Biological Invasions: a Global Perspective
Edited by J. A. Drake *et al.*

CHAPTER 22

Biological Invasions: a SCOPE Program Overview

H. A. Mooney and J. A. Drake

22.1 INTRODUCTION

Here we give a general overview of the results of the SCOPE program on the Ecology of Biological Invasions. We concentrate our attention on species invasions as a global phenomenon rather then a local event. The biological invasions program provided a global appraisal of the phenomenon of species invasions, and the effect such invaders have on the ecosystems they colonize. We define a species as being an invader when it colonizes and persists in an ecosystem in which it has never been before. Essentially we are viewing invasions in ecological rather then evolutionary time. Those wishing an in-depth treatment of the dynamics of biological invasions are referred to Elton's (1958) classic work, and to the publications which arose out of this program (Appendix 1).

22.2 HOW MANY INVADERS ARE THERE?

One of the primary outcomes of the program was to provide new documentation on the extent of invasions of different types of organisms in various parts of the world. For example, there are between 1500 and 2000 introduced species of plants in Australia, and nearly half of the flora of New Zealand (1570 invading species) is composed of invaders (Heywood, this volume). Over 1300 species of insects have successfully invaded the United States, and we do not doubt that the catalogue of invaders worldwide greatly underestimates the extent of species invasions.

Of the many data sets available, we highlight just two—that of invasions into nature reserves around the world and invasions onto islands, with Hawaii as our central example. These contrasts illustrate two extremes in ecological systems, unmanaged island systems versus carefully managed reserves which are primarily continental. Islands have incurred some of the greatest numbers of invaders, whereas reserves are managed to prevent invasions or to eliminate them, if possible, when they do occur. These examples also serve to illustrate that certain types of organisms have been more successful invaders than others and certain regions have been comparatively more resistant as well as prone to invasion.

22.2.1 Invasions into nature reserves

Twenty-four nature reserves distributed throughout the world were examined for the numbers of invading organisms, with an emphasis on higher plants and vertebrates (Usher *et al.*, 1988). Usher (1988) comments that 'No nature reserve included in the case studies is without at least one species of invasive vertebrate and at least several species of invasive vascular plants.' In the case of island reserves about 30% of the vascular plant species, and almost 18% of the terrestrial vertebrates are invaders (Usher, 1988). Interestingly, reserves on continental land masses are somewhat less heavily impacted. Further, certain kinds of ecosystems like savannas and dry woodlands appear less vulnerable to invasion. This was a particularly important evaluation since it yielded information about invasions into systems that are being biologically protected and are subjected to minimal disturbance. Despite this fact, many invaders have been successful in these systems.

22.2.2 Invasions on islands

All else being equal, ecosystems subject to disturbance and those not directly protected from invasion appear more likely to be successfully colonized by an invading species. As our example of the impact of invaders on a non-protected island system we point to the data provided by Vitousek *et al.* (1987) for the Hawaiian Islands. In Hawaii nearly half of the approximately 2000 species of flowering plants are invaders. These species have radically altered the character of the flora. Before the influence of humans over 90% of the flowering plants were totally endemic to the islands. Similar impacts are seen on other indigenous groups. In the case of reptiles and amphibians the invaders represent the only members of this group. Essentially all of the mammals are likewise established introductions. Around 100 species of birds have invaded or have been introduced to the Hawaiian Islands. A direct result of these invasions has been the extinction of numerous native bird species (Moulton and Pimm, 1986).

Thus, these data from both protected and non-protected regimes indicate that invasive species have substantially altered the nature and patterning of the earth's biota. Essentially, after an invading species becomes established the ecological 'rules' or ecological processes which operated in a given system change. In some cases this change is negligible and the invading species simply adds to the species richness of the system. In other cases the 'rules' or processes which operated, permitting coexistence of a species complex, are drastically altered leading to the extinction of native species. Concomitant with changes in the flora and fauna of an ecological system are changes in that system's resistance and vulnerability to subsequent species invasions. A species which formerly was excluded from a community may now be a successful colonist.

