PHILOSOPHICAL TRANSACTIONS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

The Analysis and Modelling of British Invasions [and Discussion]

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Phil. Trans. R. Soc. Lond. B 1986 **314**, 505-522
doi: 10.1098/rstb.1986.0070

Phil. Trans. R. Soc. Lond. B **314**, 505–522 (1986)
Printed in Great Britain

The analysis and modelling of British invasions

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The SCOPE programme on the ecology of biological invasions addresses three questions: What are the factors that determine whether a species will become an invader or not? What are the site properties which determine whether an ecological system will be relatively prone to or resistant to invasion? How should management systems be developed to best advantage, given the knowledge gained by attempting to answer the first two questions? The answers that have been offered to these questions earlier, and during the course of the programme, are reviewed. The consensus is that, although certain habitat and biological features increase the probability of invasion and establishment, these features are neither necessary nor sufficient, and that the prediction of invasion is not yet feasible. These points are illustrated by examples and generalizations from a survey of British invaders. The probability that an established invader will be a pest in Britain seems to be around 10%. Mathematical modelling may help in understanding and, later, in predicting invasions. Models indicate that establishment may be more critical than spread, and that a successful invader will spread at a constant linear speed. Models and data suggest that both an accelerating rate of spread and occasional major jumps can be expected; consequently, efforts to eliminate an invader at an early stage will be the most effective.

GENERALIZATIONS ABOUT INVASIONS

The SCOPE Programme on the Ecology of Biological Invasions is concerned with important questions, which have been discussed for many years. In so far as there is conventional wisdom, it stems from the important 1964 symposium at Asilomar, California (Baker & Stebbins 1965), and from Elton's (1958) well known, useful and influential book. As there are extensive reviews in the other symposia of the SCOPE programme (Mooney & Drake 1986; Groves & Burdon 1986; Macdonald *et al.* 1986) we will just mention some salient points, so that the study of British invaders may be set in context. In table 1, we set out some of the features mentioned most frequently, and must note at once that none of these features seems either necessary or sufficient to account for observed invasions, let alone to predict future ones.

With regard to habitats, the most commonly expressed view is that disturbance, particularly man-made disturbance, is needed for a new species to invade. There is no doubt that many species do invade disturbed habitats and that synanthropic species and species of disturbed

TABLE 1. SOME SUGGESTED CHARACTERISTICS OF HABITATS AND INVASIVE SPECIES

(For origin and validity, see text.)

habitats:	disturbed open seasonally dry anthropogenic	
species:	from distant areas climatically matched	(origin)
	r selected high dispersal rate	(autecology)
	competition lack of natural enemies	(synecology)
	inbreeding single-parent reproduction	(genetic)
	finding an empty niche	(circular?)

habitats are nearly coterminous sets. Some workers, such as Harding & Sutton (1985), have used synanthropy as almost the only indicator of whether a species is an invader. Crawley (1987) directly addressed the first two questions of the SCOPE programme and showed the marked differences between the invasibility of different habitats, but concluded (perhaps going slightly beyond his data) that all habitats were invasible. For that matter, all habitats probably suffer natural disturbance to a greater or lesser extent. In the same way, generalizations that invasive species prefer open habitats or seasonally dry ones are best phrased as probabilistic statements, that species of such habitats are much more likely to be invaders. This topic is discussed further by O'Connor (this symposium).

There are features, associated with biological characters such as the origin, autecology, synecology and genetics of species, which have been thought to be useful indicators; some are listed in table 1. As with the habitat features, these seem at best to give an indication of the variable probability of an invader's success, and have very little value in predicting which species will next appear. The SCOPE programme talks about species from distant areas which arrived lacking their natural enemies; the papers of Lawton & Brown and Hickley (this symposium) are relevant. In this symposium, Coope discusses the climatic matching of species; we return to this topic below. Grime touches on the question of *r* selection, Bennett dispersal rates, and Gray the genetic factors. Studies of the interactions between the demographic aspects of species and their habitats underlie the papers of Anderson & May, Ross & Tittensor, and Crawley.

In table 1, we have distinguished between the characters of the species by itself as autecology, and those involving other species as synecology. One area of disagreement is the importance of species interaction in species establishment. Simberloff (1981) showed, from a survey of surveys, that most invaders (about 80% of his list) had no recorded effect on the indigenous species. This is perhaps not inconsistent with the view that a successful invader often lacks natural enemies in its new colonies. Certainly immunity from attack, especially perhaps from generalist predators, will result in a higher effective rate of natural increase. The parameter *r* is the intrinsic rate of natural increase, but what predatory effects are allowed for in its calculation is not always clear.

The most contentious point in table 1 is the question of *r* selection. Partly because of Stearns' work (1978), many ecologists now doubt the usefulness of the once fashionable *r–K* distinction, and in particular have not found successful invaders to be *r*-selected (Drake & Williamson 1986) although Crawley (1987), in a survey of successfully introduced biological control agents, found a correlation of *r* with success. In contrast, Newsome & Noble (1986) find a variety of character suites associated with invasion, which they label as competitors, gap grabbers, survivors, swampers, etc. They are in agreement with geneticists, such as Barrett & Richardson (1986) who conclude that 'there is no single optimal solution to the challenge facing the colonist'. The view that colonists need to find an empty niche has little value for prediction, as niches are in general only recognized once occupied, as Crawley (1987) notes. He also points out that many successful invaders are widespread and common in their country of origin.

The weakness of all these rules of thumb can perhaps be illustrated most simply, not by quantitative survey, but by discussing two marine species that seem to break most of the rules. The first is the planktonic diatom *Biddulphia sinensis*, which invaded the North Sea in 1903 (Ostenfeld 1908). It was a well-known species before the invasion, having first been described from Hong Kong harbour. It appeared to be a species of tropical waters, found from the Pacific around to the Red Sea in waters that are both warmer and of a higher salinity than any of those around northwest Europe. As there are already many European species of *Biddulphia*, both planktonic and benthonic, *B. sinensis* would seem an unlikely invader on any of the criteria of table 1. Neither its known habitat nor its biological characteristics suggested in any way that it could be an invasive species. Nevertheless, it spread rapidly through European waters and established itself as a permanent member of the plankton in the least saline and, in winter, coldest areas of the continental shelf (Robinson 1961). The reason for its success appeared to have been that it had found an empty niche; 'it differs from all others diatoms found in the Irish Sea in having its average peak of abundance in November' (Johnstone *et al.* 1924). Figure 1, and the analyses in Williamson (1987) show that this is only partly true. It does have its main peak of population in November, but from figure 1 it can be seen that it is not the dominant diatom even in November, and that the period of population abundance covers all of the colder half of the year when other diatoms, including other species of *Biddulphia*, are commoner. In a principal component analysis of the plankton of Port Erin Bay, Isle of Man, the effect of the invasion of *Biddulphia sinensis* was the dominant one on the community after the two principal components describing the standard seasonal cycle (Williamson 1986). So there are detectable though weak interactions with other species, rather than the occupation of an empty niche.

