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Deliberate Introductions of Species: Research Needs

Benefits can be reaped, but risks are high

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The silent invasion of Hawaii by insects, disease organisms, snakes, weeds and other pests is the single greatest threat to Hawaii's economy and natural environment.... Even one new pest—like the brown tree snake—could forever change the character of our islands. (Coordinating Group on Alien Pest Species 1996, p. 1)

Reforestation in the tropics is so vastly behind deforestation that we cannot wait to fully appraise all the potential negative elements of domestication. Weediness is of consequence perhaps in Honolulu, but not in Addis or Delhi. (James Brewbaker, quoted by Hughes 1994, p. 244)

Introductions of nonindigenous organisms can be both a boon and a bane to society. Humans depend heavily on non-native organisms for food, shelter, medicine, ecosystem services, aesthetic enjoyment, and cultural identity. Over 70% of the world's food comes from just nine crops (wheat, maize, rice, potato, barley, cassava, soybean, sugar cane, and oats; Sattaur 1989, Prescott-Allen and Prescott-Allen 1990), each of which is cultivated far beyond its natural range. Similarly, 85% of industrial forestry plantations are established with species of just three genera (*Eucalyptus*, *Pinus*, and *Tectona*), which are also largely cultivated as exotics (Evans 1992). Thus, although native organisms fulfill some human requirements, non-native organisms play an integral role in the economies and cultures of all regions (Figure 1). In New Zealand, for example, more than 95% of export earnings derives from alien species (New Zealand Department of Statistics 1996).

Most proponents of purposeful introductions understand the risks, and most conservation biologists recognize the potential benefits to be derived from carefully controlled introductions

Escalating human population growth and improved transcontinental transport have led to skyrocket-

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Figure 1. A universally welcomed introduction. The coconut palm, *Cocos nucifera*, is a widely introduced species now found on tropical beaches everywhere, such as this one in Hawaii. Although it probably originated in Melanesia (Purseglove 1985), it was rapidly moved throughout the tropics by mariners and farmers and has become widely naturalized. Now found all over the globe, the coconut palm provides a host of products that support subsistence economies on Pacific atolls, agroindustries in the Philippines, and international tourism in the Caribbean. Photo: Jack Jeffrey.

ing rates and increasing scales of movement of nonindigenous organisms. The once slow, erratic, and small-scale transfer of species has shifted to a rapid and large-scale translocation of large numbers and great species diversity; pathways for inadvertent transfer have also multiplied. Several examples underscore the scale and taxonomic scope of these movements: North American seed and nursery catalogues offer over 59,000 plant species and varieties for sale to national and international markets (Isaacson 1996); the rate of invasions in San Francisco Bay has accelerated from an average of one new species established every 55 weeks during the period 1851–1960 to one new species every 14 weeks during the period 1961–1995 (Cohen and Carlton 1998); and microbial pathogens, mostly viruses and viruslike organisms, accompanied more than half of the apple and potato accessions inspected in quarantine in the United States between 1985 and 1994 (White and Waterworth 1996).

Despite the many benefits provided by non-native organisms, the increasing rate of naturalization and spread (i.e., of invasions) of species introduced both deliberately and accidentally poses an increasing global threat to native biodiversity, one ranked second only to habitat loss (Vitousek et al. 1996, Wilcove et al. 1998). A small proportion of introduced organisms, representing many taxonomic groups, has had significant negative economic and environmental impacts (e.g., OTA 1993). These impacts include crop failures, altered functioning of natural ecosystems, and species extinctions (Figure 2). In just 1 year, the impact of the introduced golden apple snail (*Pomacea canaliculata*) on rice cost the Philippine economy an estimated $US 28–45 million, or approximately 40% of the Philippines' annual expenditure on rice imports (Naylor 1996). In the water-scarce fynbos (shrubland) of South Africa, introduced *Hakea* and *Pinus* species have reduced water yields from invaded watersheds by between 30 and 70% (van Wilgen et al. 1996). The accidental introduction of the blight-causing fungus *Cryophonectria parasitica* from Asia led to the loss of the economically important American chestnut tree from deciduous forests of the eastern United States (McCormick and Platt 1980), and newly introduced fungal and insect species continue to reduce the diversity and alter the economic values of these forests (Sinclair et al. 1987, Harrington and Wingfield 1998). Similarly, the devastating impacts of introduced carnivorous mammals on native birds in New Zealand (King 1984) vividly demonstrate the scale of damage that invasive alien species can inflict.

