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Summary and Conclusions: Characteristics and Consequences of Biological Invasions

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Summary and conclusions: characteristics and consequences of biological invasions

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INTRODUCTION: THE CENTRAL QUESTIONS ABOUT INVASIONS

The mechanisms of colonization, competition and extinction have fascinated biologists since they began to appreciate that ecological patterns, however stable they might appear, are the outcome of complex dynamic interactions. The pioneer naturalists who recorded the similarities and differences between floras and faunas in different regions were often confronted by the question of whether todays patterns were the relict consequence of processes that operated in the past but no longer did no, or could be explained by the dispersal capacity of species in a world with todays geography. Darwin and Hooker corresponded over the cause of the floristic and faunistic similarities between widely separated temperate lands in the southern hemisphere, and Darwin once wrote to Hooker about one widely dispersed island tree 'I believe you are afraid to send me a ripe *Edwardsia* pod lest I should float it from New Zealand to Chile'. The study of the disjunct and distinctive biotas of oceanic islands has always involved assumptions (if not calculations) about the isolating influence of ocean barriers and about the rates of colonization as a source of new genes diluting the pool already present and moderating the trend towards endemism.

The vulnerability of such disjunct, impoverished, highly endemic island biotas to change following human settlement, with its accompanying disturbance of natural ecosystems and introduction of plants and animals, including mammalian herbivores, previously excluded by ocean barriers, itself became accepted wisdom in ecological literature at an early stage. The accelerated flux of species between continents, also linked to human impact, has become a matter of both academic fascination and practical concern. Nearly 30 years ago, Elton (1958) pointed out that the study of biological invasions brought together aspects of faunal history, ecology and conservation. He also posed a number of central questions, which the papers in this volume seek to answer. Why have some species, like the malaria mosquito (*Anopheles gambiae*), the asiatic chestnut blight (*Entothia parasitica*), the muskrat (*Ondatra zibethica*), the starling (*Sturnus vulgaris*), the cord-grass (*Spartina anglica*), the sea lamprey (*Petromyzon marinus*) or the chinese mitten crab (*Eriocheir sinensis*) spread dramatically, apparently into undisturbed habitats, after their introduction into other continents, whereas other species, carried to new lands in a deliberate policy of introduction, failed? More seriously today, as people travel ever more widely and disturb the world's natural pattern on an ever-broadening scale (for example converting eleven million hectares of tropical forest to cultivation, rangeland or secondary woodland every year) what kind of opportunistic colonist will take advantage of the new situations, and what problems will this create? How far can we predict invasions by those highly successful species we call pests? How far can ecological management techniques make

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† The views expressed in this paper are those of the author and not necessarily those of the Department of the Environment.

environmental systems resistant to them so that we avoid the cost and secondary effects of chemical control? What principles must we apply if we want to maintain the world's genetic richness in samples of natural ecosystem that will resist invaders?

The papers in this volume were chosen to have a strong quantitative component. Their aim is to provide more than mere anecdotes of biological destiny. They address three questions, posed by the Scientific Committee on Problems of the Environment (SCOPE) in its programme on the ecology of invasions, which are not significantly different from those posed by Elton (1958). These questions, set out by Williamson & Brown (this symposium), but reordered here, are:

1. What properties of a species make it capable of dispersion to invade new habitats, and what features determine whether it will successfully establish itself if it does arrive in a new setting?
2. What features of a receiving habitat (physical or biological) make it prone to invasion?
3. What management strategies are appropriate to control invading species?

The papers in this volume do not address these questions with equal weight. Less emphasis is placed on the factors governing species dispersal than on those determining establishment, less on the role of habitats than on that of species, and very little consideration is given to management questions. In this paper of summary and conclusion, an attempt is made to redress the balance.

Dispersion

It is an often neglected fact that species do not disperse. Individual organisms do, whether as plant propagules or immature or adult animals. Such individuals (unless from a genetically uniform clone) carry only a fraction of the genetic variability of the parent stock; there is therefore an element of lottery in the process from the start. The physiological condition of those dispersing individuals can also be crucial to their invasive success. For example, many bird stragglers to oceanic islands arrive with severely depleted body reserves, so that individual survival in an inclement season must be in jeopardy even if climates are matched, food is potentially available and enemies and competitors are not impossibly resistant. These individual features introduce a stochastic element into the system at the outset.