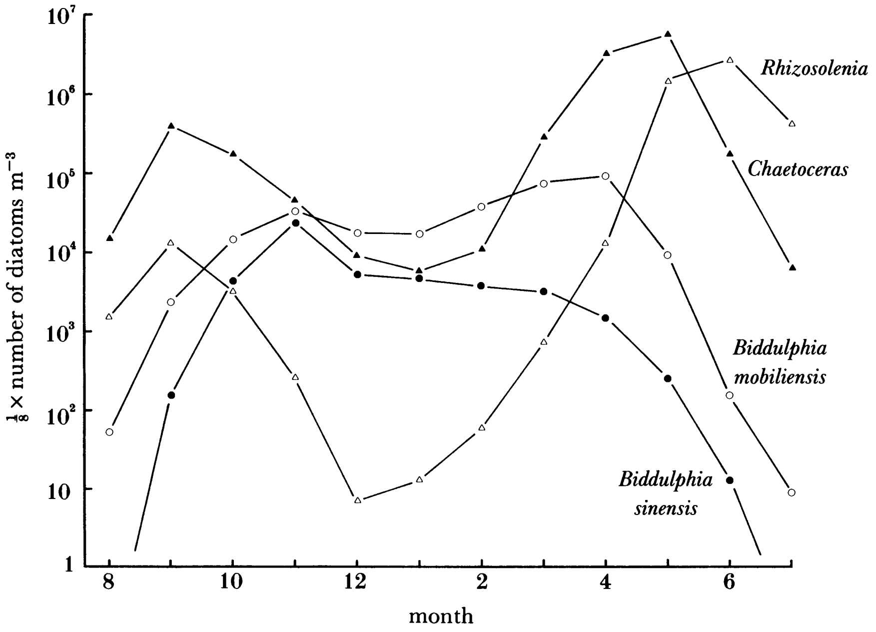

FIGURE 1. Average annual cycles of some diatoms in Port Erin Bay, Isle of Man. The year is shown from August to July to emphasise the pattern in winter. *Buddulphia sinensis* invaded in November 1909, and the data for it are for 1910–1920. For the other diatoms, the data are for 1907–1920. All average numbers are the squares of the averages of the square roots of the monthly data in Johnstone *et al.* (1924), and are plotted on a logarithmic scale.

The barnacle *Elminius modestus* is another example of a species from a remote area, in this case Australia, which has successfully invaded a community with similarly well-established species. It was first found on the south coast of England, and has now reached Shetland (Hiscock *et al.* 1978). Crisp (1958) tabulated in a semiquantitative way the partial overlap of the habitat requirement of *E. modestus* and indigenous British barnacles. *E. modestus* is notably tolerant of low-salinity sites around the high water mark, and so occupies zones further up estuaries than other barnacles; however, in the mid-zone of the ordinary rocky shore it settles in exactly the same areas as *Balanus balanoides*. In some cases the suppression of small specimens of *Balanus* by *Elminius* results in the remaining *Balanus* being individually larger than usual, healthy and successful.

What *Elminius modestus* and *Biddulphia sinensis* show is that, even in communities of relatively small number of species, in which the biology has been studied extensively, our knowledge is still insufficient for us to recognize empty niches in any useful way, and even insufficient to say quantitatively, after the event, what were the important characteristics that allowed the invasion to occur. Crawley (1987) gives similar examples from terrestrial plants and insects.

INVASIONS INTO BRITAIN

Background

The study of British invasions is a subjective process. Apart from a few arctic–alpine species, all the British biota have invaded in the last 10000 years or so (Bennett, this symposium; Coope, this symposium) and species continue to arrive both spontaneously and with varying amounts of assistance from man. We have attempted to study invasions in the last century or so, regarding earlier arrivals as indigenous. The definitions of such terms as 'introduced', 'established' and 'pest' are far from agreed, but the biggest difficulty in the way of a quantitative survey of British introductions is the variation in effort and taxonomic knowledge in different groups. For birds and mammals, where there are many amateur observers, where the taxonomy is reasonably established and where there are also archaeological and fossil records to call upon, it is possible to be reasonably sure which species have become introduced by man, or as a result of man's activities, in historical times, and which were here earlier.

We have surveyed the literature, consulted taxonomic experts, and attempted to count the number of invasive species in different taxonomic groups and to classify these as having become established or not, if established, how widely, and again if established, whether they have become a pest generally or in more restricted areas. The results of this survey are tabulated in Appendix 1. The object of doing the survey was to attempt to see how far it is possible to predict, from general biological features, which species will invade and which will become pests. The conclusion, which will not surprise field biologists, is that only rather general statements about probability can be made. On our present knowledge, almost any sort of species might become a pest; however, knowing that the probability of its doing so was low would be no consolation once it had become one.

In many groups, there is much uncertainty about which species are recent invaders. Some workers, as noted above, have taken synanthropy as an indicator, but that begs the question of what proportion of invaders are synanthropic. Others (Kloet & Hincks 1964–1978) have not attempted systematic listing, saying 'introductions established under natural conditions are not differentiated, as the total number of species that qualify for this category is unlikely to be discovered'. Nevertheless, there are clear records for invasions of many species, and there are at least three types of satisfactory evidence that a species has been introduced. The first is an historical record of such introduction, requiring good data before and after the introduction. Such data are available, for instance, for many birds; in Appendix 2 we list all those birds that have introduced themselves into Britain without the direct help of man, by extending their natural range. The second type of evidence is archaeological or palaeontological, and applies not only to vertebrates and molluscs, but also to some arthropod and plant groups (Coope, this symposium). The third type of evidence is when a species is associated only with another species known to be introduced. This can apply to certain insect herbivores, such as *Dendrocnotus* on spruce (*Picea*). However, the food preferences of insect species can change, and the extensive planting of a new agricultural crop may bring a previously native species up to the level at which its presence in the country is recognized (Strong *et al.* 1984). In our list we have attempted to exclude species found only in greenhouses and other habitats that do not match the general British environment, and we have tried to include only species that might establish populations here, that is excluding vagrants.

