed at best a 30% success rate (Crawley 1989; Sheppard 1992; Williamson 1996).

Modeling

Ecological models can improve our understanding of the population dynamics of an nonindigenous species or how best to control it. Demographically based matrix models have been used by conservation managers to explore the consequences of management options for rare or endangered species (e.g., Crouse et al. 1987). In a similar manner, sensitivity analyses of matrix and other population models are being used increasingly to evaluate the contribution of different life stages and various biotic interactions to population growth, and to identify key factors that could be manipulated to reduce the viability of a nonindigenous species (Lonsdale et al. 1995; Rees & Paynter 1997; Shea & Kelly 1998; Courchamp & Sugihara 1999; McEvoy & Coombs 1999; Parker 2000; Byers & Goldwasser 2001). Also, a few spatially explicit, large-scale models have successfully evaluated specific control strategies by which to limit the spread of nonindigenous species (Higgins et al. 2000; Wadsworth et al. 2000).

Few nonindigenous species population models incorporate interactions with native species, but they may provide useful insight. For example, Byers and Goldwasser (2001) isolated and evaluated life-history attributes of a native and an introduced estuarine snail. Their model identifies differential parasitism and exploitative competition as important advantages for the nonindigenous species. But the low mortality rate of the nonindigenous snail compared with that of the native snail was most responsible for its invasion success. The model therefore informs management strategies by demonstrating that manipulating parasites or the density of food resources are less effective means by which to mitigate the impact of the nonindigenous species than simply manipulating mortality. Although creating such a model can be time-consuming and complex, it may be one of the most effective tools with which to aid intervention efforts by exposing the mechanism(s) of success of a particular nonindigenous species.

Models can also help us evaluate and design monitoring programs. In their model, Byers and Goldwasser evaluated several different monitoring metrics within a biological monitoring framework to try to detect the impending extinction of the native snail. None of the monitored metrics reflected significant change until at least 20 years after the invasion, suggesting that our accepted monitoring practices may be inadequate to detect effects early enough within a problematic invasion.

Remote Sensing and the Geographic Information System

Despite the urgent need for better methods with which to detect incipient invasions and the spread of established species, it is unlikely that we will ever have all the trained personnel needed to perform adequate ground surveys across large areas. Particularly for conspicuous, sedentary species, however, it may be possible to detect infestations and their patterns of spread by satellite remote sensing, aerial photography, hyperspectral imagery, or other spatial-information technologies (Anderson et al. 1993; Carson et al. 1995; Everitt et al. 1995, 1996; Birdsall et al. 1997). Even if a species is not visible from satellite images, community types invaded by the species may be. The communities can then be inspected (Dewey et al. 1991). These methods of early detection deserve considerable research effort as valuable tools for detecting and tracking nonindigenous species.

Acting Effectively Once Priorities are Set

Research to Improve Control of Harmful Nonindigenous Species

Once targets are chosen, managers need to know how best to allocate resources to the strategies of exclusion, early detection, eradication, monitoring, and control of nonindigenous species (Myers et al. 2000). Although control is often viewed as a highly applied issue, research relevant to controlling invasive species may also make fundamental contributions to our understanding of population ecology. An excellent example of this is biocontrol. Research on biocontrol releases has long been used to test and model theories in basic ecology and invasion biology (e.g., Levins 1969; Murdoch et al. 1984). Biocontrol studies could be used even more extensively to address the establishment, spread, and impact of invasive species, principally by expanding the scope of research beyond simply how much they damage the target species of interest. For example, studies of biological control agents can provide data on how introduced species spread through time, switch to other hosts or prey, or interact with other species within native communities.

Culling or physically removing nonindigenous species is one of the more common techniques for their control, but it is labor-intensive, costly, and often ineffective. Managers need to know if such techniques are truly the most effective means of not only controlling a nonindigenous species, but ultimately protecting native biodiversity. In some cases, mitigation measures for an invaded ecosystem may be worse than the problem (Arnold et al. 1998; Pickart et al. 1998). We have little information on the effects of nonindigenous species themselves, but we have even less information about the effects of control efforts on the communities and species we are attempting to protect. These effects should be examined over different time scales, because acute and chronic effects may differ.

Innovations are needed that make controlling invasive species faster or more efficient and less damaging to desirable species. Many areas of ecological and physiological research may yield ideas for improving control methods. One such area is the study of seasonal changes in vulnerability to pesticides, fire, or other control methods. For example, a major weed of coastal Australia, the introduced shrub bitou bush (*Chrysanthemoides monilifera*), is vulnerable to low concentrations of herbicide at a time of year when the native vegetation is dormant (Toth et al. 1996). Changes in land use may retard or facilitate invasion, and control might therefore be possible through indirect pathways (Vitousek et al. 1997). Population models of nonindigenous species, discussed above, can be used to simulate and test the efficacy of various control strategies.