The classic display of dispersion capacity is transoceanic. The floras of many young, isolated island habitats contain a high proportion of bryophytes and pteridophytes, which produce large numbers of small, airborne spores. An extreme example of what such dispersion can do is provided by the concentrically zoned hepatic and moss communities, studded with small basidiomycete fungi and with lichens in the outer zones, around steam-emitting fumaroles on the isolated volcanoes of the South Sandwich Islands in the Atlantic sector of the maritime Antarctic, some of them on flows probably erupted only a few decades ago (Longton & Holdgate 1979). Clearly, the actual business of dispersion is not limiting in such wind-distributed *r*-strategists; it is habitat match that counts. More generally, cryptogams with light propagules, clearly likely to experience transoceanic spread by wind, do occur in larger than normal proportions on oceanic islands (see, for example, Wallace 1880; Ridley 1930; Wace 1960; Wace & Dickson 1965). Grime (this symposium) states, however, that the ease of dispersion of pteridophytes is not matched by success as actual colonists in the habitats he has studied, showing again the key role of habitat interactions. Various authors (e.g. Van Steenis 1936; Cain 1944; Good 1953) have also pointed out that within the angiosperms there are less clear relations between seed type and successful colonization of remote islands.

The invertebrate faunas of remote islands show certain parallels with the makeup of aerial plankton, and the relation can be surprisingly exact at the generic level, as Holdgate's (1965) analysis of the fauna of Tristan da Cunha shows. Less obvious candidates for wind dispersion, although within the theoretical scope of the model developed by Mollison (this symposium), but candidates for marine drift on vegetation masses and driftwood, also include gasteropods and curculionid beetles, which are common on temperate islands around the southern hemisphere and show considerable radiation onto food plants that are unlikely to be the same as those of their ancestral continental forms.

The problem with such analyses is that many are essays in *post hoc* rationalization. Looking at a species on an oceanic island, it is often easy to frame a plausible hypothesis of how it got there. Sometimes experimental tests may confirm field observations. For example, the leguminous shrubs of the section Tetrapterae of the genus *Sophora* are widely distributed in the temperate regions of the Southern Hemisphere, occurring in New Zealand, Southern Chile, and the oceanic habitats of Islas Juan Fernandez, Easter Island, Hawaii, Marquesas Islands, Rapa, Austral Island, Lord Howe Island, Chatham Islands, Réunion and Gough Island (Wace & Dickson 1965). It was originally thought that the stout, rather corky pods of the genus might float and account for this pattern. But observations in Southern Chile indicate that the pods split on the trees, and because the species is in part a streamside one, the seeds are liable to be scattered into rivers and so reach the sea. They were noted in the sand on the west coast of the island of Chiloé in Southern Chile in December 1958 (E. J. Godley, personal communication), and experiments showed that, of eight seeds put into sea water 10 months after gathering from the tree, three floated for three years, and two of these germinated successfully (Godley, in Wace & Dickson 1965). More direct tests of dispersion capacity, by trapping of spores and insects on remote islands or at sea (as undertaken by Gressitt and others; see, for example, Yoshimoto & Gressitt 1961), would be a useful validation exercise, especially if preceded by hypotheses of the expected patterns.

Although there appears to be a broad relation between ease of dispersion and establishment, at least for some taxonomic groups, it is clearly not exact. Many more species disperse than succeed in establishing viable populations. However, records of the dispersion process are very incomplete. Records of invertebrate vagrants to remote islands are, for example, few because of limited trapping. Massive dispersion incidents may, however, be less rare than we suppose. There are anecdotal pointers in that direction; for example, on 6 December 1833, Darwin (1845) set down a record of several observations of 'vast numbers of butterflies' accompanied by some moths and Hymenoptera and one coleopteran some miles off the Atlantic coast of Patagonia. On 17 November 1961, in much the same area, with a warm offshore *pampero* wind blowing, I recorded vast numbers of Macrolepidoptera and Odonata moving over the waters of the estuary of Rio de la Plata and a few Odonata were still alive 4 days later aboard the RRS *John Biscoe* on her arrival at Stanley, Falkland Islands (Holdgate 1965). A few spectacular arrivals of invertebrates on oceanic islands have been recorded, like the large Brazilian moth *Othreis apta* Walker, taken at light on Gough Island in the mid-South Atlantic, over 2750 km from South America, and several other South American insect stragglers recorded elsewhere in the Tristan da Cunha group (Holdgate 1965). It is reasonable to deduce that there must be a continuous 'rain' of invertebrates over the great oceans, largely unrecorded by scientists. Such dispersion is likely to be episodic, associated with particular meteorological conditions. The same is believed to hold good for the dispersal of bird vagrants across oceans such as the Atlantic.

