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CHAPTER 14

Mathematical Models of Invasion

MARK WILLIAMSON

14.1 INTRODUCTION

Models have many uses. The aim of this chapter is to examine some of these uses in relation to the problem of the ecology of biological invasions, and to note what has been said about models elsewhere in the SCOPE programme.

It is possible to examine the use of models for understanding a particular problem either by considering different levels of understanding or by considering different aspects of the problem. For invasions, the latter is more convenient simply because there are many different aspects. So sections below consider separately models of establishment, models of spread and models of community equilibration. While different levels of understanding emerge from the discussion of these stages, I will preface these discussions with a consideration of what models can and can not do.

Amongst the many uses of models there are four I wish to highlight. The first is prediction. It would be highly desirable to be able to predict the success or otherwise of potential invaders. The problem of predicting the consequences of the release of genetically engineered organisms increases the need for successful prediction. But what emerges from the SCOPE programme is that reliable prediction in individual cases is still not possible. What is possible is a statistical indication of which invasion type is more, or less, likely, and *post hoc* explanations, with reference to models, of why a particular invasion has or has not happened.

Models have had appreciable success in two other ways, which are the second and third uses I will mention here. These are to explain what has been observed and to indicate the possible behaviour of ecological systems subject to invasions. Much of this chapter deals with these two uses of models.

The fourth use of models that I wish to mention is to bring out gaps in existing knowledge. In a study of invaders of the British Isles, Williamson and Brown (1986) found, in round terms, that 10% of invaders became established, and 10% of those established became pests. Lawton and Brown (1986) tried to see to what extent establishment could be related to the standard demographic parameters r, R_0 and K, but had to resort to indirect measures of these three. As will be seen. there is not only a dearth of direct measurements of these parameters but also, to some extent, a vagueness about precisely how these and other parameters should be measured.

As Beddington (1983) points out, there is now a great variety of models available in ecology, but the interface between theory and experiment (or observation) is weak. Regrettably few ecologists concern themselves with the problems of testing models and of parameter estimation. So a major theme underlying this chapter is that while models can now offer explanations of invasions in broad terms, detailed understanding and prediction require better and more extensive measurements of population parameters.

The SCOPE programme has included a modelling working party (Drake and Williamson, 1986) and much of this chapter draws on material developed there. All the SCOPE national symposia involve models in many places in passing, but in the South African and Dutch symposia there are no papers explicitly on modelling. In the Australian symposium, Newsome and Noble (1986) set out as a model, if not as a mathematical model, the properties of invaders. In the American symposium, Roughgarden (1986) reviews aspects of establishment, spread and community interactions. However, the major contribution to models is the British symposium, which was deliberately focussed on quantitative aspects of invasions. There are detailed discussions of models in Anderson and May (1986), Crawley (1986), Holdgate (1986), Lawton and Brown (1986), Mollison (1986) and Williamson and Brown (1986), with some discussion in most of the other papers. The joint British Ecological Society and Linnean Society symposium, which was also part of the British contribution to the SCOPE programme, mentions models here and there, particularly in Lawton (1987) and Usher (1987). In this volume, models are also dealt with explicitly by Crawley, by Levin and by Noble.

14.2 ARRIVAL AND ESTABLISHMENT

If an invasive species is going to become a problem, which is what the SCOPE programme is about, it has to arrive and establish itself. There is no doubt that it is in general cheaper, easier and more effective to control an invader as early as possible, preferably at arrival; there is also no doubt that many invaders have evaded and will evade efforts to prevent their arrival. Many arrivals, certainly almost all those at regions remote from their centre of origin, are brought by people, and there is little to be learnt from modelling those processes. Nevertheless, the frequency with which they are brought will affect the probability of establishment, as has often been shown on a more local scale. Grime (1986) gives examples in the British Flora.

Between arrival and establishment, there may be a period of adaptation. It is tempting, despite the lack of evidence, to suppose that this period involves genetic change. Both Orians (1986) and Kruger *et al.* (1986), using data spanning centuries, suggest that establishment is more likely the longer the time since the original introduction. However, the data on weed biocontrol, covering a much shorter period, show such delay in only 7% of releases (Crawley, 1986).