22.3 WHO ARE THE INVADERS?

22.3.1 Functional groups

In considerations of invading species accounting is usually made in terms of the taxonomic groups to which they belong. An alternative approach is to categorize invaders by the role they play in community and ecosystem processes. For example, the invader might be a specialist or generalist consumer, it may function as an herbivore, woody plant, predator, pathogen, or nitrogen fixer. To date few analyses have searched for trends in invasion success as a function of the role species play. However, there are some robust theoretical predictions about what kinds of species are better colonists in differing ecological situations (Drake, 1983; Sugihara, 1983). Using radically different models Drake (1983) and Sugihara (1983) have found that invasion success is a function of both community complexity (number of species) and the degree of trophic specialization. As community complexity increases species which are more specialized in diet tend to be more successful invaders. An empirical evaluation of this trend is forthcoming.

Here we explore invasions in a single functional group—that of plant pathogens. Von Broembsen (this volume) gives an assessment of the extent and effect of invading plant pathogens into natural ecosystems. She noted that there are only five examples of highly successful and destructive invading pathogens into natural forested systems: chestnut blight, white pine blister rust, dutch elm disease, pine wilt disease, and phytophthora root disease. The pathogenic agents in these cases are varied, and include nematodes and fungi but not bacterial or viral phytopathogens. The types of forests attacked have been in temperate regions and have been characterized by uniformly distributed dominant trees of one or a few closely related species. Some of the invading pathogens have relatively complex life cycles, dependent on insects or alternate hosts for portions of their life cycles. All are the result of introductions of diseased plant materials prior to strict quarantine procedures.

Although there have been only a few cases of successful invading pathogens, it should be noted that these cases have had impressive impacts. The chestnut blight effectively eliminated the American chestnut throughout its range. Similarly, large areas of jarrah eucalyptus forests have been affected by phytophthora with impacts on the water balance of these regions. There are many additional examples of invading pathogens which have had only minor effects or no discernible effect at all; however, many of these have been into agroecosystem and are not considered by Von Broembsen.

Why have there been so few invading plant pathogens natural ecosystems? Von Broembsen suggests that they often have specialized hosts (although this is not the case for phytophthora) and are thus not good invaders into new systems. Intact ecosystems appear particularly resistant to invasions; however, it may be that invasions are often unnoted or there have been limited opportunities for invaders. It is instructive to note that of the successful examples given above none are important pathogens at their origins. The picture is substantially altered if one considers the successful invading pathogens of crops, where a given crop species may have large numbers of potential pathogens.

What of other functional groups? Unfortunately, much of the data on invaders does not suggest which functional group species belong to. Hence, an analysis of trends is not currently possible. Nevertheless, we offer a few thoughts based on theoretical considerations. Given a species' ability to tolerate a new environment, a species which represents a new functional role, or perhaps fills a vacent role, might be expected to be a better colonist then a species which invades a system containing a species which already fills that role. If this is the case, we may be unable to find general trends across communities because there is no reason to expect that all communities will be missing the same functional groups. We suggest that at the level of functional groups trends are not likely to exist.

22.3.2 Taxonomic groups

As noted above, invading species may be found among all types of organisms, microorganisms, plants, and animals. However, certain taxa appear to be more successful invaders than others. Unfortunately, it is not possible to evaluate all groups uniformly because of an inadequate data base. Heywood (this volume) has, however, been able to assess terrestrial plants. He notes that of the 250 000 species of higher plants only about 250, or 0.1%, are serious agricultural pests although a much larger number, 8000, are considered weeds of agriculture. Of the world's 18 worst weeds, over half are grasses and all of these are of tropical origins. Heywood notes that the most common plant families from which weedy species originate are Compositae, Gramineae, and Leguminosae. This is not surprising since these represent the largest families of flowering plants, with approximately 20 000, 13 000, and 8 000 species respectively, occupying a tremendous range of habitats throughout the world. In the case of insects, Simberloff (1986) notes though that the invading species into North America are not representative of the taxonomic pool; some taxa are significantly more successful then others. this may be function of differences in opportunity for successful transport.

22.4 HOW DO THEY GET THERE?

The increasing breakdown of the biogeographic barriers that once limited the interchange of the world's biota has been accomplished through the intercontinental transport of humans and their goods. The biological invaders have either been purposely carried with humans or have inadvertently accompanied them. The history of these movements has been chronicled by Crosby (1986) and di

Castri (this volume). Although quarantine efforts have altered the rate of invasions of accidental introductions they have not totally controlled them. Further, as the means and frequency of human transport has changed so have the kinds of organisms accompanying them (Sailer, 1983). Unfortunately, although in many countries there are strict quarantine programs directed toward agricultural pests there is often free interchange and continued introductions of organisms not associated with agriculture that have the potential to alter the properties of native ecosystems.