The concept of an established species, i.e. one where at least one population has been recorded continuously over many years, and which is reproducing in that population, is a rather more precise one than that of an introduced species. Whether a species is recorded as established only in one or two localities, or somewhat more widespread, or through the whole country, depends not only on the success of a species but also on the diligence of those who record it. Such information is reliable for most groups of vertebrates, arthropods and vascular plants, but much less reliable for fungi and nematodes, and totally unreliable for almost all groups of microorganisms. In these less worked groups there will be a clear bias towards recording introduced pests and diseases in species cultivated by man, at the expense of introductions that lack that impact.

There are also taxonomic difficulties, which result both from lack of work and from lack of agreement between workers on what constitutes a species. For many zoologists, the so-called 'biological species' concept (a set of individuals potentially capable of exchanging genes) is a general standard. Even here there are difficulties. Should the Sika deer (*Cervus nippon*), introduced from Eastern Asia and Japan, really by regarded as different from the red deer (*C. elaphus*)? The two species can hybridize, and it has been suggested that the Eastern Asiatic mainland populations are all hybrid (Lowe & Gardner 1975). By standard ornithological criteria, the Japanese races would be regarded as distinct subspecies. This does not alter the fact that the Japanese race has frequently been introduced into Britain and thrives. As is well known, the conventions in botany remain different, and a more morphological species concept is the rule. Consequently, interbreeding forms from different geographical regions, such as the European larch and the Japanese larch, are regarded as distinct species (*Larix decidua* and *L. kaempferi*) although, like the deer, they hybridize readily. The presence of microspecies in genera such as *Rubus* and *Hieracium*, and of chromosomal forms in other species, makes the comparison of botanical counts with zoological counts uncertain.

Generalizations

Despite the above difficulties, useful generalizations can be made. Four are discussed here; some others are discussed by Lawton & Brown (this symposium). The first is that, whereas the probability of a species' being introduced in relation to the number of species in the same taxonomic group that are already native varies very widely indeed, the proportions of introduced species becoming established and of established species becoming pests are very much more stable. The frequency of these three classes as a function of the total number of indigenous species, derived from Appendix 1, is shown in figure 2.

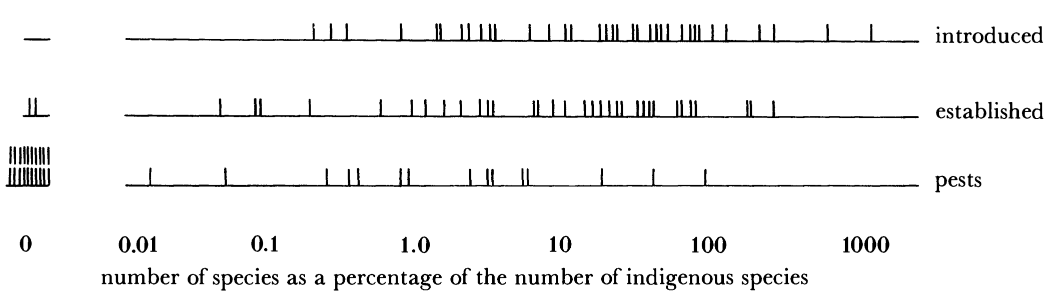

FIGURE 2. Introduced established and pest species shown as a percentage of the indigenous British species. The data for this figure are derived from Appendix 1. A pest species must be established, and an established species must have been introduced, so each distribution is to the left of the one above it. Despite the large variability in rates, the shifts are fairly consistent.

Some of the variation, however, relates to the difficulties discussed above. Perhaps unexpectedly, if one divides the established species into 'pests' and 'others', in three wide groups of vertebrates, insects and vascular plants, there is no significant difference in the proportions; about 1 in 9 becomes a pest ($\chi^2 = 3.8$, DF $= 2$). This figure is a useful starting point for discussing future introductions. Because the evidence is based on large, heterogeneous groups, and only three of them, it would perhaps be least misleading to say that it indicates that very roughly 10 % of established species become pests in Britain.

The second and third generalizations relate to plants. Figure 3 shows that plant families with many species globally are not only more likely to produce invaders, but are more likely to

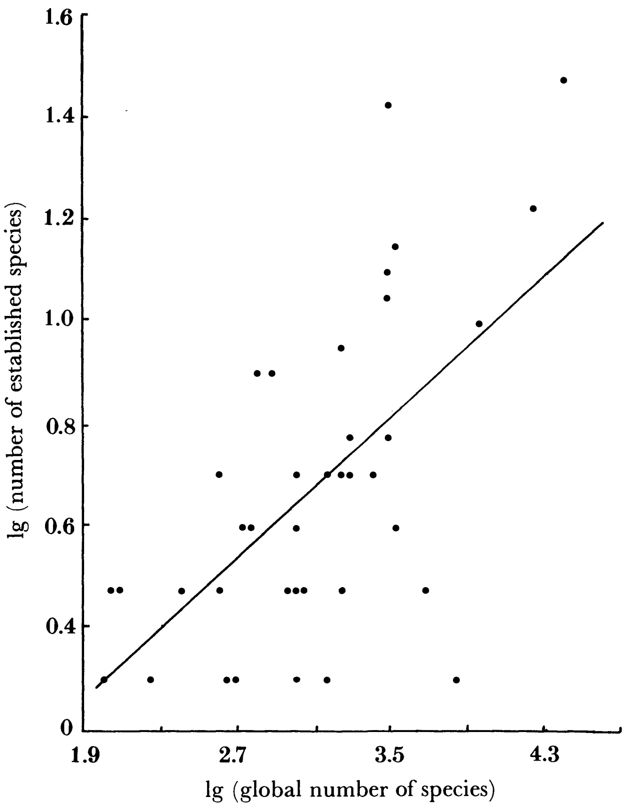

FIGURE 3. The positive relation between the number of angiosperm species in a family established at more than one or two places, and the global number of species in that family.

produce widespread established populations. The first part of that conclusion seems common sense, whereas the second part, shown in the figure, follows from the first generalization above, as shown in figure 2. However, figure 4 shows that this result hides some complexities. By defining an establishment coefficient, it is possible to remove the effect of family size. This coefficient compares the proportion of each family that has invaded Britain with the proportion for all families that have invaded Britain. Formally,

$$(f_B/f_W)/(a_B/a_W),$$

where f is the number of species in a plant family and a the total in all families that have invaded Britain. The subscript B refers to established invaders in Britain, W to the total species in the world (from Heywood (1978)). An establishment coefficient of 1 for a plant family means that that family has invaded Britain to an exactly average extent, as measured by the proportion of its global number of species that have invaded Britain. Values greater than 1 indicate a more successfully invasive family: values less than 1, less successful ones. The result (figure 4) is a strong negative relation, showing that on this criterion it is the smaller families globally that are more likely to produce successful invaders. Various speculations could be put forward to explain this. For instance, the smaller families globally might be small from a relative lack of dispersal ability, so leaving more species that could establish in Britain when their dispersal is assisted by man. Other explanations could involve niche size, but we have not been able to find sufficient critical data to test this. For the moment, we merely warn that generalizations about the probability of invasion, based on some measure of 'commonness', should be taken cautiously.