Both the potential benefits and risks of nonindigenous species (which we define as including genetically modified versions of native organisms) are difficult to quantify, so it is not surprising that scientists differ on the value of deliberate introductions. For example, some scientists believe that the need to restore productivity to degraded lands is so great that, in some places, concerns about possible harmful effects of potential invasions are frivolous. In contrast, others stress the biological, economic, and social costs of some introductions. Appropriate and inappropriate introductions were the subject of an international workshop held in Waimea, Kauai, Hawaii, in June 1997, that forms the basis for this article. The workshop had two goals. First, the 21 participating scientists and managers, whose expertise ranges from plant domestication to biological control to conservation biology, and who include both advocates and opponents of deliberate introductions, sought to identify aspects of introductions about which there was general agreement. Second, discussions focused on how research can help to resolve the remaining differences. In this article, we highlight key areas in which research is needed and outline a set of specific research questions that participants consider necessary to evaluate and address the issues.

Areas of agreement on species introductions

Workshop participants identified eight key areas of consensus on introductions of nonindigenous species. These include the following: some introductions have great potential to provide society with large economic and ecological benefits; species introductions will continue and their impacts will be unevenly distributed; human activities facilitate not only species movements but also species establishment; long delays often occur between introduction and spread, but once a naturalized species is well established it is almost impossible to eradicate; and invasive behavior elsewhere is a potent predictor of invasiveness in untested habitats.

Further introductions of nonindigenous organisms could be the basis for maintaining productivity in agricultural systems, for environmental remediation, and for new economic development. The overwhelming majority of the world's agricultural and horticultural species are nonindigenous where they are cultivated. Most intentional plant introductions have been in horticulture (e.g., Wells et al. 1986), but large numbers of introduced species are also used in agricultural systems. New crops and garden plants that will inevitably be introduced continue to be developed, and biological agents to control pests are being identified that will be used in areas where they are not indigenous. New species and seed sources of the major industrial forestry genera continue to be sought, introduced, and tested internationally (Barnes 1988, Dvorak and Donohue 1992). In addition, the recent development of "multipurpose" tree species for agroforestry has resulted in a new wave of purposeful introductions across the tropics (Hughes 1994, 1995, Richardson 1998).

Inadvertent introductions of nonindigenous organisms will continue in the future. Improving global transportation, increasingly free trade, and the continuing quest for economic growth will all result in an expanding exchange of organisms among biogeographic regions of the world (Jenkins 1996). For example, the globalization of trade, involving the intercontinental movement of raw timber and packaging materials, has made the inadvertent introduction of new forest pests inevitable (Harrington and Wingfield 1998). International port cities, such as Miami and Honolulu, tend to have more species of nonindigenous invaders than other cities (OTA 1993). State and federal inspectors in Hawaii, which is visited by nearly 7 million tourists annually and imports 80% of the goods consumed, intercepted 2275 individual nonindigenous invertebrates in a single year, including 259 species not known to already occur in Hawaii (Holt in press). Furthermore, deliberately introduced organisms may carry undetected viruses, fungi, or other small parasites that will become serious economic or environmental pests (Guy et al. 1998).

Figure 2. An example of good intentions gone astray. Valued in the Andes for its edible fruits and attractive flowers (photo at right), banana poka (*Passiflora tripartita*) was deliberately introduced into Hawaii early in this century. It now blankets the canopy of many native forests (photo above), and its spread is facilitated by nonnative birds and mammals. Photos: Jack Jeffrey.

Benefits and costs of introductions are unevenly distributed among ecosystems, within and across regions, among sectors of society, and across generations. Although an introduction may meet a desired objective in one area, at one time, or for some sectors of society, unwanted and unplanned effects may also occur. Introduced organisms can, therefore, simultaneously have both beneficial and costly effects. Furthermore, the relative magnitudes of costs and benefits vary both in space and over time. The issue is made more complex by the fact that many non-native species have clear benefits and costs within the same region. For example, in South Africa, Australia, and New Zealand, some *Pinus* species are commercially important forestry crops but also cause expensive problems when they spread from plantations into watersheds and conservation areas (Richardson and Higgins 1998). In the United States, the weevil *Rhinocyllus conicus* contributes to the control of exotic thistles (*Carduus* spp.) on rangelands, but it also reduces the reproductive success of native thistles (*Cirsium* spp.) and, consequently, their insect fauna in national parks and nature reserves (Louda et al. 1997). In south-eastern Australia, the introduced forb *Echium plantagineum* is known as "Salvation Jane" in semi-arid South Australia, where it is an important dry season forage, but it transmogrifies into "Patterson's Curse" in southern New South Wales, where it is considered a livestock poison and competitor with preferred pasture plants (Cullen and Delfosse 1984).

Human acceleration of invasions. Biological invasions are a natural process. Occasionally, long-distance transport between biotic regions, or between continents and islands, occurs without human intervention. Nevertheless, human activity has accelerated the rate of invasions, often by orders of magnitude, and has resulted in the transportation of some organisms into habitats they could not have reached on their own. Humans began to significantly facilitate invasions in Neolithic times but have tremendously accelerated both intentional and inadvertent transport of species over the last 150–200 years (di Castri 1989, Reichard and Hamilton 1997). Before human settlement of the Hawaiian Islands, for example, the combined rate of colonization by vascular plants and metazoans is estimated to have been approximately one species per 50,000 years. After the arrival of the Polynesians, in the fourth century, the colonization rate increased to 3–4 species per century. During recent decades, the rate has increased to more than 20 new species per year (Loope and Mueller-Dombois 1989). Invasion rates in Australia are comparable: Between 1870 and 1970, the rate of naturalization of plant species is estimated to have been 10–30 per year (Groves 1997). Human intervention has also broken down dispersal barriers for entire classes of organisms. For example, until human arrival, oceanic islands lacked ungulates and, sometimes, ants.