The stage after the arrival, or introduction, of a species I prefer to call establishment. Some authors call it colonization, and certainly historically, as used by the Greeks, a colony is a population that has introduced and established itself away from its home ground. However, a colonizing species is often considered to be one whose life history and habitat requirements lead to most of its populations being new colonies, a species that habitually invades and occupies transient habitats (Gray, 1986; and in the discussion of Grime, 1986). As there is no particular connection between this type of species and those invading species that cause environmental problems, the invaders that are the concern of SCOPE, I shall, as far as possible, avoid the use of the term colonization in this chapter.

14.2.1 Minimum viable population size

Small population sizes or low population densities may result in a species being more vulnerable. This general phenomenon was referred to as undercrowding by Allee *et al.* (1949) and is now often known as the Allee effect. The original Allee effect was the physiological effect on an individual of the presence of other members of the same species; a social effect, such as is seen in flocks and swarms. Other possible effects can be listed. A newly arrived individual may be unable to find a mate, or, more immediately, unable to find the resources to sustain itself. Small populations may be more vulnerable to general predators, and are, by hypothesis, subject to competition from larger populations of other species. A small population may lack genetic variability, and, if it remains small for long, may suffer inbreeding depression. These effects, and others, are reviewed by Roughgarden (1986).

Each of these effects can be put in mathematical form, admittedly quite a complex form for the genetic effects. It is much harder to get quantitative measures of these effects in the field, or to distinguish, say, the difficulty new arrivals have in finding resources from a failure of establishment because of a lack of long-term resources. If the concept of a minimum viable population size is to be useful in controlling and predicting invasions, more measurements need to be made of the relevant parameters of invasion models. Roughly speaking only the epidemiological models discussed below (Section 14.2.3) have been tested and shown to include real effects of small population size.

Nevertheless there is evidence that small population size is critical in determining the success of establishment in some species. Table 14.1 gives data on biological control insects in Canada, based on the numbers released of each species. Ehler and Hall (1982) show similar results with a larger data set, but classified by the number of individuals of all introduced species released against a given pest species. There are explanations other than small population size and Allee effects for the type of data in Table 14.1. For instance: species that are better

Table 14.1. Success rate in biological control of insects by insects in Canada. Data from Beirne (1975)

	Success	Failure	% Success
Total individuals released			
< 5000	9	89	9
5000–31 200	13	20	39
$> 31\,200$	22	6	79
Individuals in a single release			
< 800	—	—	15
> 800	—	—	65
Number of times released			
< 10	—	—	10
> 10	—	—	70

climatically matched may be easier to breed and so release in large numbers; the species that can adapt to the conditions of the breeding cage may also be those that can adapt to the alien environment into which they are being introduced; species with larger r may be easier to breed; an experimenter finding a successful biological control species may go to more trouble to breed large numbers; and so on. Still, the failure of about two-thirds of releases for biological control of insects (Beirne, 1975) and one-third for releases of weed biocontrol agents (Crawley, 1986) can be compared with the failure of around 90% of introductions into Britain (Williamson and Brown, 1986), and so suggest that a large proportion of failures to invade may be ascribed, at least in part, to the effects of small population size.

14.2.2 The parameters of establishment

If the resources are sufficient, and the environmental conditions adequately favourable, can the conditions for the establishment of an invader be summarized in a few parameters? Or, to put it another way, can simple single species or oligo-species models help us understand, explain or predict invasions?

The best known parameters are r and K from the logistic equation

$$\mathrm{d}\ln n/\mathrm{d}t = r(1 - n/K) \tag{1}$$

where n is the population size (number or density) of a single species, t is time, r is the rate of increase at zero population density, K the equilibrium population size, frequently, if inaccurately, referred to as the carrying capacity. Following the introduction by MacArthur (1962) of the concepts of r and K selection, many authors related life history characteristics, and in particular colonizing ability, to r and K. This idea has fallen into disfavour since the empirical tests of Stearns (1977) and the criticisms of Boyce (1984). In any case, colonizing in the sense used in most r and K studies is, as I have indicated above, not necessarily relevant to invasion.