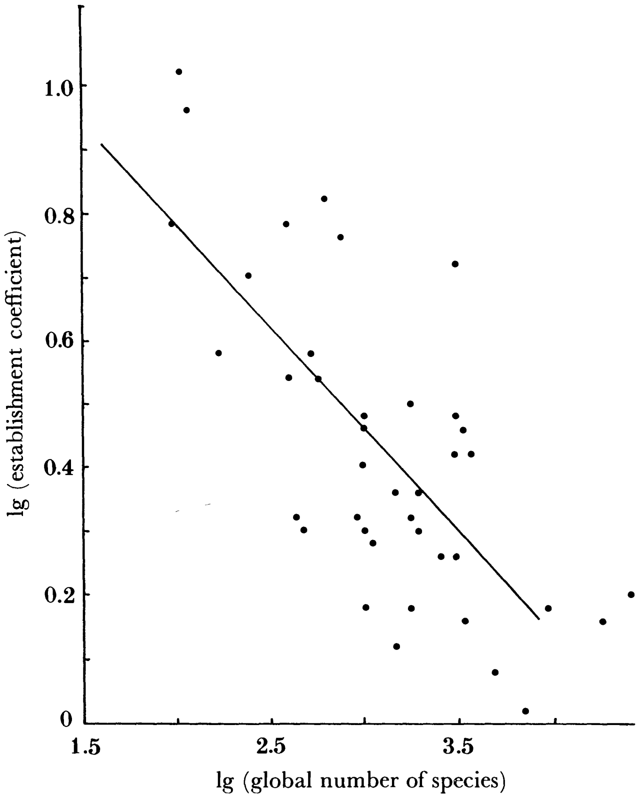

FIGURE 4. The negative relation of the establishment coefficient for invading angiosperm families and the global number of species in different families. The coefficient is defined in the text.

One factor that could be involved in the relation in figure 4 is easy to examine, namely the climate of origin. This seemed not to be involved in that relation, but our climatic analyses are rather broad. The fourth generalization presented here confirms the standard view that climatic matching is important in invasions, but shows that such matching is far from all-important.

A difficulty in testing the importance of climatic matching is that the information on the country of origin of many invading species is rather vague. We have therefore been forced to take very broad categories of climate; the major ones are shown in table 2. The climatic regions used here are derived from Fullard & Darby (1973). Tropical rain climates include both rain forest and savannah; dry climates include deserts and steppes. The distinction between warm temperate and cool temperature is based primarily on winter temperatures, so western Europe is classified as warm temperate. The number of invaders from cool temperate areas is small, and those from the fifth broad classification, of polar climates where there is no warm season at all and relatively few species, is negligible. The data in table 2 shows the percentage establishment at more than one locality out of the total number of recorded invaders for these four classifications for the three major groups. As expected, success is greater for invaders from so-called warm temperate regions. Nevertheless, both vertebrates and plants from tropical rain climates have a surprisingly high probability of success of establishment, much higher than insects from such habitats.

TABLE 2. PERCENTAGE OF INVASIVE SPECIES BECOMING ESTABLISHED AT MORE THAN ONE LOCALITY

climate	vertebrates	plants	insects
tropical rain	44	38	3.75
dry	53	44	21.6
warm temperate	66	56	35.1
cool temperate	33	66	50

These generalizations confirm the general view, discussed above, that invaders, and the invasive species that establish, are a distinctive subset of possible species, but nevertheless include representatives of almost all types of species. A new conclusion of practical import is that the probability of becoming a pest is not negligible, although the figure of 10% is only approximate.

THE VALUE OF MODELLING STUDIES

For a quantitative biologist, the conclusions from the study of table 1 are surprising. Characteristics like 'disturbed habitats' or 'empty niche', which are very difficult to put into quantitative terms, seem to have better predictive values than a quantitative measure, such as the intrinsic rate of natural increase, when comparisons are made between species. Can studies of mathematical models improve on this? Can they suggest which characteristics of an organism should be measured, and can they help in answering the third question of the SCOPE programme, on the techniques that should be used to manage invaders? A short report on the working party on mathematical models under the SCOPE programme has been published (Drake & Williamson 1986); a fuller report will appear in the SCOPE final volume on the programme. Here we set out the structure of the problem, and consider a few examples that are relevant to British invaders.

The process of invasion can be divided into arrival, establishment and spread. As with other terms in this field, precise definitions have not been generally agreed. In particular, we use 'establishment' as we have before, to mean an invasion leading to a firmly established, more or less permanent, population. It may sometimes be convenient to divide the arrival stage into the dispersal leading to an invasion and the initial colonization. Most colonists, as has been seen, will fail.

Although many mathematical models exist, analytic and simulation, deterministic and stochastic, simple and complex, that bear on the modelling of invasions, only two sets are sufficiently developed and well regarded to help managers directly. These are the epidemiology models, discussed in this symposium by Anderson & May and by Mollison, and models of the third division of the process of invasion, namely models of spread, reviewed by Okubo (1980). The modelling working party were of the view that, for practical purposes, the number of parameters should be kept small, and that the parameters should be measurable and interpretable. The advantage of such an approach has been shown, for instance, by Ludwig & Walters (1985), who showed, in a fisheries context, that predictions were more accurate from a simple model than from an age-structured one, because in the former the parameters could be estimated more accurately. The model of spread considered below may be important simply because it has only two parameters.

Colonization and establishment

On first arrival, the population of an invader will be small. There are many well-known biological effects that indicate that small populations may be more vulnerable than large, sometimes known collectively as the Allee effect, or as undercrowding. Individuals may have difficulty finding mates, the population may become inbred, competition from and predation by indigenous species may be stronger at low population densities, a small population may be more susceptible to extinction from chance events, and so on. If one also takes into account what is known of variation in the rate of spread (discussed below) it would seem that managers would be well advised to control invading populations at the earliest possible stage. The established quarantine procedures of many countries take this to the limit.