22.5 WHERE DO THEY COME FROM?

Plant invading species of the New World have their principal origins in 'the eastern and southern fringes of the Mediterranean Basin and the adjacent Mediterraneo-Irano-Turanian steppes of the Middle East' (Heywood, this volume). It is these regions that have had a long history of human modification and where agriculture originated. It is not surprising that plants that co-evolved with agricultural practices have attributes that make them successful invaders. These regions have also served as centers of world commerce and thus as sources of plant materials.

Insect invaders of the New World also are predominately from the western palearctic region (Sailer, 1983). Simberloff (this volume) argues, however, that these origins reflect principally pathways of commerce, and thus opportunities for invading species, rather than any intrinsically aggressive properties they may possess. This trend is likely to be found with plants as well as animals.

22.6 HOW DO THEY GET ESTABLISHED?

Once an invading species arrives in a new environment its successful establishment is contingent on a variety of environmental and biological factors. Successful established represents a significant barrier in the invasion process. It is difficult to present quantitative estimates of the proportion of unsuccessful invasions; one must of course witness the invasion to know it even occurred. Nevertheless, some information on the proportion of invaders that become established is available in the biological control literature (DeBach, 1964, 1974). Simberloff (1981) summarized the attempted introductions reported by DeBach (1974), and found that for over 11 of 30 control efforts one or more of the species introductions failed (100 attempted introductions). Hypothetically, the proportion of unsuccessful invaders should be considerably lower then in natural invasions, because in biological control efforts an attempt is often made to match the ecological and environmental requirements of the introduced species to the target environment.

Given that environmental conditions are sufficiently benign to permit an invading species to colonize, what factors are likely to influence whether or not that population will persist? A variety of factors ranging from the genetics of small populations to community level interactions have been implicated in affecting invasion success. We will begin by considering the process of successful invasion as a sequence of barriers that must be overcome for successful establishment.

22.6.1 The minimum viable population

The concept of the minimum viable population is central to any consideration of species establishment after invasion. Simply stated, a minimum viable population represents some population abundance that is immune to local extinction due to genetic, demographic and environmental stochasticity (Shaffer, 1981; Gilpin and Soule, 1981; Richter-Dyn and Goel, 1972; Leigh, 1975; Frankel and Soule, 1981; Schoenwald-Cox *et al.*, 1983; MacArthur and Wilson, 1967). Given the magnitude of population fluctuations caused by such factors, a population might have a minimum size below which extinction is likely and above which extinction is unlikely.

Richter-Dyn and Goel (1972) modelled the population dynamics of a hypothetical invading species that was resource-limited. They considered the effect chance fluctuations had on invader population dynamics by adding a simple stochastic term to the population growth equation. Although their conclusions are model-dependent, Richter-Dyn and Goel found that a population of about 20 individuals could increase in abundance and persist in the face of stochastic fluctuations in abundance. Conversely, a population below 20 individuals either became extinct at a rate equivalent to the reciprocal of the per-capita birth rate, or, due to random fluctuations the population eventually exceeds the threshold above which extinction is unlikely.

Clearly, factors other than those subject to stochastic variation in population size also influence successful invasion and persistence. These factors effectively increase the minimum viable population size, that is they increase the likelihood of extinction. Because invading species tend to be rare upon colonization, the dynamics and genetic structure of small populations are likely to be important. For example, the sex ratio, breeding system and genetic diversity of an invading population can be a critical determinant of success as an invader. A sex ratio skewed towards females will have less of an effect in some mating systems (say polygyny) than others. Additional complications such as genetic bottlenecks, which arise from the often severe reduction in genetic diversity of the founder population, may have serious consequences as well. These are but a few of the factors which can influence a species' minimum viable population size.

22.6.2 Higher-order effects

If all communities had the same structure and organization one might expect that a successful invader in one system would be equally successful in another.