More elaborate schemes, usually with three categories (Grubb, 1985; Vermeij, 1978) which implies at least three parameters, have been proposed. For instance, Grime's three factors relate to the loss (or failure to grow) from competition (with other species), the constraints on plant production, which he calls stress, and the destruction of biomass, which he calls disturbance. All three imply negative terms, the loss of actual or potential population, in any model (see the discussion after Grime (1986)). In principle, the scheme could be related to invasion into any type of community. Newsome and Noble (1986) find 10 suites of ecophysiological characters associated with success in invasion in Victoria (Australia) and suggest that these can be spanned by three types of invaders: gap-grabbers, competitors and swampers. This is another, verbal, three character model, much like those listed by Grubb and by Vermeij. All these models, which are clearly similar but not identical, are useful in describing and explaining some community patterns, and suggesting parameters that might be measured. Grubb (1985) discusses some of the difficulties of definition. Until measurements have been made, it is impossible to say if the models will be helpful in prediction. The scheme proposed by Newsome and Noble (1986) brings out the point that invaders can be found in all three categories and so, conversely, knowing the category that a species belongs to says nothing about its invasion potential. Noble (this volume) points out further weaknesses in the use of three character schemes in discussing invasion.

Invasion, of the type that is of importance to the SCOPE programme, is perhaps more analogous to succession than to the colonization of transient habitats. So models of succession (Connell and Slatyer, 1977; Lawton, 1987; Usher, 1987) might be helpful in studying invasions, but these models are more closely related to the models of community structure considered in Section 14.4 than to simple few parameter models for the establishment of single species.

Another, possibly important, parameter arises naturally in the mathematics of a population with age structure. This is R_O, the expected number of female offspring produced during a single female's entire life, that is the number of eggs produced by an egg, or the number of seeds produced by a seed. In standard notation, where l_x is the number of survivors to age x, and m_x is the reproductive rate (of females) of age x, then

$$R_O = \int l_x m_x \,\mathrm{d}x \tag{2}$$

and is independent of the age structure of the population. Its value, obviously, depends on the life table and the birth table, and so assumes whatever conditions produce those values. Conversely R_O is dependent on all aspects of the environment and in particular those causing the death rate. Salisbury (1942) seems to have been the first to suggest that the commonness of a plant, that is, both its abundance in one place and its geographical range, reflected the reproductive capacity of the plant. He measured, in many species, seed output in one season. This differs from R_O by ignoring juvenile mortality and by not measuring the reproductive output of one plant over its lifetime (except in annuals), but nevertheless seed output is clearly a major component of R_O.

For an age structured population an important parameter is the intrinsic rate of natural increase, first called r and championed by Lotka (see Smith and Keyfitz, 1977), and defined as the dominant root of the equation

$$\int e^{-rx} l_x m_x \, dx = 1. \tag{3}$$

As with R_O, this assumes a particular schedule of death rates, conventionally not dependent on the density of the population. However, while r is a rate of increase, it is the rate of increase only in the stable age distribution. Few natural populations are actually in the stable age distribution as that normally requires several generations of density independent increase, so usually r has to be calculated rather than observed. In fact the majority of estimates of r refer to populations in the laboratory, and are always dependent on such variables as temperature and humidity (Williamson, 1972). What r would be for such species under natural conditions is not known, but it would probably be smaller at any given physical conditions because of natural mortality.

Lotka's r may be regarded as composed of an intrinsic birth rate b, and an intrinsic death rate d (Lotka, 1924; Pielou, 1977), giving

$$r = b - d \tag{4}$$

and it is natural to equate it with r in the logistic equation, so bringing together r, K and R_O.