Human alteration of ecosystems often increases the probability that introduced organisms will become invasive. Human population growth and demands on natural resources have increased disturbance frequency, scale, and scope, providing ample sites for colonization by introduced organisms that are able to disperse and rapidly become established (Elton 1958). Humans alter land in ways that favor humans; species that do well in human-altered habitat in one area may be more likely to do so in another. Repeated colonization across the landscape can result in small, scattered populations from which population expansion proceeds rapidly (Moody and Mack 1988). Soil disturbance, fire, grazing, soil movement, nutrient input, trampling, hydrological shifts, habitat fragmentation, and human introduction of alien symbionts have all been implicated in facilitating invasion by nonindigenous organisms (Janzen 1983, 1987, Hobbs and Huenneke 1992).

A time lag of several decades or longer often exists between the initial introduction of an organism and evidence that it is invasive and having unanticipated effects. Range expansion of many introduced organisms often follows a logistic pattern, with slow initial spread (Orians 1986, Moody and Mack 1988, Hengeveld 1989, Hobbs and Humphries 1995, Williamson 1996, Shigesada and Kawasaki 1997). This lag is clearly demonstrated by the woody weeds invading in the vicinity of Brandenburg, Germany, where continuous records of introductions have been kept for 400 years. Of 184 currently invasive woody species, 51% did not appear to be invasive for over 200 years after their introduction (Kowarik 1995). Similarly, a 20-year lag occurred in the buildup of the biocontrol weevil *R. conicus* on native plants (Louda et al. 1997). Reasons for the "lag phase" phenomenon are poorly understood but may include difficulty of detection, exponential growth, local adaptation, increased availability of sites appropriate for seed germination and seedling establishment, low frequency of occurrence of the exact combination of biotic and abiotic conditions that favor reproduction (e.g., Richardson et al. 1992), lagging introductions of mutualists (e.g., McKey and Kaufmann 1991), and climate change (Kowarik 1995).

Most invasions are irreversible. Small populations of naturalized introduced organisms can sometimes be eradicated if action is immediate; animals successfully eradicated in this way include rabbits in Haleakala National Park in Hawaii (Loope et al. 1992), a fire ant in the Galapagos (Abedrabbo 1994), and medfly outbreaks in California. However, once reproduction, dispersal, and subsequent adaptation have occurred, control becomes problematic and eradication increasingly unlikely. Generally, the probability of locating and eliminating all individuals is inversely proportional to population size and spatial extent. Consequently, eradication of such invaders as European starlings in North America (and Australia, New Zealand, and South Africa), avian malaria in Hawaii, the European rabbit in Australia, and any soil microorganism anywhere is probably impossible.

A strong predictor of invasiveness and ecological change resulting from invasion is whether the organism has been invasive and caused change elsewhere. Post-hoc analyses of species and ecosystem attributes to identify predictors of species likely to become invasive have concluded that the best single predictor of invasiveness is the invasive behavior of introduced organisms in other parts of the world with similar environments (Forcella et al. 1986, Crawley 1989a, Lodge 1993, Scott and Panetta 1993, Williamson and Fitter 1996, Gordon and Thomas 1997, Reichard and Hamilton 1997). For example, 90% of exotic invasive plant species in Australia are also invasive in other locations to which they have been introduced (Panetta 1993).

Research needs

Although proponents and opponents of intentional introductions agree on some points, many issues about potential benefits and risks remain unresolved. Research in four main categories—risk–benefit assessment, alternatives to introductions, safeguards to accompany purposeful introductions, and impact mitigation—would provide the scientific basis for improved policy decisions about prospective introductions. Examples of broad research questions are listed in the box (page 623).

Research to better evaluate risks and benefits. The risks associated with

Research questions about introductions

Several research questions need to be answered to help ensure that proposed introductions are done wisely and safely.

Guarding against risks without sacrificing benefits:
- How can the potential benefits and costs of introductions best be evaluated in economic, environmental, and social terms?
- Should all introductions be regulated?
- How different must organisms or recipient ecosystems be from those assessed previously to warrant independent assessment?
- When is it appropriate to assess and regulate taxa other than species?
- What are appropriate ecological and political boundaries for regulation?

Alternatives to introductions:
- How and when can indigenous organisms be domesticated so that they can substitute for proposed uses of nonindigenous organisms?
- How can the retention of indigenous species and natural food webs be integrated into agroecosystems so that the risk of pest problems is minimized?