Communities, however, are not all the same—indeed they posses such a diversity of structures and patterns that a community-level 'phenomenology' does not yet exist (see, however, Drake, 1989). What makes one community vulnerable to invasion while another is resistant to invasions? Clearly, disturbed systems tend to be more susceptible to invaders than intact systems, although we note cases where disturbance prohibitis invasion by many species (Hobbs, this volume; Mooney and Drake, 1986). But what of two undisturbed systems or two equally disturbed systems; what factors are responsible for differences in vulnerability to invasion? Should species-poor communities be more susceptible to invasion than species-rich systems, all else being equal? These are difficult questions to answer and represent a potentially rich avenue of future research.

At least part of the answer will come from integrated community-level studies. Resistance and susceptibility to invasion is a community-level property, not a property of guilds, trophic levels or plant, bird, fish or insect ensembles. Demonstrations of unlikely interactions across disparate trophic levels or levels of scale are common. Such interactions define the boundary of the system that must be explored if progress is to be made in understanding vulnerability to invasion.

22.7 HOW FAST DO THEY MOVE?

After an invading species becomes established in a new environment it is unlikely that it will remain localized. The final stage of a species invasion is usually the spread or dispersal of the invading species into the surrounding environment (Williamson, this volume; Elton, 1958; Levin, this volume; Okubo, 1980, Skellam, 1951; Williamson and Brown, 1986; Anderson and May, 1986). Clearly, a species that invades but does not spread is unlikely to become as serious a problem as an invader that rapidly expands its range. For example, both the gypsy moth (*Prostoia dispar*) and the Africanized honey bee have rapidly expanded their ranges across many habitat types. However, many invaders remain localized, dispersing only short distances from the original introduction.

An important component of spread is the rate at which the invading species colonizes new territory. Absolute rate of spread depends on two population parameters, namely the population's rate of growth and dispersal ability (Levin, this volume; Williamson and Brown, 1986; Williamson, this volume). A species with a low rate of increase but substantial dispersal ability may spread at a rate roughly equal to a prolific breeder but poor disperser. Williamson and Brown show that the spread of the muskrat (*Ondatra zibethica*) and grey squirrel (*Sciurus carolinesnsis*) appears as a '...generally steady advance, which could be ascribed to random dispersal with occasional major advances.'

Rate of spread is not only a function of species characteristics but the ecosystems through which the species spreads. Mack (1986) has suggested that the successful invasion of some non-native grasses into the Intermountain West occurred only when disturbance from large mammals was removed. The spread of zander (*Stizostedios lucipperca*), a piscivorous fish now invading England from eastern Europe, is strongly limited by characteristics of the lakes and rivers themselves (Hickley, 1986). Hence zander spreads more rapidly in slow moving riverine systems then in rapidly moving waters.

Generally, the rate of spread of an invader is a complex function of a species' population ecology and the amount of consequential habitat heterogeneity. Spread through a patchy environment is likely to depend on the degree of habitat heterogeneity, size and distribution of patches, distance between suitable patches, and population characteristics such as growth rate and vagility or dispersal ability.

22.8 WHAT IS THE NATURE OF THE SYSTEMS THEY INVADE?

A primary goal of the invasions program was to assess the significance of invasions of organisms into natural systems. Elton (1958) had argued that the lack of invaders into natural systems was due to some resistance attributes they had that were determined by their complement of competitors, predators, parasites, and diseases. Successful invasions occurred when this resistance system was in some way broken down by disturbance. Simberloff (this volume) argues that the greater apparent vulnerability of native systems is not necessarily related to such system properties but simply to the greater frequency of introductions into the human-dominated disturbed systems. Crawley (1987) makes similar arguments. The data do not yet exist on successes and failures into matched natural and disturbed systems to resolve this issue.

22.9 HOW DO THEY IMPACT THE SYSTEMS THEY INVADE?

Since the time of Elton's book there has been a significant development in the study of the properties of ecosystems. It is thus not surprising then that one of the most important contributions of the SCOPE program on the ecology of biological invasions has been an analysis of the impact of invaders on ecosystem properties. The most telling examples are again from nature reserves—systems that are managed for the maintenance of natural processes. Macdonald *et al.*, (this volume), in their analysis of nature reserves around the world, found examples of ecosystem disruption of the following types:

1. Accleration of soil erosion rates (feral mammals)
2. Alteration of biogeochemical cycling (feral pigs, invasive nitrogen fixers, salt accumulators)
3. Alteration of geomorphological processes (dune and marsh grasses)
4. Alteration of hydrological cycles (phreatophytes, *Phytophthora*, invasive trees)

5. Alteration of fire regimes (invasive grasses and shrubs)
6. Prevention of recruitment of native species (alien plants, mammlas, and ants)

The important point of the above list is that virtually all ecosystem functional (water and mineral cycling, productivity) and structural properties (community structure and succession) can be influenced strongly by an invading species. Further, invaders from all taxonomic categories may play this disruptive role (microbes, plants, and animals).