Just as there are reasons to suspect that different taxonomic groups differ in their dispersion frequency, so it is plausible to argue that ease of dispersion may vary as atmospheric and oceanic circulations change over the millennia. Coope (this symposium) suggests that short periods of critical oceanic circulation lasting a few centuries or so may have provided 'windows' for immigration to the north Atlantic islands, and emphasizes that climatic and geographical history must be known in order to make sense of distributions.

INVASION

Coope (this symposium) stresses the importance of a match between climate at source and in the receiving habitats as a major determinant of successful establishment. The analysis of climatic similarities is itself a topic for much current research, and for oceanic habitats there are indications that the analysis of the relation between seasonal and diurnal temperature ranges may be a valuable predictive tool (Nix, cited by Gibbs, in discussion; N. M. Wace, personal communication). What is clear from the papers in the present discussion is that many species reach potential new habitats, but that establishment depends critically on habitat features and that success may have counterintuitive attributes.

Such distinctions between dispersive capacity and invasive power emerge from the analysis by O'Connor (this symposium) of British and Irish avifaunas. He demonstrates that long-distance dispersive powers as illustrated by seasonal migration are not the key to establishment. Non-migrant species produce more young per brood and season, and dominate favourable habitats, extending and contracting their range as climatic and other conditions vary. Migrants are shown to be marginal in the system, taking seasonal food surpluses, and they are less productive of young. Accordingly, the successful bird colonists are the less frequently translocated sedentary species, whose high reproductive capacity enables them to establish a population swiftly once colonization occurs.

O'Connor demonstrates that, in Britain, new colonization has taken place, particularly in Scotland and southeast England, especially where a trickle-feed of new immigrants is most likely to help the process. His general conclusion is reinforced by evidence from southern hemisphere oceanic islands, where there are numerous records of episodic arrivals of straggling migrants, such as swallows, egrets, blue herons and sandpipers, at times when weather patterns drive individuals off track. One of the most fascinating examples is provided by the American purple gallinule, *Porphyrula martinica*, which migrates seasonally along the Atlantic coast of South America and is a regular vagrant on Tristan da Cunha, surviving there for weeks at a time, but not remaining to breed. Individuals of this species, whether or not strengthened by feeding on the mid-Atlantic islands, have been known to move right across the ocean to reach South Africa. In contrast, the resident flightless gallinule on Tristan da Cunha and Gough Island is a *Gallinula* species from a non-migratory genus, which incidentally has a very high reproductive capacity (Wilson & Swales 1958).

The papers in this meeting may perhaps be criticized for not discriminating as clearly as they should between long-distance dispersion (or dispersion that jumps to new areas) and the more continuous spread of species over continental habitats, imprecise though the distinction may be. There has also been imprecision in the use of the terms 'colonization' and 'invasion', although this is usefully resolved by Gray (in discussion of Grime, this symposium), who defines colonizers as a subset of invaders, specializing in disturbed areas. The implication is that invasion is a larger-scale process than colonization. Several papers deal with the spread of species through continuous land and water habitats, and with the invasion of new host populations by pathogens (Williamson & Brown; Bennett; Hickley; Ross & Tittensor; Anderson & May).

Bennett's references to data on the rapid rate of northward extension of range of *Quercus* and *Fagus* in the postglacial are striking, with implied advances of up to 1 km per year, and populations doubling in a few decades. There may be parallels with O'Connor's analysis of birds, in that both can involve sudden extensions of varying distance from an advancing front, and outward spread thereafter; both also involve failure and withdrawal from time to time at the margins. Rates of spread clearly depend critically on interactions of species with habitats, and these (with differing sources from refugia and differing competitive patterns) appear to underlie the contrasting forest development sequences in Europe in the different interglacials. In a similar way, species–habitat interactions explain the slow spread of the predatory fish described by Hickley (this symposium), which succeeded only in slow waters and appeared largely man-dispersed, with natural spread of at most 0.5 km per year, and that by the extension of range of non-reproductive individuals. Muskrat and grey squirrel, reviewed by Williamson & Brown (this symposium) and mink and coypu, covered by Usher (this symposium), show steady advances at rates of the order of kilometres or tens of kilometres per year and a near-linear relation between the square root of the area invaded by the first two species and time; this result suggests that there is little ecological obstruction to invasion. At the other extreme, the dramatic invasions of rabbit populations by myxoma virus, described by Ross & Tittensor (this symposium) at 5 km per day in Australia and up to 0.5 km per day in Britain in the initial stages, demonstrate the potential of a virulent pathogen when a mobile vector like a mosquito is also available. The detailed analysis of the myxoma study indicates clearly that modelling must take account of the interactive processes between pathogen, vector and host, and this also comes out from Anderson & May's analysis of virulent human infections, including plague, rabies and AIDS.