Purposeful introductions:
- What common guidelines can be developed for deliberate introductions of all kinds of organisms?
- Have screening procedures differed for introductions that proved successful or harmful?
- How can the potential for nonindigenous organisms to disrupt ecosystem processes be assessed and reduced?
- Can the demand for introductions be reduced by improving the effectiveness of introductions that are attempted?

Reducing negative impacts:
- When can reduction of human-caused disturbance within natural areas be used to control nonindigenous species impacts?
- Can subtle, indirect effects of potential introductions be predicted?
- Can enough be learned from the population growth lags, booms, and crashes of previously introduced organisms to make useful generalizations?
- Should special guidelines accompany release of sterile forms, which may pose less risk than fertile organisms?
- Can protocols be developed to predict when an introduced species will hybridize with natives and what the ecological and economic consequences of such hybridization might be?
- Should special guidelines related to invasion and hybridization potential be added to those that already regulate release of genetically engineered organisms?

introducing nonindigenous organisms depend on the attributes of both the organisms and the recipient ecosystems. How can the potential benefits and risks of prospective introductions best be evaluated? Given that any introduction is potentially risky, what are the appropriate units of biological organization and levels of spatial scale at which scientists and regulators should weigh the chances of an introduced organism becoming invasive?

Scales of biological organization. Risk assessments for screening candidates for intentional introduction are often converted into recommendations on whether to accept, reject, or further evaluate a candidate species (e.g., New Zealand's Biosecurity Act, New Zealand Government 1994; Australia's Weed Risk Assessment System, Pheloung 1995). Quarantine to prevent accidental introductions of pests is based on lists of prohibited species, but risks associated with taxonomic units below and above the species level need to be considered as well (Daehler 1998). Different populations (provenances), varieties, subspecies, progenies, and genotypes within the same species can have different invasion potentials and may require independent risk assessment, as Hughes (1998) has documented for subspecies of the leguminous tree *Leucaena leucocephala*.

Conversely, infraspecific classification units may provide sufficient information about risks for species within certain higher taxa. For example, within pines, invasive species (*Pinus* spp.) are concentrated in the subgenus *Pinus*, and noninvasive species are concentrated in the subgenus *Strobus* (Rejmánek and Richardson 1996). Nevertheless, some assessment systems consider congeners of known invaders to be especially risky (e.g., Reichard and Hamilton 1997), whereas others do not (e.g., Pheloung 1995). The same units of biological organization are not equally appropriate for application to all kinds of organisms, and research is needed to define the appropriate taxonomic levels at which to carry out risk assessment for different groups of invertebrates, vertebrates, and plants. Further research is needed to evaluate which unit(s) of biological organization provides the most reliable and cost effective information about the risks of introductions.

Scales of environmental heterogeneity and movement. Areas of sociopolitical jurisdiction (e.g., states, countries, and trading blocks) are currently the units used for managing the movement of nonindigenous organisms. Nevertheless, biogeographic barriers, uniqueness of local biotas, and dispersal capacities of nonindigenous organisms do not necessarily mesh with political boundaries. For example, cordgrasses (*Spartina* spp.), which are native to the Atlantic and Gulf coasts of the United States, are invading mudflats and saltmarshes of the Pacific coast of the United States (Daehler and Strong 1996). The same species are therefore native and desirable in one locale and alien and widely regarded as undesirable in another—all within the same (albeit huge) country. And on a smaller scale, several nonindigenous ornamental species that are invasive in southern Florida are not problems in northern Florida.

Furthermore, nonindigenous organisms that are introduced into one political jurisdiction without causing problems often spread to another, where they can cause problems. For example, if the nonindigenous cactus moth, *Cactoblastis cactorum*, arrives in Mexico by dispersing from the United States across the Gulf of Mexico, it may have economic impacts due to the extensive use of *Opuntia* (prickly pear) products in Mexico; its ecological impacts could also be severe because Mexico is rich in native *Opuntia* species. Studies are needed to determine whether the current focus on political boundaries in regulating introductions produces substantially incorrect answers about their benefits and risks. It may be that a system such as that recently proposed for Australia—in which natural ecological subdivisions, or bioregions, have been proposed to govern movement of nonindigenous organisms—will prove to be most effective.

Benefits and risks in economic, environmental, and social terms. Even when benefits appear to outweigh risks, making a decision about whether to release a nonindigenous organism may be difficult. In such cases, costs may be considered excessive if they are distributed unevenly across locations, generations, or segments of society. For example, in Florida, Christmasberry (*Schinus terebinthifolius*) is valued by beekeepers as a winter source of nectar yet is despised by conservationists because it invades native ecosystems (Bennett and Habeck 1991). Research is needed to identify conflicting interests regarding benefits and risks of introductions, to substantiate purported valuations of those benefits and risks, and to determine the likely distribution of benefits and risks among sectors of society.