There is little agreement on how to model the processes involved in a colony becoming established. Ecologists do not agree on how communities are structured. For the SCOPE programme, models are required which would indicate which invasive species would disrupt the structure of communities, but that presupposes agreement on models of community structure. Simberloff (1981) argued that, as 80% of recorded invaders appeared to have no effect on the communities invaded, interactions are weak. However, it is the 20% where there are effects, some of them very striking, that are important to the SCOPE programme.

Some computer models of communities suggest further reasons why the process of establishment is difficult to understand. Post & Pimm (1983) and Drake (1983) built model communities, the latter with a pool of 125 species and the former with an infinite pool. The community built up by their assembly rules remained invasible for long periods, involving much species change, and new invaders sometimes produced cascades of extinction. These communities evolved towards stability, but it was difficult to see why particular sets of species were more stable than others. In some cases, the detailed history of succession seemed important. If this is so in model communities where all the parameters are known, it will be much more difficult to understand natural communities, if the interactions between species in the models are indeed a reasonable representation of natural communities.

Spread

The simplest model of spread relates to the spreading out of a homogeneous population, that is without age structure or other distinction, into a homogeneous environment. The population is presumed to be increasing exponentially, and diffusing outward randomly as in Brownian motion. This gives the expression

$$\frac{\delta n}{\delta t} = rn + k\frac{\delta^2 n}{\delta x^2},$$

where n is the population size, t time, r the intrinsic rate of natural increase and x the radial spatial dimension; k is the diffusivity (sometimes written as D,) and is equivalent to $\frac{1}{4}\sigma^2$ in two dimensions, where σ^2 measures the variance in position of individuals.

In this form, the equation was first studied by Kendall (1948) and, independently, by Skellam (1951) and is a simplification of the earlier genetical equations of Fisher (1937) and Kolmogoroff *et al.* (1937). Even these apparently simple partial differential equations have surprising mathematical complexities, discussed by Murray (1977). However, the basic ecological equation given above has an approximate asymptotic solution, namely

$$x/t = 2r^{\frac{1}{2}}k^{\frac{1}{2}}.$$

This represents a wave of advance with constant linear speed. Is this a good representation of what is actually seen in real populations?

Skellam (1951) examined the spread of the muskrat, *Ondatra zibethica*, in central Europe. Ulbrich (1930) published a map (reproduced in Elton (1958)) of the contours of spread of this American invasive species from 1905 to 1927. Skellam took just five of these contours, treated them as approximate circles and showed a satisfactory linear relation between the square root of the area and time. He did not estimate the parameters r and k.

Several questions can be asked. Is the square root of the area the best linearization of the time course of spread? Does it include all the salient features of the variability of spread? Can the parameters be estimated, and if so, are the estimates reasonable? We have examined the spread within each full contour given by Ulbrich, and also the rate of spread along the eight radii in the direction of the principal points of the compass. Somewhat different analyses have been made by Andow *et al.* (in preparation). We have also estimated the intrinsic rate of increase for the muskrat, and (from that and its rate of spread in Europe) estimated its diffusivity, k.

From figure 5, it is clear that the square root of the area plotted against time gives a good straight line, albeit with some slight variation, which comes out more strongly in figure 6. The logarithm of the area, and the area itself, both give strong curves over the 22-year period, though both might well be thought straight if data for only five or ten years, say, were available.

Figure 5 suggests that it is reasonable to follow Skellam and use the slope of the linear relation as an estimate of $(rk)^{\frac{1}{2}}$. Independent estimates of the slope, of r and of k, would test the consistency of the model, but these are not available. The intrinsic rate of natural increase can be estimated, roughly, from the known reproductive rate of muskrats, and guesses of the mortality may be obtained by using a modification of a Leslie matrix in which adult survival is independent of age (Williamson 1959). The transition matrix from September to September,

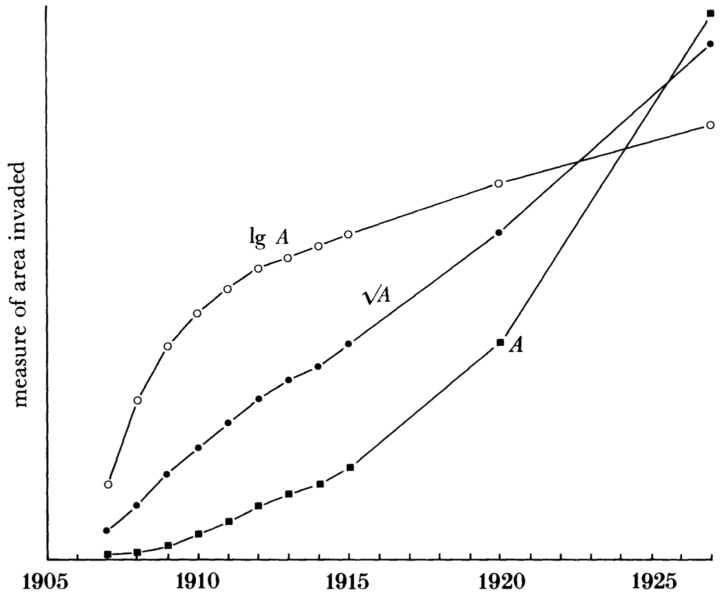

FIGURE 5. The rate of spread of the muskrat in central Europe, measured on different scales. The three graphs show the area occupied by muskrat (A), as measured from the map in Ulbrich (1930), plotted directly, as a square root and as a logarithm, with the scales adjusted so that the linearity of the graphs may be compared.

the end of the breeding season, derived from one brood of five animals from first-year muskrats, two of six from older ones, and a one-to-one sex ratio, is

$$\begin{bmatrix} 2.5 & 6.0 \\ 0.8 & 0.9 \end{bmatrix},$$

giving $r = 1.39$, in years. From this, $k = 22.97$, and the mean dispersal, $(8k/\pi)^{\frac{1}{2}}$, is 7.65 kilometres per year. As mean dispersal has not been measured, it is only possible to say that this seems plausible if rather high, particularly bearing in mind that this is a mean of random dispersal, with no interaction between individuals, and no habitat effects.