The impact of invading species on non-protected, yet non-agricultural ecosystems can be considerable. Mack (this volume) notes that 'in less than 300 years...much of the temperate grassland outside Eurasia...has been irreparably transformed by human settlement and the concomitant introduction of alien plants. Few other changes in the distribution of the earth's biota since the end of the Pleistocene have been as radical...or as swift...'. In these instances there has been a complete transformation of the properties of these systems. Mooney, *et al.*, (1986) note, for example, how the perennial grasslands of California have been totally transformed by the apparently irrevocable conversion to a grassland dominated by annuals originating in the mediterranean Basin.

The degree of specific impact an invader can have on an ecosystem will vary depending on its function. Vitousek (1986) has noted that large animal invaders can alter such system properties as productivity, soil structure, and nutrient cycling. Plants, particularly those that differ in functional properties from the native species, can have similarly dramatic impacts.

Pimm (1987), (this volume), on the basis of theory and natural history observations, provides the following guidelines for predicting the potential impact of introductions on biotic communities:

1. Species introductions where predators and competitors of the introduced species are absent are likely to have severe impacts.
2. Introductions into relatively simple communities (few species) are also likely to have large impacts.
3. Finally, animal introduction that utilize multiple food plants are likely to have large effects especially if predators are removed.

22.10 WHAT CAN WE PREDICT AT PRESENT?

In reviewing the information available on biological invasions with the goal of building a predictive base the SCOPE program has been hindered by two fundamental data lacks:

1. Most of the evidence comes from qualitative natural history observations. There has been very little experimentation utilized in the study of biological invasions.
2. Although we have abundant information on the number of successful invading

species for most groups we have essentially no information on the numbers of failures nor an analysis of why they failed. Thus we cannot easily give adequate probabilities of establishment of a given organism into a new system.

Although, as noted above, there are some general rules relating to invasibility based on the properties of systems, there are fewer general predictive guidelines relating to properties of the organism. There have been, however, repeated attempts to make predictions of the potential invasibility success of a given organism based on their traits. These attempts (Baker, 1986, for plants; Ehrlich, this volume, for invertebrates) have generally taken the form of lists of attributes, genetic, physiological, and ecological, that are most often associated with successful invaders. Crawley (1987) presents a somewhat pessimistic assessment of these analyses, though, stating that 'reluctantly, it has to be admitted that at the moment we have virtually no predictive ability in relation to the species characteristics of plants associated with invasibility in a particular kind of community.' He does note, however, that the intrinsic rate of increase, for insects at least, is a predictor of probability of successful establishment as is the widespread nature of their distribution.

Increasingly we are beginning to understand the significance of episodic events in structuring biological communities. Rare events entrain a whole series of responses that may totally change the dynamics of a systerm. An invading species may be successful during these brief intersections of the chance of being there just at the right time. These intersections may be rare indeed and very difficult to predict for an untested species (Crawley, this volume).

Simberloff (this volume) nevertheless believes that detailed studies of the natural history of a particular organism and of the physical and biotic characteristics of the host environment should yield the information necessary to make sound predictions of potential invasion success. In spite of this lack of predictability for a specific case, knowledge of traits of organisms and of the target environment gives important generic guidelines of the probability of success that can be utilized for planning.

The emphasis in the SCOPE program has been on the numbers and impacts of the invading species and very little on the failed introductions because of the lack of data on the latter. There are some studies on certain groups of organisms that do, however, indicate the difficulty of establishing an alien organism in spite of a concerted effort and considerable knowledge of the biology of the organism. Only about a quarter of the attempts to introduce exotic birds have established breeding populations. In some cases (Japanese quail into the United States) no breeding populations have been established in spite of the release of hundreds of thousands of individuals (Long, 1981). In cases of carefully planned introductions, where there was great care to match host and target habitats in biocontrol efforts, high establishment rates have been achieved.