Research on alternatives to introductions. Introductions of nonindigenous organisms that successfully establish and spread are usually irreversible and frequently cause undesirable ecological impacts (Howarth 1991). Therefore, it is the assumptions that lead to introductions, rather than the use of indigenous organisms per se, that require scrutiny. For example, the assumption often made in using biological control to treat pest problems (i.e., "absence of natural enemies is the cause, addition of natural enemies is the cure") may lead scientists to overlook other management alternatives—including predicting and preventing further pest entry or treating pest problems with integrated pest management, which combines cultural, mechanical, chemical, and biological control methods.

Similarly, in tropical reforestation, it has frequently been assumed that introducing nonindigenous trees is the best way to create ecosystems that give first priority to human needs (e.g., for fuel, timber, fodder, and soil protection). The presumed advantages of such exotics over native species have often been their apparently greater economic value, better tolerance of unfavorable environmental conditions, or escape from specialized natural enemies (Hughes 1994, 1995, Richardson 1998). Nevertheless, indigenous organisms often do as well as exotics (Butterfield and Fisher 1994, Haggar et al. 1998, Leakey and Simons 1998). Furthermore, the escape-from-enemies argument often loses its validity with time because enemies often finally do arrive (e.g., the psyllid defoliator *Heteropsylla cubana* on *L. leucocephala* in tropical forestry; Hughes 1995) or new enemies may be acquired (as is often the case with biological control agents; Goeden and Louda 1976). The relative benefits and costs of indigenous and alien species therefore need to be studied and evaluated over the long term, not just the short term.

Direct substitution of indigenous organisms for nonindigenous organisms. One underutilized approach to reducing the rate and number of deliberate introductions is to obviate the demand for them by meeting needs in other ways. Evaluation of potentially useful indigenous organisms rather than nonindigenous ones is an alternative that needs more consideration. Large numbers of indigenous plant and animal species have been used by local people, especially in the tropics and subtropics. Nevertheless, these species, which often figure prominently in local markets, have generally been overlooked by science (Leakey and Newton 1994). Part of the reason for this oversight is ignorance—scientists and managers have simply not explored the potential utility of all species in all places—and part of the neglect stems from a focus on the small numbers of species that lend themselves to ready industrialization and global marketing. The potential of native species to substitute for nonindigenous organisms could be harnessed and enhanced by their domestication to provide economic, social, and environmental benefits (Sanchez and Leakey 1997, Leakey 1998a, Leakey and Simons 1998). More funding, such as that provided by the International Plant Genetic Resources Institute, should be made available to local governmental and nongovernmental agencies and farmers for research and selection of indigenous organisms to domesticate. All stages of domestication should be studied: identification of priority species; exploration, characterization, and conservation of genetic diversity and the capture of desirable genotypes (e.g., Simons 1996); and incorporation of domesticates into low-input production systems, such as multi-strata agroforests (e.g., Leakey 1998b).

Retention of refugia and food webs. Homogeneous plant communities, whether naturally occurring ecosystems, forest plantations, or agricultural monocultures, are more susceptible to outbreaks of pests and diseases, including nonindigenous organisms, than more heterogeneous communities (Barbosa 1987). Introduction of biological control agents, which are usually nonindigenous themselves, is a common management response to disease or pest outbreaks. An alternative way to protect against such outbreaks, and to reduce the need to introduce alien species for control purposes, may be to sustain a landscape-scale mosaic of habitats and land uses that contain refugia for indigenous natural enemies of the pests (Secord and Kareiva 1996). Research is needed to better integrate the role of habitat structure across spatial scales in the management of introduced pest species and to determine if food webs of indigenous and nonindigenous species vary at a similar scale and level of complexity. For example, a nonindigenous pest species on a farm with forest patches joined by corridors through cropland may be more or less harmful, depending on the scale of the system, the distributions of natural enemies, and the dispersal of the pest and its natural enemies.

Research on purposeful introductions. If indigenous organisms cannot be managed to provide necessary or desired economic benefits or ecosystem services, introductions of nonindigenous organisms may be called for. Research in several areas could increase the benefits of purposeful introductions and decrease their risks.

A single framework for all types of introductions. Comparative analyses of the rationale and effectiveness of the various approaches to the release of different classes of nonindigenous organisms (e.g., exotics introduced for fisheries, pets, agriculture, horticulture, forestry, and biological control and genetically modified organisms) are needed. Experts currently disagree about the relative risks of those different classes of introductions, but the ranking of risks would be easier if all introductions were considered in a coordinated way, independent of their origins or purposes.

Retrospective analyses of introductions. Retrospective analyses could shed light on the establishment and unwanted impacts of purposefully introduced nonindigenous organisms. For example, to what screening were harmful nonindigenous organisms belonging to various broad taxonomic groups (e.g., marine invertebrates, trees, insects, and pathogens) subjected before introduction? Why did the screening fail to exclude them? What kind of screening would have been necessary to prevent these introductions? In most countries, these questions might pertain to biological control agents or pathogens on nursery stock only because little other screening is in place. An example from New Zealand is instructive: Retrospective screening of invasive nonindigenous plant species using the controls of the 1993 Biosecurity Act revealed that 98% of the current major weed species would not have passed initial border security (Williams 1996); approximately half of these were probably introduced deliberately.