In discussing the immigration of species onto islands MacArthur and Wilson (1967) suggest that b/d is a better measure than r for the probability of succesful establishment. Armstrong (1978) shows by an ingenious argument that, for a population with age invariant rates, $b/d = R_O$. Unfortunately this is not true for a general age structured population, as can be seen with a little trouble from (2), (3) and the analytic expression for b in the stable age distribution

$$b^{-1} = \int l_x e^{-rx} \, dx. \tag{5}$$

Nevertheless, if invasion success can be predicted to some extent by r or R_O, it might be better predicted by b, d, or some combination of them, or by some other parameters derived from the l_x and m_x distributions. A fundamental point is the definition of conditions assumed for l_x and m_x. Conventionally, the distributions are measured at minimal population density. Even so, which mortality factors are included and which left out is not always clear, but such decisions will have a marked effect on the usefulness of these parameters in understanding and predicting invasions. Lotka (1924), starting from human populations, includes all forms of mortality; Crawley (this volume) follows the modern convention of excluding all mortality appearing elsewhere in his models. For studying invasion, the density independent mortality associated with the site of the invasion would seem to be what is wanted. The discussion of equations (12) and (13) in Section 14.4.3 elaborates on this point, as does Boyce (1984).

These basic models of population dynamics suggest examining r, K and R_O for their importance in invasion simply because there are no other standard parameters in these models. The difficulty, as already noted for r, is that there are very few measurements of these parameters, and these measurements are not in the natural environment. Lawton and Brown (1986) observe that over groups of animals as a whole, large animals are more successful invaders than small in Britain, but that among insects, small insects are more successful than large. They note that these differences could result from either the mode of introduction, or the biology of the invaders, or both, but nevertheless they attempt to relate these patterns to what has been reported in the literature about the relationships of r, R_O and K to size. Lawton and Brown conclude 'there are neither theoretical nor empirical grounds for believing that r alone is the principal, or necessarily even an important, arbiter of invasion ability'; but Crawley (1986), using similar arguments with different data, concludes that r is important.

The basis of these contrary conclusions would seem to be both a lack of knowledge of r in real environments, and a well-known generalization which is possibly misleading when comparing invasions by closely related species. The generalization, which dates from Smith (1954), is that larger organisms have smaller r. Smith's diagram, which relates r to R_O and the generation time T, has been repeated with some additions by several authors; Fenchel (1974) makes the direct comparison of r to size. All these diagrams cover several orders of magnitude. Smith has six orders of magnitude for r and T, Fenchel six for r and 21 for weight.

Fenchel (1974) notes that published estimates of r come mostly from opportunistic, colonizing or pest species, and indicates that the relationship of r to size would be weaker if other types of species had been included. In the study of invasions, and in particular in predicting invasions, it is important to be able to say of closely related species, of species in the same genus or family, which will be the most successful. In contrast to the Smith–Fenchel generalization, it is well known that within a species the largest individuals generally have the highest reproductive rate (Vermeij, 1978). This is particularly striking in angiosperms with their marked phenotypic plasticity (Salisbury, 1942). Maaløe and Kjeldgaard (1966, p. 63) show a four-fold increase in r with a four-fold increase in cell mass for the bacterium *Salmonella typhimurium*. Dobzhansky *et al.* (1964) show a 20–30% variation in r over five genotypes of *Drosophila pseudobscura*. The flies, as far as is known, do not differ significantly in size. In Fenchel's relationship, this difference in r corresponds to a 10-fold difference in weight. So if r decreases with size between organisms in different classes, but increases with size in a species, how does it behave in families and genera?

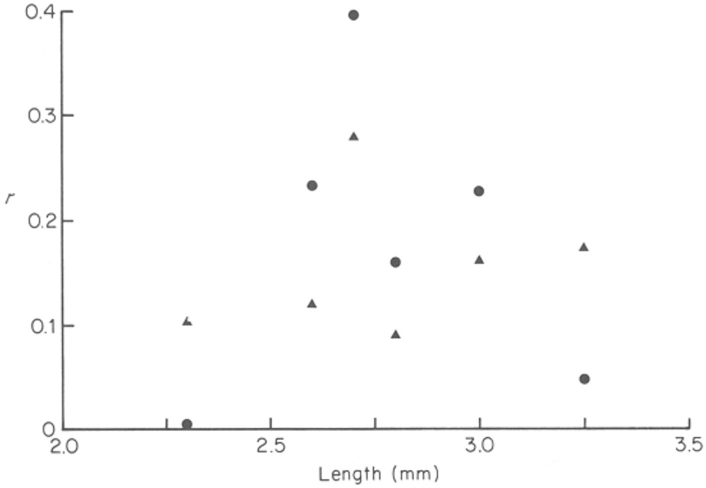

Figure 14.1. The intrinsic rate of increase (r) at two temperatures for six species of ptinid beetles. Lengths from Joy (1976), r from Howe (1953, 1955, 1959) and Howe and Bull (1956). ▲ 20°C, ● 25°C