22.11 GOOD INTENTIONS ARE NOT ENOUGH

Of course all purposeful introductions have been with good intentions—increasing agricultural productivity, providing erosion control, enhancing recreation and so forth. In most cases these objectives have been achieved, but in some cases at costs not originally envisioned. As our understanding of biological systems becomes more complete we should be able to reduce the probability that an intentional introduction will have an adverse effect. We should be beyond making such mistakes as we did in purposefully introducing plants such as crabgrass and Johnsongrass, two of North America's most noxious weeds, and animals such as carp. Other purposeful introductions into North America include water hyacinth, dandelion, (Foy *et al.*, 1983) and kudzu vine. Yet even in fairly recent times there have been examples of purposeful introductions that have had fairly drastic ecological and economic consequences. The point of the following example is that great care must be taken to consider all aspects of the consequences of an introduction, not just an immediate one of interest, such as increasing productivity.

In 1957 the Nile perch *Lates niloticus* was introduced into Lake Victoria in East Africa because it was large and relatively easily caught. The consequences of this introduction, as chronicled below, are given by Barel *et al.*, (1985). The intent of the introduction was to increase the availability of food for human populations. This act was taken in spite of concerns over the consequences of introducing a large carnivorous fish weighing over 200 kg into a system where few other fishes exceed 1 kg. These concerns were validated as subsequent events proved. The introduction was very successful in terms of establishment but had many detrimental effects including driving to extinction many endemic fishes. It is claimed that 'the potential loss of vertebrate genetic diversity as a result of this single ill-advised step is probably unparalleled in the history of man's manipulation of ecosystems.' Other undesirable consequences of this introduction have been considerable. The larger fish proved to be a less favored food besides being difficult to preserve. The oily perch have to be smoked rather than sun dried as was done with the native smaller fish. Wood to support the drying has led to deforestation of a number of islands (Coulter *et al.*, unpublished manuscript). Establishment of the Nile perch is now so entrenched that there appears little possibility of removing them. Thus a lake ecosystem, the size of Switzerland, has been irrevocably modified in a relatively short time. The changes, in spite of good intent, have been mostly detrimental. Barel *et al.*, (1985) note that except in the cases of fishless lakes and man-made reservoirs, all examples of movement of fish from one system to another with the intent of increasing yields of human food have been either unsuccessful or simple disasterous. They note that although the basis for these failures could be predicted in some cases often they cannot since information from controlled experiments has not been available.

The lessons from the above example are many and include having a control program in place before a release and utilizing experimental data to base predictions of possible system impact. Importantly the total impact of the introduction should be carefully considered before release.

22.12 THE COSTS AND BENEFITS OF CONTROL

Once an invading species becomes established eradication may become virtually impossible, although there are some success stories, more so for animals than for plants (Macdonald *et al.*, this volume). Attempts to completely eradicate pest insects have generally been costly exercise that in time fail and occasionally cause environmental damage (Dahlsten, 1986). Greater emphasis is generally placed on keeping populations of invading organisms down to an acceptable level. Usher (1988) has proposed that the most likely cases of successful eradication of invading mammals will be those which are naturally poor dispersers and occupy a circumscribed geographical locality.

Since most generally there are no target-specific eradication methods for most kinds of organisms there will be unavoidable elimination of individuals of other species in addition to the adverse environmental effects. The question of whether control efforts are positive depends on the effect the invader is having on the system in relation to the possible effects of the controlling methods utilized. Whether control is actually attempted depends on the economics of the effort as well as the public perception of the problem.

Comprehensive approaches to pest control (integrated pest management) that carefully consider the control options (mechanical, chemical, and biological); the details of the biology of the target organisms; and the economic, social, and ecological impacts of control efforts have unfortunately not been utilized extensively against invasive organisms in rangelands or natural ecosystems (Kluge *et al.*, 1986). The needs are there and the techniques are available for these approaches, but evidently economics has limited their application.

22.13 THE NEW ORDER

The characteristics of the earth we inhabit are being transformed at an ever accelerating rate principally due to the burgeoning human population and accopanying industrialization. Our atmosphere is being transformed as are our waterways. The terrestrial landscapes are being modified, in many instances, inalterably. Eight of the 30 major global vegetation types have been reduced to between 25 and 45% of their original area. Thirteen percent of the total ice-free area has been totally transformed by cultivation (Macdonald *et al.*, this volume). In specific regions the impact of agriculture has been profound. In Great Britain agriculture affects 80% of the land surface and the native vegetation was mostly destroyed several hundred of years ago (Heywood, this volume).