Holistic view of the invasion process. Purposeful introductions of nonindigenous organisms should be developed in stages—from assessing the need through collecting, identifying, screening, evaluating, releasing, establishing, and distributing the organisms and ultimately assessing their economic, environmental, and social effects. In current introductions of biological control agents, attention focuses on all steps except the last (McEvoy 1996, Louda et al. 1997). The situation is even worse for introductions of exotic plants into the United States, where there is little or no screening of any kind for potential adverse impacts (OTA 1993). Better tracking of the total traffic in nonindigenous organisms moving through each stage in the process—from need assessment through impact assessment—is necessary to reduce the adverse affects of deliberate introductions, as are analyses of the stages at which introductions succeed, fail, or cause unexpected problems.

Fewer, more effective introductions. Most species introduced for specific purposes perform below expectation, and a few perform far above expectation (e.g., Crawley 1989b). For example, of 463 grasses and legumes introduced to improve pastures in northern Australia, only 5% increased pasture productivity; over 60% of the remaining species naturalized and became weeds (Lonsdale 1994). Proponents of introductions are inclined to introduce more and more organisms to find the one (or few) that really works or is most profitable. However, each introduction brings an increment of risk, and the more introductions that are made, the more casualties even a low mishap rate can cause. Given that the risks associated with new introductions vary among both organisms and recipient ecosystems, research is needed to quantify those risks. Research is also needed on the attributes of human cultures that determine what leads to preferences of indigenous or nonindigenous organisms, so that managers and policymakers can reduce the number of introductions required to meet local needs (Hughes 1994, 1995, Hopper 1996, McEvoy and Coombs 1999).

Research to evaluate and mitigate impacts of introductions. Nonindigenous organisms can potentially harm the environment and its inhabitants in a variety of ways—from a direct trophic interaction that arises when nonindigenous organisms consume a nontarget organism, to direct competition, to indirect interactions that can occur when nonindigenous organisms and nontarget organisms are affected by the same intermediate species (e.g., shared hosts, natural enemies, and mutualists) or ecosystem components (e.g., habitat and resources). Indeed, some of the very characteristics that make nonindigenous organisms effective in providing such useful services as pest control, soil amelioration, and soil conservation also make them potentially dangerous invaders that can harm indigenous organisms.

Breadth of impact of biological control agents. Host specificity is one of the primary criteria used to evaluate and rank the risks that control agents pose to nontarget organisms (Thomas and Willis 1998). Host specificity testing protocols to prevent harm to nontarget species have been developed and tested for biological control of weeds, but protocols for predators, parasites, and pathogens used to control arthropod pests need to be developed (Hopper 1995, McEvoy 1996). Some scientists and managers have suggested that more attention be paid to potential indirect effects and evolutionary changes in assessing the risks of introducing exotic biological control agents (Secord and Kareiva 1996, Simberloff and Stiling 1996). Follow-up studies of a variety of long-standing introductions are needed to assess the probability and consequences of nontarget effects, to measure rates of evolution following introduction, and to update risk assessment protocols accordingly.

Evaluation of impacts on ecosystem processes and services. The impacts of introduced species on ecosystem functioning are poorly understood. Rates of ecosystem processes can change in the presence of invaders (Vitousek and Walker 1989, Gordon 1998), but invasive species do not inevitably reduce the services society derives from an ecosystem. Whereas some invasive species cause enormous economic costs to human enterprise, others invade and modify degraded or polluted sites, thereby countering the negative effects of humans on the biosphere. For example, the post–World War II revegetation of northern Guam by aerially seeding the alien leguminous tree *L. leucocephala* protected soil, replenished nitrogen, provided habitat for wildlife, and most likely restored water quality. Research is needed to evaluate the positive and negative effects of invasive species on ecosystem processes in many different ecosystems.

Post-introduction population oscillations. Some introduced organisms reach and maintain high populations, whereas others undergo an initial population explosion in the new habitat but then decline (D'Antonio et al. in press). Non-native species that become dominant in their new habitats over the scale of decades may eventually be outcompeted by native species and cause fewer long-lasting changes than might initially be thought. Research is needed to identify the mechanisms involved in such declines and to answer the following questions: Can long-term dynamics be predicted by characteristics of the nonindigenous organism and recipient community? Is it possible to estimate how long such declines are likely to take? Do native communities return to their preinvasion state following the decline of the invader?

Post-introduction range expansions. Most nonindigenous organisms fail to spread beyond their original site of introduction, and research is needed on the specific mechanisms that control this failure. Are barriers to invasion more often biotic or abiotic, and does the nature of the barrier depend on the broad taxonomic group to which the nonindigenous organism belongs (Mack 1996)? What traits of noninvasive aliens cause them to differ in their rate and extent of range expansion from those that are invasive?