Establishment and impact

Many disperse, but few establish. Williamson & Brown (this symposium) analyse the pattern in Britain, concluding that about 10 % of introductions succeed in establishing themselves, and about 10 % of these become numerous and ecologically disruptive enough to be termed 'pests', a term whose imprecision they recognize and which others rightly castigated in the course of discussion. What is interesting in their analysis, and that of Lawton & Brown (this symposium) is the counterintuitive aspect of the process. The former authors state that smaller families are proportionately more likely sources of successful colonists, and that, when major taxonomic groups are compared, larger organisms do better than smaller ones. Lawton & Brown find the inverse relation within the insects, with a much stronger correlation. Both relations pose questions: first, as to whether the data are spurious, being skewed by uneven observation, and second, as to what the cause might be.

The invasion of hosts by pathogens clearly provides a model that attracts because the systems have a superficial appearance of simplicity and the parameters appear more susceptible to measurement. Anderson & May (this symposium) show yet again that two-species systems can be modelled fairly readily but three-species systems continue to pose difficulties. Mollison (this symposium) returns to this point, demonstrating the use of relatively simple models covering such attributes as dispersal, colonization, persistence, equilibrium and stability. Those who recall the 'mega-models' of the IBP, with their very large number of terms and attempts at synthesis of the behaviour of very complex systems, will be inclined to agree with Mollison in rejecting undue complexity. Crawley (this symposium) argues for somewhat more complex models than Mollison's, involving six central parameters: increase rate, resource limitation effects, interference effects, natural enemy effects, mutualist effects, and immigration effects. He demonstrates that analysis based on the demographic parameters he lists seems to fit the data. Perhaps the key point is that models should never be over complicated and that there should always be critical questions about the need to include particular terms (given adequate data to permit this to be done in a meaningful way). The omission of terms whose value is doubtful or whose quantification cannot be reasonably undertaken is probably wiser than their inclusion on theoretical grounds when the actual values entered are largely guesswork.

The papers about pathogens in this volume demonstrate that the establishment of these, as of other species, depends very much on habitat circumstances. For myxomatosis, the availability of a vector was crucial, whereas the persistence of measles depends on a sufficient host population: Anderson & May (this symposium) demonstrate that the population was not sufficient to sustain the disease in Iceland. For rabies, the critical ratio appears to be that between the production of young foxes in the host population and the high mortality rate of the disease itself. The importance of habitat change arises here, with the reminder that human aggregation in large groups was the key to the availability of our species to pathogens that previously infected other organisms. A shift in human social tolerance has clearly been an important factor in permitting the spread of AIDS, although less clearly in its invasion from macaque monkeys, if that indeed has been its origin. Southwood (in discussion of Anderson & May) comments that this is not without parallel in the wider ecological world, with the colonization of conifer habitats in England by species that presumably reached the southern counties regularly over recent centuries, but failed to establish themselves for want of sufficient food plants.

Lawton & Brown (this symposium) return to certain hypotheses about establishment that were posed by Williamson & Brown at the outset of this volume. The latter authors comment that traditional wisdom says that invadable habitats are open and disturbed (whether by erosion, glaciation, fire or human agency); that invading species are likely to come from climatically matched zones; that such species are probably r-strategists because rapid spread helps establishment; that they are likely also to be able to compete successfully with pre-existing biota (more of a K-character); that a lack of natural enemies in the new habitat is an advantage, and that such species are characterized by high inbreeding, and succeed by finding an empty niche. Williamson & Brown point out that the latter argument is circular: success succeeds. As to the other characteristics, these authors demonstrate that none of the generalizations is universally true. Some invaders, for example, appear to match the ecological characteristics of those already present, as the winter-peak diatom *Biddulphia sinensis* matches *B. mobiliensis* in the Irish Sea.