Examining the rate of spread along radii, on the other hand, suggests that dispersal may not be random. The rate of spread each year, and the distribution of such rates, is shown in figure 6. The median rate of spread seems to fluctuate in time, with fairly well-marked peaks in 1909 and 1922. Individual rates are very variable, from 0 up to almost 60 kilometres per year. The modal rate is 4.0 km per year, the median 8.2, the mean 11.3 and the standard deviation 10.04. The overall distribution of rates seems quite well behaved, but with a long tail.

The deviations from the expectations of the model are all such as to make control more difficult. The rate of spread perhaps fluctuates systematically, and, if so, may reflect the underlying population structure. The effect is an acceleration of spread in the first few years, an effect found more systematically and over longer periods in some other studies (Andow *et al.* in preparation; Easteal & Floyd 1986; Usher, this symposium). More seriously, there are occasional major leaps, an effect that Crisp (1958) thought was shown by the barnacle *Elminius modestus*, and predicted in some stochastic models (Mollison 1977).

Whether more elaborate models (discrete time, non-normal distributions and stochastic processes) would be sufficient to explain the very fast dispersal of forest trees since the end of

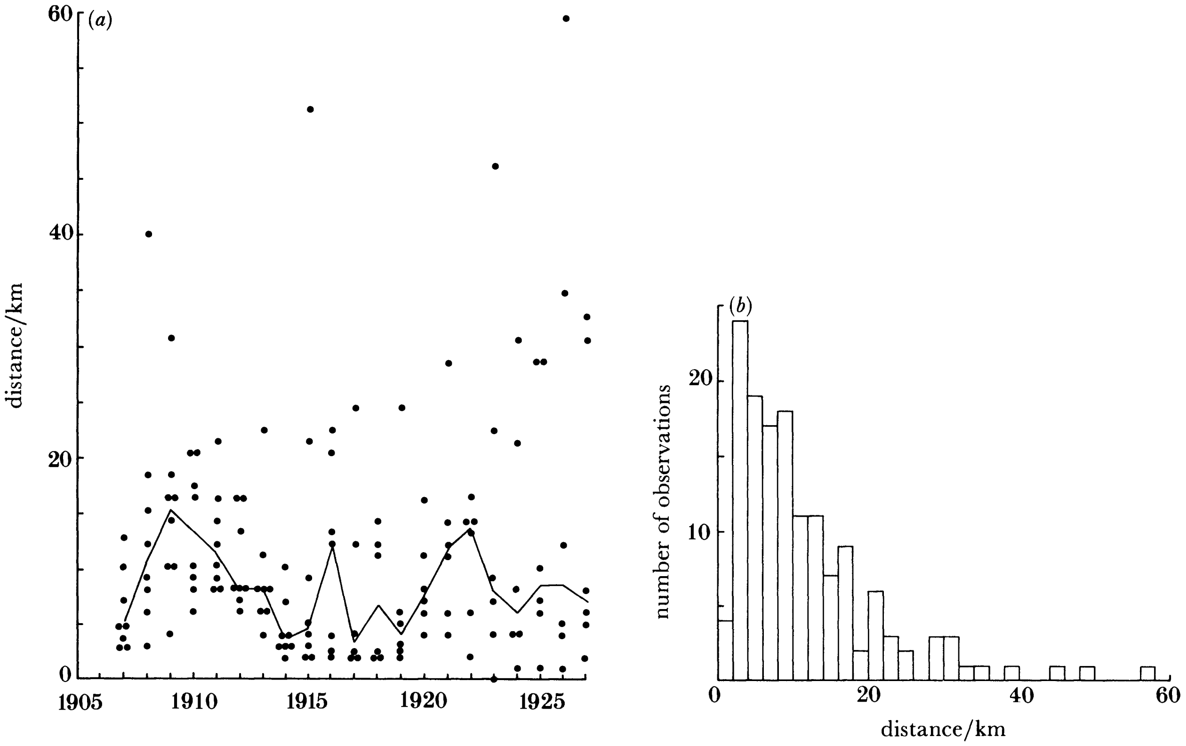

FIGURE 6. (*a*) The rate of spread of the muskrat in central Europe, measured along eight radii drawn on the map of Ulbrich (1930). Each point is a measurement between two contours on a radius. The continuous line is the median of the points. (*b*) Cumulative frequency of the data in (*a*).

the pleistocene (Skellam 1951; Bennett, this symposium) remains to be seen. What is clear is that a manager wishing to control such a population would be well advised to act as soon as possible.

There is no case known to us of an invader of Britain which spreads out quite so uniformly as the muskrat in central Europe, but the grey squirrel, *Sciurus carolinensis*, comes close to it. This was introduced from North America on a number of occasions in the nineteenth century and the early years of the twentieth centry. Lloyd (1983) summarizes what is known of its spread up to 1971. By that time grey squirrels had been recorded in all parts of England and Wales other than the offshore islands of the Isle of Wight and Anglesey, parts of East Anglia, and most parts of the four northern counties of Northumberland, Cumberland, Durham and Westmorland. Since then its spread through East Anglia has been completed (Reynolds 1985) and spread has started in the Westmorland part of Cumbria (Voysey 1985). As Elton (1958) points out, once grey squirrels arrive in a district, red squirrels disappear within a few years, 20 at most. The picture is confused by red squirrels' showing violent population fluctuations in the absence of grey squirrels, and by the occasional failure of the grey squirrel to spread into areas occupied by red squirrel, as for instance from Yorkshire into County Durham.

The process of the spread of the grey squirrel has been meticulously recorded by Reynolds (1985) in East Anglia, where the grey squirrel advanced from the south, being bounded on the west by the fen country and on the east by the sea. Figure 7 shows an analysis of Reynolds' data, comparable to the analysis in figure 6 of Ulbrich's muskrat data. The pattern is remarkably like that shown for the muskrat, a generally steady advance, which could be ascribed to random dispersal with occasional major advances.