If a species is controlled or eradicated, can we be certain that its removal will actually benefit native species? What steps need to be taken to restore the site? Some nonindigenous species have integrated themselves into the local food web, and their removal may harm native species that have become dependent on them. In San Francisco Bay, for example, the Asian clam (*Potamocorbula amurensis*) is now a major food source for native crab and duck species (Carlton et al. 1990). In several cases, removal of nonindigenous species without full consideration of ecological ramifications has led to increased problems with other nonindigenous species that merely fill the created space (Groves 1989). Or, rapid removal can represent a problem for native species that have started using the nonindigenous species as habitat, such as monarch butterflies on *Eucalyptus* trees in California (Westman 1990).

Because management is monetarily limited, the most useful studies on impact might be those that evaluate the relative ease and expense of control strategies to reduce the waste of human and financial resources on futile control efforts. For example, cheatgrass has invaded a vast area of western North America and has had severe effects, but managers often give it low priority for control because it is deemed too difficult to eradicate (Mack 1986; Roberts 1991). Similarly, San Francisco Bay, where nonindigenous species comprise up to 99% of the biomass in certain areas (Cohen & Carlton 1998), may be impossible to restore to its native state. It is therefore a sink for limited resources, although controlling nonindigenous species may be important for other reasons, such as reducing the potential for introductions to neighboring water bodies.

Risk Assessment

Ecological theory alone cannot evaluate the quality of information available to decision-makers, synthesize information, or weigh the relative costs of control options. Policymakers should borrow decision-making tools from other disciplines and should use appropriate methodologies to compare and test these tools (e.g., Office of Technology Assessment 1993; Smith et al. 1999; Lonsdale & Smith 2001). Risk analysis and cost/benefit analysis could be usefully employed to answer questions such as which invasive species should be controlled first, and whether money should be spent to control these weeds or build a buffer zone.

Research into risk assessment will not result in the fail-safe screening of individual nonindigenous species, but it may lead to an overall reduction in the number of newly establishing nonindigenous species that cause significant harm. Risk assessment is a decision tool, usually employed when there is a small chance of a potentially catastrophic event occurring as a byproduct of implementing a new technology or process. Typically it is the first step to identifying measures to minimize the risk at each stage of the process in question.

For biological invasions these stages may include (1) arrival (risk analysis of pathways), (2) establishment (risk of the organism forming viable, reproducing populations), (3) spread (risk of the organism expanding its extent), and (4) impact (risk the species having a measurable effect on existing species or communities). The "tens rule" (Williamson 1996) estimates that 10% (between 5% and 20%) of imported species will make the transition from one stage to the next. But this rule provides only a rough guideline; better knowledge of actual transition probabilities could benefit conservation managers by elucidating whether they are consistent across taxonomic or functional groups, enabling more vigilance over highly invasive ones. Comparing these rates would help us assess whether, for example, plants intentionally introduced for horticulture are more or less likely to invade and become established than are plants accidentally imported into a given region (Williamson & Fitter 1996). Although progress has been made in the assessment of risk for the first three pathways listed (Ruesink et al. 1995; Rejmánek & Richardson 1996; Reichard & Hamilton 1997), the risk of impacts from nonindigenous species has not often been rigorously assessed (Parker et al. 1999); thus extending risk assessment could lead to new insights.

Conclusions

Experimentation with and management of invasive species can be advanced by partnerships between researchers, planners, and conservation managers. Time and resource constraints often limit the ability of conservation managers to participate in day-to-day research activities. However, managers can identify questions most important to their conservation efforts, indicate sites of crucial conservation concern, and provide essential information about these sites and their current and historical management. Direct scientific feedback from researchers will hasten the progress of adaptive management (Walters & Holling 1990; Randall 1996).

Research is needed to measure the costs associated with different control strategies and with immediate, delayed, or no reaction to the presence of invasive species. This requires knowledge of how nonindigenous species affect native biodiversity—specifically, which species have high impact and which have low impact in particular areas. Research that quantifies effects using metrics other than presence or abundance alone is therefore central to this endeavor. Research designed to integrate control methods and measure the effects of control on the target and nontarget species is also vital. Studies on the variation of ecosystems in terms of probability of invasion and on lag phases between the establishment and extensive spread of invasive species (Smith et al. 1999) are useful for prioritizing ecosystems at risk. Risk assessment, decision theory, and epidemiology all offer useful insights for the development of policies to control nonindigenous species through a process involving scientists and policy makers.

Conservation managers and quarantine officials are on the front line in the struggle against nonindigenous species and are now racing against time as the damage from established nonindigenous species mounts and new invaders continue to arrive. Much useful knowledge of nonindigenous species already exists—it merely requires reanalysis or reassembly into a form that managers can use. Many of those doing research on nonindigenous species intend their work to inform conservation efforts and protection of native species. In designing research on invasive species, researchers should therefore consider carefully how to best organize and present their data to address the critical conservation challenges faced by resource managers.

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