Lawton & Brown draw together the pattern which emerges from the unruly, multivariate ecological world. They conclude that invasive ability is likely to be related to a low coefficient of variation in population size, high r (although this alone is not a main determinate of invasion), high K (in the sense of high potential population size) and avoidance of high mortality due to enemies or competitors. No single factor dominates; nor are the same ones important in all circumstances. This is evident if the examples in the case studies in this volume are examined and scored against Lawton & Brown's parameters.

The parallels with the plant colonization patterns examined by Grime (this symposium) are obvious and interesting. Grime also examines the balance between the intrinsic properties of species and the characteristics of habitats as determinants of colonization of localised, small, man-made and rather specialized, mineral-rich sites. Dispersal, notably by wind, but also by seeds entrapped on mud on vehicles, has clearly been one key factor. Grime's analysis demonstrates an interplay in that dispersion mechanisms are clearly important in 'spoil specialists' as they are (by a rather obvious circularity) in 'oceanic island specialists', but not so important for other, more opportunist, colonists, where high population densities in the general region and high reproductive capacity appear crucial. The parallels with O'Connor's analysis (this symposium) of birds are interesting, and superficially appear to be in accord.

Is there something genetically special about colonizers? Gray (this symposium) proposes the question but seems to demolish it equally effectively. His paper shows that the alleged relation between polyploidy and colonizing potential does not emerge clearly from analysis, perhaps partly because of confounding variables. Genetic characteristics of invaders are not easy to establish, for these reasons; the best approach is likely to be experimental, where founder populations of known genetic makeup are tested in particular situations – always assuming that we do not allow new pests to emerge thereby. Harper (in discussion) makes a rather similar point in saying that the *post hoc* rationalization of how success has succeeded is likely to be less stimulating than the question of why particular organisms have not invaded apparently suitable situations. Joysey (in discussion) also emphasizes the need for much better understanding of whether a source population and an invader are genetically the same and if not, how they differ.

MANAGEMENT

Finally, we turn to questions of prediction and management. Anderson & May (this symposium) make some suggestions about the likely course of AIDS infections, showing the sensitivity of predicted peak infection and mortality levels to assumptions about the incidence of the actual disease, with its high mortality in seropositive cases. It is clear that social, behavioural measures, reducing the frequency of sexual contact, may be crucial in containment and more effective in the short-to mid-term, if not on a longer timescale, than any vaccine is likely to be. Mollison (this symposium) comments more generally that the models now available are helpful in giving qualitative and sometimes quantitative explanations on a basis of explicit logic, but they are not predictive, and the output often depends on one or two central parameters, such as the net reproductive rate, R_0.

If we are to maintain assemblages of natural vegetation as reservoirs of genetic diversity, as we clearly wish to do on nature reserves, we will also be concerned that they do not undergo ecological change as a result of invasion. Usher (this symposium) is reassuring to the extent that, even on oceanic islands like the Hawaiian group, with a large number of introduced plants, few species are actually invasive of undisturbed habitats. The same is true of South Atlantic temperate oceanic islands. However, Usher's paper shows the major ecological disruption that an aggressive undershrub like *Rhododendron ponticum* can cause, especially if aided by an introduced herbivore such as sika deer (*Cervus nippon*). This paper also displays the difference between species, and the problems of stopping invasive species once established.

Grime (this symposium) makes a point which has more than a touch of predictive significance. He points out that in Britain we have moved from a flora dominated by long-lived, slow-growing species with conservative reproductive strategies to more rapidly growing, short-lived r-strategist species, and he correlates this with human disturbance and eutrophication. In the tropics, deforestation is also removing classic K-strategist forest trees, but with impoverishment rather than eutrophication. The dominants of those stripped soils are certainly going to differ in life strategies from those on nutrient-enriched, cleared land, but if we can work out a fundamental classification of organisms, as Grime proposes, and build into it the fourth dimension of habitat as Southwood advocates in discussion, and make the whole model operational by being able actually to measure each variable as a true independent without automatically constraining the others (Harper, in discussion) we may then have something that will put land management on a sounder ecological basis.

Crawley concludes the series in this volume by analysing the data available for successful invasions of plants, especially *Opuntia* and *Lantana*, by control species, and the causes of success or failure. This paper also emphasizes the subtleties of success, for example in the account of successful biological control of a wrongly identified *Salvinia* species by a wrongly identified weevil, and, conversely, the failure of control of the oak knopper gall wasp, *Andricus quercuscalicis*, whose establishment in Britain occurred in the face of a whole series of potential enemies. It is conceivable that this is but a transient phase, and that the future will bring the progressive extension in habit of these control species so as to curb *A. quercuscalicis* in Britain, as they apparently do in its country of origin.