Table 14.2. Rates of increase of three species of *Daphnia* (Crustacea, Cladocera). Data from Bengtsson (1986)

Species	Adult size (mm)	$r(\text{day}^{-1})$	R_O
D. magna	3.7	0.185	64
D. pulex	2.0	0.215	75
D. longispina	1.8	0.140	38

Adult size is the mean of the size range, r and R_O are averages of the values under four conditions of temperature and food.

In Figure 14.1, I show the best information I can find, which is for spider beetles, which are pests of stored products. The variation in size is not great, and derived from a taxonomic work not from the cultures; overall the two variables are independent. Nevertheless the highest r goes with a middle-sized species, the commonest pest, while the lowest r's are found in the largest and smallest of this set of six species. Bengtsson (1986) measured r (and also R_O) for three species of *Daphnia* under four conditions of temperature and food, and found the highest r in each case in the middle-sized species, *D. pulex*. His data are summarized in Table 14.2. The order of species is the same for r in all four conditions. For R_O the results are more variable. *D. magna* has the lowest R_O of the three at 20 °C and low food, but the highest with both feeding regimes at 15 °C. *D. pulex* is apparently the commonest species of the three. In both ptinids and *Daphnia* middle-sized species have the largest r, and maybe the highest K if commonness is a reliable guide.

For plants, r has scarcely ever been estimated (Crawley, 1983). Salisbury (1942) gives the seed production for adults, which may be related to R_O and hence to r. In his data it seems that the highest seed output is associated variously with the largest or a middle-sized species in each genus. As already noted, seed production is related to commonness; so presumably R_O is related to K measured as biomass. For birds, O'Connor (1986) suggests that reproductive output, again an approximate measure of R_O, is relatively high for successful invaders.

All this work shows that the modelling invasions of macroorganisms there is much to be done in defining the important parameters and measuring them. For pathogenic microbes the situation is somewhat better, as will be seen in the next section.

14.2.3 Models of epidemics

Although the life table and its parameters are a powerful aid in human demography, the logistic curve and similar forms are based more on mathematical convenience than biological reality (Allee *et al.*, 1949). There are, however, two areas of population biology in which simple equations have been developed with parameters with real biological meaning, and in which the equations have been tested by observation and experiment. These are studies on continuous cultures such as chemostats (Williamson, 1972) and the mathematical theory of epidemics (Bailey, 1975).

Conditions for invasions into chemostats have not been studied systematically, except for genetic mutants which are usually the only invaders readily available. Tilman (1977) gives conditions for the stability of a two species, two resource system, and so, by implication, the conditions for one of the species invading a system containing only the other. In simple systems the number of species can not exceed, and may be less than, the number of controlling factors (Williamson, 1957), and Tilman's results are an example of this. It is possible that the study of density-dependent controlling factors might be helpful in understanding invasions.

In contrast to continuous cultures, much is known about invasions by micropathogens, and this shows, as will be seen, how complex the conditions for invasion are even in systems of only three species. The simplest epidemic model has two species and considers a host species with susceptible, infected and recovered individuals, and a parasite (disease) population. Transmission from infected to susceptible is taken to be proportional to random contact. This gives

$$x + y = n = \text{constant} \tag{6}$$

$$\mathrm{d}x/\mathrm{d}t = sxy - (a + b + c)y \tag{7}$$

where x are the susceptibles, y the infecteds, s the transmission rate, a, b and c are loss rates from natural death, disease caused death and recovery. Anderson and May (1983) emphasize the comprehensibility that results from using as few dimensionless parameters as possible, a standard technique in physics. So they rescale the time t on to the natural time scale $(a+b+c)^{-1}$, and call it t', and define a dimensionless parameter R

$$R = sn/(a+b+c) \tag{8}$$

so that (6) becomes

$$\mathrm{d} \ln y/\mathrm{d}t' = (R-1) - Ry. \tag{9}$$

So growth is only possible with $R > 1$. R is the expected number of secondary infections produced within the infectious period of one newly infected host. Anderson and May (1983) say R is precisely analogous to R_O; Anderson and May (1986) call it R_O. Note that R depends on n, which is assumed constant for any one epidemic. If $n < (a+b+c)/s = n_T$, the epidemic can not develop. For an epidemic, the population must be greater than the threshold density n_T. This is the famous threshold theorem of Kermack and McKendrick (1927).