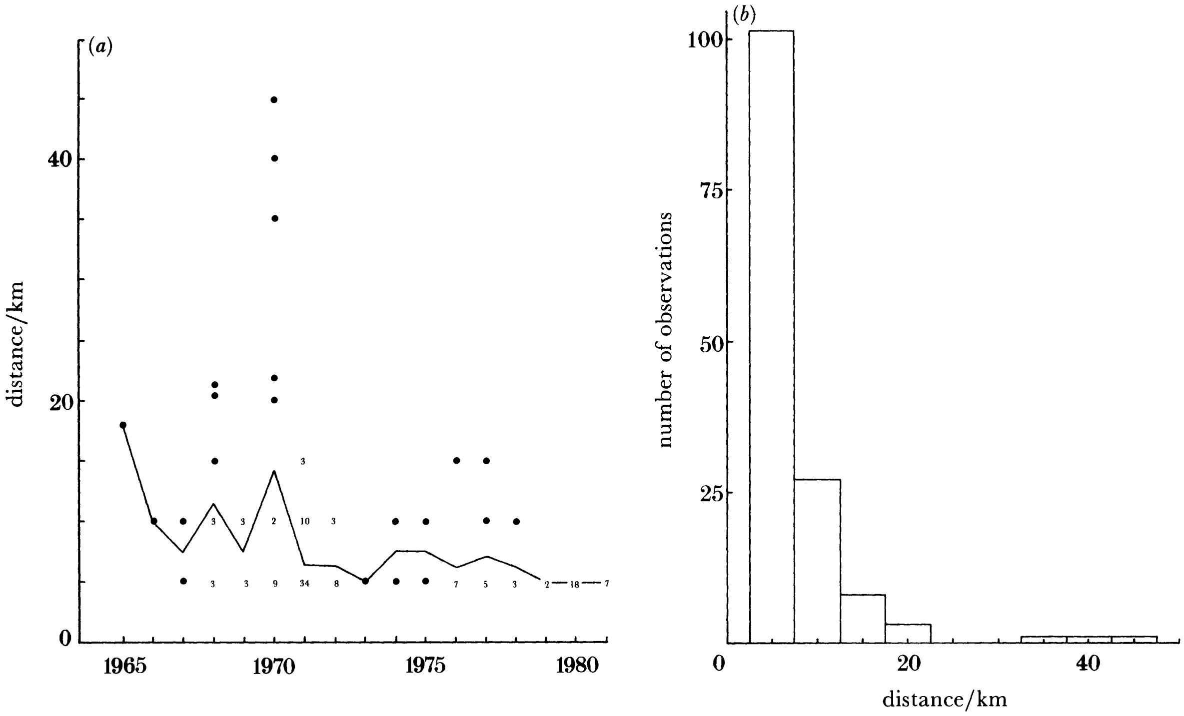

Figure 7. (*a*) The rate of spread of the grey squirrel in eastern England, from the maps in Reynolds (1985). These maps show presence and absence of the species each year on a grid of squares 5 × 5 km. Each point shows the shortest distance from a previously occupied square to a newly occupied one. (*b*) Cumulative frequency of the data in (*a*).

Although the reasons for the spread of the grey squirrel have been obvious in broad terms for many years (its larger size and its better adaptation to deciduous woods as shown by its higher density of individuals per unit area) there is still little agreement on the biological details of the interaction between the species, despite many studies. Perhaps the SCOPE programme, by drawing on a wider base of experience, may lead to a greater consensus and a greater ease of interpretation.

CONCLUSION

These models and examples show that simple spread of a newly established species can only be explained in outline; many details remain to be understood. The other examples discussed in the following papers in this volume show the advantage of a variety of pragmatic and theoretical approaches. The characteristics and consequences of invasive species that emerge from these studies are discussed in more detail by Holdgate (this symposium). The study of invasions shows how primitive our knowledge of ecological systems, as systems, still is. The most difficult problem remains that of predicting which species will establish, and that difficulty shows the need for caution and precaution in introduction into the general environment of any new species or genotype, whether natural or resulting from genetic manipulation.

The survey of British invaders was done by K.C.B. under a grant from the Department of the Environment to M.H.W., and they are both most grateful for that support and for Professor Lawton's many contributions to this work. We thank Dr A. H. Fitter for his comments.

The Modelling working party met at Fontana, North Carolina, in September 1985 (Drake

& Williamson 1986) under the chairmanship of M.H.W.; he is grateful for the contributions from the members of that working party (Dr D. A. Andow, University of Minnesota; Dr J. F. Drake, Stanford University; Dr S. Levin, Cornell University; Professor I. Noy-Meir, Hebrew University of Jerusalem; Dr S. J. Pimm, University of Tennessee; Dr N. C. Stenseth, University of Oslo; and Dr M. Rejmanek, University of California, Davis). He is also grateful to his fellow members of the Scientific Advisory Committee for the SCOPE programme (Chairman Professor H. A. Mooney, Stanford University; Dr F. di Castri, CNRS, Montpellier; Mr F. Kruger, Forestry Research Institute, Pretoria; Dr R. H. Groves, CSIRO Division of Plant Industry, Canberra; Dr J. Sarukhán, Instituto de Biologia, Mexico; Dr M. Rejmanek) for their advice and discussion on various points, and particularly to the Assistant to the programme, Dr Drake, who acted as a rapporteur for the Modelling working party.

Appendix 1. Tabulation of outcomes of invasions, from an unpublished report by K. C. B. for the Department of the Environment

The list excludes species living only in greenhouses and other artificial habitats, and in the sea. The distinctions between the columns are necessarily arbitrary and subjective. For instance 'pest' is used for species regarded as such by some authorities; others regard some of the pests as non-pests and vice versa.

This list has been compiled from 119 books and papers, and from personal communications, and is no doubt incomplete. The following works have been particularly useful: for mammals, Corbet & Southern (1977); for birds, British Ornithologists' Union (1971) and Sharrock (1976); for fish, Maitland (1972). For insects, Kloet & Hincks (1964–78) is basic, but of varying use depending on the order of insects considered. For spiders, Locket *et al.* (1974); for woodlice Sutton (1972) and Harding & Sutton (1985); for molluscs, Kerney & Cameron (1979); and for triclads, Reynoldson (1978). For all animal groups, Lever (1977) and Ministry of Agriculture, Fisheries and Food (1981 and earlier) are useful. For vascular plants, Clapham *et al.* (1962) and Perring & Walters (1962) are complementary. For all groups, the papers in Hawkesworth (1974) are a guide.