Post-introduction time lags. As described earlier, recognition that a nonindigenous organism has become a pest often lags well behind its introduction. For example, the oldest herbarium specimen of Christmasberry from Florida is dated 1846; a detailed survey of south Florida vegetation in 1941 did not report it as a conspicuous plant in the wild, yet by the mid-1950s it was recorded as an invasive weed tree of major importance (Ewel 1986). Similar stories have been reported throughout the world (Hobbs and Humphries 1995). Research is needed to investigate why lags occur and whether they vary among taxonomic groups. A related research need concerns how long it is necessary to wait after small-scale trial introductions to estimate their risks and benefits.

Sterile forms. Reducing dispersal and reproductive potential might be the best way to contain plants introduced for horticulture and forestry—this mode of containment can be accomplished by using sterile varieties. For example, sterility is one of the presumed virtues of certain races of vetiver grass (*Vetiveria zizanioides*), which is used widely for erosion control (NRC 1993). Research is needed to assess how reduced dispersal or fertility in a nonindigenous organism will influence the probability that it will have unintended effects. Under what restrictions should the introduction of sterile cultivars or breeds be permitted? What is the probability that a sterile cultivar or breed will revert to fertility, and what are the conditions under which reversion is most likely to happen?

Spontaneous hybridization. Nonindigenous organisms may hybridize with indigenous organisms (Abbott 1992, Levin et al. 1996, Rhymer and Simberloff 1996, Daehler and Strong 1997), resulting in contamination of native genotypes and the production of novel weeds. For example, some varieties of the nonindigenous shrub *Lantana camara* hybridize with endemic members of the genus in Florida and are feared to be genetically swamping the native species (Sanders 1987). Sometimes the hybrids themselves present new and unpredictable threats of invasion, even though the hybrid may be reproductively isolated; a well-documented example is *Spartina anglica* (a cordgrass), which arose as a polyploid hybrid between a native species and an introduced one (Gray et al. 1991). Hybridization between introduced species can be equally problematic, as is the case in Australia, where 7 two-way and 2 three-way hybrids have resulted from some 100 introductions of species and varieties of willows (*Salix* spp.); these hybridization events have resulted in new species and new weeds, raising concerns about the impacts of willows on riparian environments (Cremer et al. 1995). Research is needed on the following questions: How often does introduction of a nonindigenous organism lead to hybridization with a native organism? What are the ecological and evolutionary consequences of such hybridization? What is the likelihood that hybridization among introduced species, or between natives and introduced forms, will lead to invasive genotypes? What are the likely risks and benefits of such hybridization?

What screening protocols could be used to assess the risks associated with hybridization?

Genetically modified organisms. Because of the potential of genetically modified organisms to induce economic and ecological change, their use is fast becoming a topic of international prominence (e.g., Levin 1990). Genetically modified organisms can affect a natural community in two ways. First, they can transfer introduced genes to other individuals of the same or related species. The finding that some transgenic plants are more likely to outcross than nontransgenic plants (Bergelson et al. 1998) raises concerns that rapid reduction in genetic variation will more often result from the introduction of genetically modified organisms than from the introduction of nontransgenic plants. However, the generality of these outcrossing results awaits study; it is still unclear whether enhanced outcrossing will be a common feature of genetically manipulated systems.

In addition, genetically modified organisms (or nontransgenic relatives into which the transgene has introgressed through a hybridization event) might increase in population size, thus invading a natural community. Despite this possibility, the recipients of genes inserted by genetic engineering have been widely assumed to have a diminished capacity to invade natural ecosystems (Bergelson 1994) because the costs associated with genes that protect against herbivores, pathogens, or herbicides would decrease fitness in the absence of these selective forces. Confidence in this assumption has, however, been undermined by the mixed results from studies that have attempted to measure a reduction in the fitness of resistant plants in the absence of selection (Bergelson and Purrington 1996, Bergelson et al. 1996, Mauricio and Rausher 1997). Therefore, reducing survival and reproduction of genetically modified organisms may be the best way to contain them under field conditions. For example, baculoviruses introduced for insect control have been engineered to increase their speed of kill (increasing effectiveness) and reduce their survival (increasing safety). Strategies for containment of genetically modified organisms need further testing in the field.

Conclusions

Although many laypeople have not given species introductions much serious thought, those with economic, political, or professional interests in the issue hold widely varying viewpoints. At the extremes, these views range from a handful of advocates of no introductions, or of such rigorous pre-introduction proof of benignness that all introductions are effectively prohibited, to an equally small group that advocates a freewheeling global eco-mix of species. Happily, such extremists are now much in the minority; most proponents of purposeful introductions understand the risks (but believe that technology can deal with them), and most conservation biologists recognize the potential benefits to be derived from carefully controlled introductions. Clearly, there is a need to bring all parties together on common ground that can lead to objective, science-based decisions by policymakers.