All of these alterations are providing a new landscape with an abundance of disturbed habitats favoring organisms with certain traits. This massive alteration of the biosphere has occurred in conjunction with the disintegration of the great barriers to migration and interchange of biota between continents due to the development by human of long-distance mass transport systems. The introduction of a propagule of an organisms from one region to a distant one has changed from a highly unlikely event to a certainty. The establishment and spread of certain kinds of organisms in these modified habitats, wherever they may occur, is enhanced. The net result of these events is a new biological order. Favored organisms are now found throughout the world and in ever increasing numbers. It is evident that these changes have not yet totally stabilized either in the Old or New World. In the former the success of invading species has changed through time with differing cultural practices and new directions and modes of transport. Old invaders are being replaced by new ones (Heywood, this volume). In the New World additional invading species are still being added.

The kinds of disruptions that non-intentionally introduced invading species can play in natural systems have been outlined above and have been the focus of the SCOPE study. These disruptions may in time stabilize on the basis of a new system equilibrium. Usher (1988) gives an example of the development of a co-existence between invading mink and native ducks in Sweden. Where at first there was widespread destruction of ducks by the mink within a couple of decades an apparent equilibrium has been reached between a stable mink population and nesting ducks. Usher comments that recent invaders may have a greater impact on a new community than long-standing invading species.

Not much attention has been centered on the ecosystem role that these invading species may serve in repairing disrupted systems. As one example, weedy herbaceous invaders may be more effective in sequestering the nitrate that is released from disturbed soils than the natives. Many of these invading species may provide fuel, fiber, and wood for certain societies although in others they may interfere with human activities and goals, e.g. papyrus, cat-tail, common reed (National Academy of Sciences, 1977).

Another viewpoint on the new order is provided by Wells *et al.* (1986), who noted that in South Africa 'most of our alien invader plants were intentional introductions and it is extremely likely that many of the rest were transported in association with them. Since these imports were made to establish industries and gardens, the problems associated with today's plant invaders can be seen as a tax being paid by the community for the prosperity and emenities that have been and are still being enjoyed'.

22.14 INVASIONS BY GENETICALLY DESIGNED ORGANISMS

An issue with which the scientific community at large is debating is the intentional introduction of genetically engineered species. What have we learned from the

SCOPE invasions program that may be of use in considering the release of genetically engineered organisms (GEO) into the environment?

First, there are many components of the issue that must be considered. These include those factors that are involved in the success of establishment and maintenance of the populations of interest. The lessons from the SCOPE program indicate that there are *general* rules for predicting success for a given organism type. However, it is clear that a detailed knowledge of the natural history of the GEO and of the characteristics of the target environment will be required if we are to make accurate predictions about organism performance in the open environment. There is no escaping the fact, however, that careful experimentation will be required to provide the information necessary to make such releases 'safe'.

Then there is the issue of spread out of the target area. If the factors for success of the GEO are the same outside of the target area as within, the organism will likely spread depending primarily on the dispersal properties of the organisms. As has been shown repeatedly, organisms of all types are accidently transferred from one region to another dependent on the degree of and direction of movement of vectors especially humans. It has further been shown that once established it may become extremely difficult to completely eradicate an invader. The lesson is that in many cases there will be no recall once a species becomes established and begins to spread.

There is abundant evidence of the considerable impact certain invading species have on the systems they colonize. Again general predictions can be made based on the properties of the invader. Introductions that perform a system function considerably different from that of the resident species can have a large impact. This may be of particular concern with GEOs since in many cases unusual functional features in relation to those of other members of the systems would generally be desired. Further introductions that assume a 'keystone' role in the organization of the total community can also have a potentially large impact. These are general guidelines that would need to be tested experimentally for any particular case.

Many of the cases of good intent in purposeful introductions that ultimately have bad consequences stem from a narrow view of the potential good that can come from the introduction. Often the desired feature of the organisms is considered in isolation from the total impact that the organism will have on the target system as well as on those who depend on that system for a variety of purposes. The potential effects of release must be considered in a total system context.

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