	established pests		established non-pests					
group	wide-spread	res-tricted	wide-spread	res-tricted	1 or 2 places	not estab-lished	total inva-sions	total indig-enous
mammals								
rodents	3	1	0	2	2	0	8	9
Cervidae	0	0	2	3	1	0	6	2
other	2	0	0	0	5	0	7	36
total	5	1	2	5	8	0	21	47
birds								
Anseriformes	1	0	2	3	0	1	7	17
Galliformes	0	0	2	4	4	2	12	5
other	0	0	2	1	3	5	11	181
total	1	0	6	8	7	8	30	203
reptiles and amphibians	0	0	0	4	6	1	1	12
fish	0	0	1	7	6	1	15	32
total vertebrates	6	1	9	24	27	10	77	294
insects								
Collembola	0	0	0	0	0	1	1	304
Phasmida	0	0	0	0	2	2	4	0
Orthoptera	0	0	1	0	1	40	42	29
Dictyoptera	3	0	0	2	1	36	42	3
Dermaptera	0	0	0	0	0	6	6	7
Heteroptera	0	0	0	0	1	11	12	532

group	established pests		established non pests			not established	total invasions	total indigenous
	wide-spread	res-tricted	wide-spread	res-tricted	1 or 2 places			
insects								
Homoptera								
Aphidoidea	4	0	46	19	5	19	93	446
Coccoidea	0	0	7	4	1	18	30	127
others	1	0	1	3	1	8	14	485
total	5	0	54	26	7	45	137	1058
Coleoptera								
staphylinids and carabids	0	0	7	4	2	6	19	1348
curculionids	1	0	2	1	5	6	15	419
others	1	0	13	8	12	32	66	1962
total	2	0	22	13	19	44	100	3729
Diptera	0	0	1	4	0	7	12	5950
Hymenoptera	1	0	0	2	0	14	17	6584
Lepidoptera	0	0	0	1	1	34	36	2357
total insects	11	0	78	48	32	240	409	20553
spiders	0	0	0	2	1	2	5	609
woodlice	0	0	0	0	1	2	3	35
molluscs	0	0	2	4	6	7	19	173
nematodes	2	0	0	0	0	11	13	?
triclads	0	0	1	3	3	0	7	10
vascular plants								
pteridophytes	0	0	0	1	1	0	2	64
gymnosperms	0	0	1	1	0	20	22	3
dicotyledons								
Cruciferae	9	3	7	6	2	44	71	62
Papilionaceae	3	0	7	7	1	5	23	67
Rosaceae	0	0	5	8	2	8	23	55
Compositae	3	2	7	22	8	19	61	110
other dicotyledons	4	13	31	79	39	56	222	716
total	19	18	57	122	52	132	400	1010
monocotyledons								
Gramineae	1	0	1	12	5	10	29	127
other monocotyledons	1	0	9	16	5	4	35	288
total	2	0	10	28	10	14	64	415
total angiosperms	21	18	67	150	62	146	464	1425
total vascular plants	21	18	68	152	63	166	488	1492
fungi	12	0	6	5	4	5	32	?
viruses	1	0	0	0	0	4	5	?
total of all groups studied	53	19	164	238	137	447	1058	—

APPENDIX 2. BIRDS THAT HAVE ESTABLISHED OR RE-ESTABLISHED NON-CASUAL BREEDING POPULATIONS IN BRITAIN IN THE LAST CENTURY

Although the arrivals are all natural, breeding has been assisted in several cases by conservation measures, nest boxes, etc. Data from Sharrock (1976) and Spencer *et al.* (1986).

English name	scientific name	first record of continuous population in Britain
Slavonian grebe	*Podiceps auritus*	1908
black-necked grebe	*Podiceps nigricollis*	1904
fulmar	*Fulmarus glacialis*	1897
bittern	*Botaurus stellaris*	1911
goldeneye	*Bucephala clangula*	1970
marsh harrier	*Circus aeruginosus*	1927
osprey	*Pandion haliaetus*	1955
little ringed plover	*Charadrius dubius*	1944
black-tailed godwit	*Limosa limosa*	1953
wood sandpiper	*Tringa glareola*	1959
Temminck's stint	*Calidris temmincki*	1969
ruff	*Philomachus pugnax*	1963
avocet	*Recurvirostra avosetta*	1941
collared dove	*Streptopelia decaocto*	1955
golden oriole	*Oriolus oriolus*	1967
fieldfare	*Turdus pilaris*	1972
redwing	*Turdus iliacus*	1967
black redstart	*Phoenicurus ochruros*	1923
Cetti's warbler	*Cettia cetti*	1972
Savi's warbler	*Locustella luscinioides*	1960
firecrest	*Regulus ignicapillus*	1962
brambling	*Fringilla montifringilla*	1981
serin	*Serinus serinus*	1981

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Discussion

M. W. HOLDGATE (*Department of the Environment, 2 Marsham Street, London, U.K.*). I was surprised by the statement that smaller families were more likely to produce successful colonists. How far is there a relation between the number of members of a family in the native biota and the success rate of introduction?

M. H. Williamson. The number of species in plant families in the British Isles is correlated with the size of those families worldwide. So the effect could either be a consequence of the mode of speciation in such families, or of the lack of related species here, or both, or something quite different.

Sir Hans Kornberg, F.R.S. (*Department of Biochemistry, University of Cambridge, U.K.*). Professor Williamson said that 10% of introduced species established themselves, and that 10% of these became pests. What is meant by the term 'pest' in the context? Does it reflect the intensity of the colonization process or the nature of the species themselves?

M. H. Williamson. The nature of the species. It is interesting that the list includes only one bird rated as a pest (the Canada goose) but many mammals (rats, mink, coypu and others). The key is the nature of the interaction with man. Because of this interaction, more than 10% of the mammals count as pests, and less than 10% of the birds; but the proportions we state in the paper are a rough general rule, which appears to fit for insects also.

Sir Richard Southwood, F.R.S. (*Department of Zoology, South Parks Road, Oxford, U.K.*). In his comprehensive overview of the field, Professor Williamson has not mentioned the phenomenon of initial waxing of the population of an immigrant species, followed by its waning. One such example is the rhododendron lace bug, *Stephanites rhododendroni*, which was very abundant in southern England in the 1940s, about ten years after its introduction, but has been rare for the last 30 years. Did the authors, in their review, come across many such examples? Is it an exceptional or a general phenomenon?

M. H. Williamson. Certainly not general, but not rare either; uncommon, perhaps. The Canadian pondweed, *Elodea canadensis*, and the little owl, *Athene noctua*, are two other examples. There are far more cases of explosive spread, including those of species once native in Britain, such as *Rhododendron ponticum*.

D. Mollison (*Department of Actuarial Mathematics and Statistics, Heriot-Watt University, Riccarton, Edinburgh, U.K.*). The definition of a 'pest' is man-centred. Would it not be better to say that if an invader has a detrimental effect on pre-existing species, then it is in an ecological sense a pest?

M. H. Williamson. That would be a very broad definition. The arguments by Rifken about the release of genetically engineered microorganisms serve to illustrate that there is no easy rule. If one looks at the 12 most severe weeds in the world, they demonstrate 12 different ways of becoming weeds.