In stochastic models, the threshold becomes blurred but the principle holds (Bailey, 1975). This threshold theorem is yet another reminder that R_O is not constant for a species but depends on conditions. Anderson and May (1986), developing Bartlett's (1957) well known result, show how stochastic modifications to this equation, which have to be solved by simulation, can explain the fluctuations in measles, and how, while a population of 6500 is needed for measles to invade, a population of 250 000 is needed for persistence, perhaps the most interesting result in all models of invasions. The prediction fits data on real island populations well (Williamson, 1981).

When these models are expanded to three species (Anderson and May, 1986), remarkable complexities arise, demonstrating once again that with a little ingenuity a model can be made to produce any result you like. But some results are simple. If a new pathogen invades a host/pathogen system it will displace the previous pathogen if it has a larger R_O, a lower n_T. Others are complex. In some cases a pathogen stabilizes a two species system allowing all three to persist, in others it destabilizes, in others the result depends on the parameter values. Worse, many of the results may depend on the particular form of the equations. There are no critical tests yet for the forms of the equations or the values of the parameters in these three species systems.

Another example of the complexity of three species systems is found in Rejmanek (1984), who developed a model of three competing plant species, together with disturbance and diffusion. Not only did he show that disturbance may mediate permanent coexistence, but he also showed that diffusion increased the zone, in parameter space, of such coexistence. Consideration of diffusion leads to the next topic.

14.3 SPREAD

An invader once established will usually spread out. The speed at which it does this is of some importance to management; it is generally easier to control a slow spreading species than a fast one. However, models of this stage are often of less importance than those of establishment, considered earlier, or those of final equilibrium population density, considered below. It is perhaps, then, not surprising that these models are those that have been best developed and best tested. But even these models can be quite complex and difficult to test.

The most elementary process in population dynamics is the exponential growth of an unconstrained population. In spatial processes, simple diffusion is the natural starting point. So the simplest and most basic model of the spread of an invading species contains exponential growth and random diffusion and nothing else. That is, spread comes from the random movement of individuals which are assumed to be not affected by the behaviour and abundance of other individuals. The model has just two parameters, the intrinsic rate of natural increase, r, and the diffusivity, k. Considering just the radial spread from the starting point gives

$$\partial n/\partial t = rn + k(\partial^2 n/\partial x^2 + x^{-1}\partial n/\partial x) \tag{10}$$

where n is the population size, t time and x the radial distance (Kendall, 1948).

Even this simple equation has surprising complications. Its origin in biology is in the genetical studies of Fisher (1937) and Kolmogoroff *et al.*, (1937), and in that form the solution has an ambiguity in the velocity of the wave of advance, though Moran (1962) shows that there is no ambiguity if the process is started from a minimal population at one point. Murray (1977) discuss many of the complications. The equation was first discussed as an ecological one by Kendall (1948) and Skellam (1951), and they showed that equation (10) leads to an approximate asymptotic relation.

$$\hat{x}/t = 2r^{1/2}k^{1/2} \tag{11}$$

where $\hat{x}$ is the position of the front, as defined by some detection threshold. This represents a wave of advance with constant linear speed, the speed being a function of the two parameters r and k. If equation (11) is a good approximation, invasions will spread in concentric circles with fixed spacing for a fixed time interval. The many maps of the spread of invasion that have been published show that the approximation is a fair fit to much data. Williamson and Brown (1986) have examined in more detail than Skellam (1951) the spread of the North American muskrat, *Ondatra zibethicus*, in central Europe from 1905 to 1927. Skellam used the square root of the area as an average of the radial distance. Williamson and Brown showed that this is indeed the best transformation of the area to produce a linear spread, but even so the rate of spread varies, and the variation in the rate is very large when the spread along individual radii is studied.