A first step toward common understanding is to ensure that all objective concerns and facts on risks and benefits of species introductions are communicated to all stakeholders. Substantial progress has been made within the past 15 years in compiling such information. For example, an international effort conducted under the auspices of SCOPE (Scientific Committee on Problems of the Environment; Drake et al. 1989) gave the issue great international visibility, and local initiatives did the same for several countries, including New Zealand (Esler 1988, Ledgard 1988), Australia (e.g., ANPWS 1991), and the United States (OTA 1993). As a follow-up to the SCOPE-sponsored initiatives, a 1996 United Nations–Norway conference signaled the urgent need for a scientifically based global strategy and an action plan to deal with invasive nonindigenous species (Sandlund et al. in press).

Synchronous with these efforts, which have heightened global awareness of the dangers of introducing non-native organisms, other scientists were calling attention to little-known plants and animals that might have great usefulness beyond their native range. In the United States, for example, the Board on Science and Technology for International Development, an arm of the US National Research Council, sponsored and published a series of studies promoting wider use of a host of plant and animal species for human benefit—from amaranth to vetiver, from buffaloes to yaks. Do proponents and opponents of purposeful introductions read the full range of available literature? Not as much as they should, and cross-viewpoint communication is an endeavor that therefore should be encouraged at every opportunity.

In the transition from research to policy regarding species introductions, there are many important roles for scientists. Greatly increased public awareness of environmental change and degradation, well-publicized concerns of the international scientific community about the effects of invasive species, interest on the part of the news media in environmental issues, and widespread concern for the development of sustainable systems of land use have combined to create a propitious environment in which to foster, promote, and fund research on species introductions. Three specific needs are identified here; they are but a subset of what is needed to fill the information gap in the policy arena.

• **Development of a broadly accessible information system to support evaluation of organisms proposed for import.** Objective decision making will be improved by access to a comprehensive, up-to-date database that provides information on the biology and environmental parameters of organisms in their native habitats and in those habitats to which introductions are being considered. Enumeration of potential benefits and harmful effects should be included. Initially, priority for inclusion in the database should be given to organisms of management concern in nonindigenous habitats or those likely to be proposed for introduction. Because potential benefits and costs from introductions are important issues throughout the world, every country needs access to such an information system. Cooperation among countries in data acquisition and sharing will be the most efficient method of timely database development.

• **Evaluation of potential impacts of introductions should be based on the attributes of the communities within recipient environments as well as of the introduced organism.** Ecosystem history and environmental conditions, as well as community species composition and timing of introduction, interact with the biological attributes of organisms to determine invasion success (Crawley 1989a, Perrins et al. 1992, Hobbs and Humphries 1995). Such interactions are likely to be important, irrespective of the source of, or genetic variation within, the organism and despite variation in invasibility of the ecosystem (e.g., Myers 1983, Bazzaz 1986, Ewel 1986, Johnstone 1986). Prediction of invasiveness is complicated by these interactions, but attempts to forecast the possibility of an introduced organism becoming invasive should not be abandoned.

• **Organisms to be considered for introduction should be classified by their potential effects, then proposed for regulation accordingly.** At least three categories need to be identified: "permitted," "prohibited," and "requiring further evaluation." The classification should be assigned based on an analysis of the full range of benefits and risks associated with the introduction of the organism within a specific region. It is feasible to develop an "expert system" that would allow a species proposed for introduction to be correctly classified. The New Zealand Biosecurity Act and proposed classification mechanisms for South Africa and Australia provide clear examples of systems that other countries can adopt. Until such an expert system is developed, most countries will need to produce a more comprehensive "prohibited" list than is provided by most current regulations of noxious weeds and pests. Tucker and Richardson (1995), Rejmánek and Richardson (1996), and Reichard and Hamilton (1997) all provide models and data to guide the development of an expert system. By the same token, past experience should be drawn on to develop lists of organisms whose introductions have not caused problems and therefore should be permitted to continue.

But research alone as an end-product will not suffice—it must be coupled to education. Knowledge imparted now to the public, especially to young people, will prove to be of critical importance in determining future rates of introductions. Ecological literacy will create a better understanding of those nonindigenous organisms that have already been naturalized and will lead to informed decisions regarding the appropriate management and use of all introductions, new and old alike. Funding to raise public awareness must be sought aggressively at all scales of government.

Educational efforts should also focus on specific audiences—decision makers, ecosystem managers, conservation groups, and institutions that maintain germplasm collections and seed banks (e.g., botanic gardens, conservation organizations, and zoos). Only when understanding of the impacts of biological invasions is incorporated by practitioners and regulators will prediction of effects, prevention, and control needs be reflected in the policies of funding and development agencies. Evidence of incorporation of this information is already apparent in the policies of some countries (e.g., New Zealand Government 1994, Commission of the European Communities 1998), giving reason to hope that the economic and ecological consequences, both good and bad, of species introductions everywhere will soon become important concerns to all members of society.

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