Conclusions

Three questions were asked at the beginning of this paper, and in preparation for the meeting it summarizes. As a basic generalization, it does appear that r-strategist species, producing large numbers of small propagules or offspring, are more likely to disperse over long distances. Certainly some plant groups with light spores, produced in large numbers, appear to reach isolated and transient habitats where those with more restricted reproductive strategies fail. Similarly, small, light-bodied arthropods appear to be widely dispersed in air currents. The lesson of the papers in this volume is, surely, that invasion depends more on species–habitat interactions on arrival in a new setting than on the dispersion process itself.

There are reasons to expect that climatic and edaphic similarity between former and new settings will predispose to invasive success. In the broadest terms, it is obvious that this is so. Foresters and agriculturalists have succeeded with translocated cultivars in areas that are broadly matched to the source of the species they use. However, within such broad generalizations there are clearly more subtle features that are particularly relevant to the vigour with which a species invades spontaneously. High reproductive capacity appears to be important. There must be at least a significant degree of mobility, bringing penetration of new situations; its lack appears to be the reason for the limited spread of zander in Britain (Hickley, this symposium). Broad-spectrum species appear to do better than those restricted to a narrow habitat or food plant. Avoidance of sensitivity to variables liable to cause wide fluctuations in population size, and the potential to reach a high population size (which follows from the two preceding attributes) are all likely to be positive. Dependence on disturbance of a habitat by other species (including man) is less obviously favourable; because so much of the world environment is being disturbed, colonists of such situations are clearly at a premium, but disturbance as a prerequisite for success is clearly limiting.

It seems to follow that the habitats especially prone to invasion are those that are not near the extremes of ecological variation, but those that are matched climatically and in other ways in many places. Complex, multilayered, multi-species climax communities, developed over long periods of time, are reasonably expected to be more resistant than younger and simpler formations. The temperate regions, still exhibiting slow changes as a result of the glacial epochs, and the regions of variable Mediterranean climate, may be expected to be more invasible than warm, humid zones with ancient forests. Disturbed habitats, where the disturbance stops short of gross dissipation of soil fertility, so that many species that are climatically compatible can succeed, will be more readily invaded than those stripped down to impoverished bedrock or laterite. Potentially productive habitats opened up to colonists by human action will clearly be more invasible than those of inherently low productivity.

Management strategies can be expected to be of two kinds. One is to retain the ecosystem, whose protection from invasion is sought, in a condition as close as possible to that which has prevailed over its long history. Commonly, this means maintaining closed conditions, or, where cycles of fire are important to the habitat, permitting these at the historical rate. Even so, this will not provide proof against invasion, because of the changes in global biogeography that are being brought about by human activity. For tens of millions of years, the land habitats of the world have been divided by sea barriers, behind which floras and faunas of those taxa not capable of long-range dispersion have diverged. The world's continents and islands exhibit much greater biological diversity than appears to have prevailed in preceding epochs when the continents were linked in a Pangaea or even a Gondwanaland. Human dispersive agencies are now acting to eliminate such isolation and translocate many species. This process can be expected to continue, and with it invasion must become a normal feature of global biogeography. Avoidance of disturbance can at best reduce the magnitude and rate of change, because it keeps out that substantial fraction of invaders that are colonists of disturbed ecosystems but show little success otherwise.

The other management strategy is interventionist. It involves deliberate action to remove invaders or suppress their spread by translocating control agencies. The analyses by Lawton & Brown and Crawley (this symposium) are pertinent here. It may, however, be postulated that this type of management will largely be concerned with damage limitation, that the examples of successful elimination of an invader (like that of muskrat from Britain) will remain limited, and that success in most cases will be reflected in the reduction of the invader's population size to a level that is compatible with the perpetuation of the invaded ecosystems in only slightly altered form. It is in the nature of today's world that interventionist, rather than protectionist, management strategies are likely to be in greater demand, because an enormous area of the earth's habitable surface has already been transformed by human action. Substantial areas are dominated by introduced coniferous or eucalypt trees and imported rangeland grasses. A whole new dimension is now being added by the prospect of the release of genetically engineered microorganisms, as agents of pest control and as facilitators of colonization (for example, by the provision of built-in nitrogen fixation capability). Against this background, it is clear that a critical scientific understanding of the causes of biological invasions, and the means of their control, is crucial to the management of the planet. This area of science is far more than a fascinating intellectual diversion.

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