If the rate of spread, the intrinsic rate of natural increase and the diffusivity were all known, it would be possible to make more critical tests of equation (11). While

r has seldom been measured, measurements of k are even scarcer (Okubo, 1980). Instead Williamson and Brown estimated r from North American works of reference, and with that and the rate of spread estimated k and thence the mean annual dispersal of muskrats in central Europe. This dispersal came out at 7.65 km per year, a rather high value for random diffusion. However, their estimate of r may have been too low for European populations at low density (Mrs A. Verkaik, personal communication to Dr M. B. Usher); if so the estimate of k, and so also of the mean dispersal, is too high.

In other studies quoted by Williamson and Brown, the rate of spread appears to accelerate, or be more irregular with occasional leaps. Both these phenomena are important for the control of invaders. Mollison (1977) discusses the consequences of models that are more complex then equation (10), stochastic, in discrete time or with different contact distributions, and shown that these can predict occasional 'great leaps forward'. Kot and Schaffer (1986) and Levin (1986) discuss other models that can show complicated behaviour. Problems of estimating parameters in these elaborate models from field data are discussed by Banks *et al.* (1985, 1986). The variability in the rate of spread shown by Williamson and Brown and by others, such as Usher (1986), may well be explicable by some of these models.

The eastern North American grey squirrel, *Sciurus carolinensis*, has been introduced into Britain, California and South Africa. Williamson and Brown (1986) found a modal rate of spread of 5 km yr^{-1} in eastern England. Millar (1980) gives maps and data for the spread near Cape Town from 1900 to 1971, which give rates an order of magnitude or more lower, 0.4 km yr^{-1}. In South Africa the squirrel is only found among introduced trees; in England it is found throughout the countryside. So while the rate of increase and the diffusivity might explain the observed spread in England, for South Africa it is necessary to know why its habitat is restricted. There are no native squirrels there, and the food supply in the natural habitats appears to be sufficient. Possibly there is a community effect of the sort considered in the next section.

14.4 MODELS OF EQUILIBRIUM STATE

Even when an invader has established and spread, it will not usualy be a problem, as the surveys by Simberloff (1981) and Williamson and Brown (1986) show. There will be management problems if the invader reaches high densities, or interacts strongly with the indigenous species, and in some other cases. Can models predict the eventual population density, or the extent of interaction with other species?

14.4.1 The number of parameters

Although some species may limit their own density, by territorial behaviour, or simply by forming a monolayer, the equilibrium of most species will depend on interactions with other species. It is possible that these interactions are diffuse, multifaceted and weak, as seems to be the case for the diatom *Biddulphia sinensis* in the Irish Sea (Williamson and Brown, 1986; Williamson, 1987). In such cases there is little point in trying to model all the interactions; there would be too many of them. Indeed an essential aim in modelling should be to keep the number of parameters small.

Complex models, with many parameters, are difficult to understand, and it is difficult to estimate their parameters with sufficient accuracy to test the models, let alone to use them for prediction. Medawar (1982) contrasts the reliance placed on econometric models with the general scepticism about weather forecasts, built on well founded meteorological models. Montroll and Shuler (1979) point out that the cost, measured in money or time, of getting a satisfactory solution from a complex model increases exponentially with the number of parameters. Usher (1987) makes a similar numerical point: 32 species have 496 possible pairwise interactions and 4×10^9 three way interactions. Mollison (1984, 1986) shows how a few parameters are more intelligible than many. Anderson and May (1983, 1986) recommend the reduction of parameters by finding dimensionless combinations. We should be wary of the claims of any complex ecological model even when we understand ecological systems much more than we do today.

It is now widely recognized that simulation models of real communities, with a large numbers of parameters, such as those used in the IBP, have been generally unsatisfactory (Holdgate, 1986). An example of the futility of this approach is Swartzmann and Zaret (1983). They attempted to build a simulation model of the invasion of Gatun Lake, Panama, by the predatory fish *Cichla ocellaris*, which spread through the lake at about 10 km a year and wrought havoc on the species there. Of eight diurnal fish species (out of about 15 total) four became extinct, two were reduced 90%, one by 50% and one increased 50% (Zaret and Paine, 1973). The simulation model had over 50 parameters, but failed to represent the rate of spread, and in the graphs published all prey species increase in density, though there is a claim of better fit to the data in later results. Watt (1975) has noted the tendency of simulation modellers to claim that their results will be right soon.

Simulation, as such, is often necessary for a solution, as for instance in the stochastic measles model of Section 14.2.3. What is undesirable is the proliferation of parameters. The firm recommendation of the SCOPE working party is that the number of parameters should be kept to a minimum and that the parameters should be both measurable and interpretable.

14.4.2 Simplified models of communities

There are many ways in which the properties of communities may be simplified. Among these are the log-normal and other descriptive distributions, analysis as food webs, and the theory of limiting similarity, all discussed below. Others include Markov compartment models (Usher, 1987), the competitive equivalence model (Goldberg and Werner, 1983), functional groups (Noble, this volume) and the concept of ecological fields (Walkner *et al*., 1986), which are all designed to avoid discussing individual species, and so are of little help in understanding invasions of particular species. Noble (this volume) emphasizes the need to measure parameters on individual invading species.

Theories of the distribution of the abundance of individual species, such as the log-normal, indicate the pattern of species abundance to be expected, and so might indicate for a given community where there are invasible gaps. However, both the theory and the fit to data are approximate. As populations vary logarithmically (Williamson, 1972), applying the central limit theorem to them will produce a log-normal distribution (Brown and Sanders, 1981). However, as Pielou (1977) points out, the argument only applies to populations of one species. It can be stretched to apply to sets of species which are in some sense of the same sort (Williamson, 1988). For instance, the abundances of the set of copepod species in the mid-Pacific (McGowan and Walker, 1985) are more or less log-normal; those of a wider set of plankton, including copepods, in the North Sea, are clearly not (Williamson, 1972). Gaps in the distribution of abundances cannot be identified, and even if they could would not indicate what sort of species could invade. If invading species come at random in the log-normal distribution, relatively few will be abundant enough to be pests, and, of course, relatively few are.

The theory of limiting similarity, which in one form suggests that species are spread out along resource axes, might indicate what type of gaps exist in real communities. Unfortunately, elaborations of the theory showed, once again, that many other results can be got (Lawton and Hassell, 1984) and this and empirical tests, for instance on size-ratios (Carothers, 1986), led to the conclusion that 'no generalizations have emerged from these studies' (Abrams, 1983), and certainly no results that are useful in studying invasions (Roughgarden, 1986).

For a given quantity of resource, Hanski (1978) develops a model that predicts that the more finely divided the resource the more species can coexist on it, and the higher the invasibility of the guild of consumers. Shorrocks and his group have developed another way of looking at communities on finely divided resources, one that involves relatively few parameters, three per species (Shorrocks and Rosewell, 1986). These are an aggregation measure based on the negative binomial distribution, a rate of increase and a competition coefficient. Green (1986) has criticized the way the negative binomial is used. No doubt there will be some argument about how best to model the aggregation within species of a guild living on a divided and ephemeral resource, but certainly aggregation could reduce competition and make coexistence easier. In this model, invasion and spread are both facilitated by much aggregation or, if there is less aggregation, by low competition rates among the pre-existing species. The invader needs a relatively high rate of increase to enter, and should be competitive and weakly aggregated to spread and become common. Not only is this an interesting theory, but Shorrocks provides measures of his parameters for some *Drosophila*.

14.4.3 Food webs

The study of food webs has become a central part of modern community theory (Pimm, 1982). I will only discuss two aspects here, the mathematics of invasion in food webs, and empirical observations on predator–prey ratios.

The ratio of predators to prey has been studied both empirically and in models. Figure 14.2 shown some data from freshwater systems, derived from taxonomically complete studies. The ratio is more or less invariant with richness, and there are rather less than three prey species to each predator on average. Although the relationship is strong, and possibly useful for explaining success or failure of invaders in some communities, it is not strong enough to produce predictions. Even at the bounding rations given in Figure 14.2, namely 1:1 ad 7:1, it is not

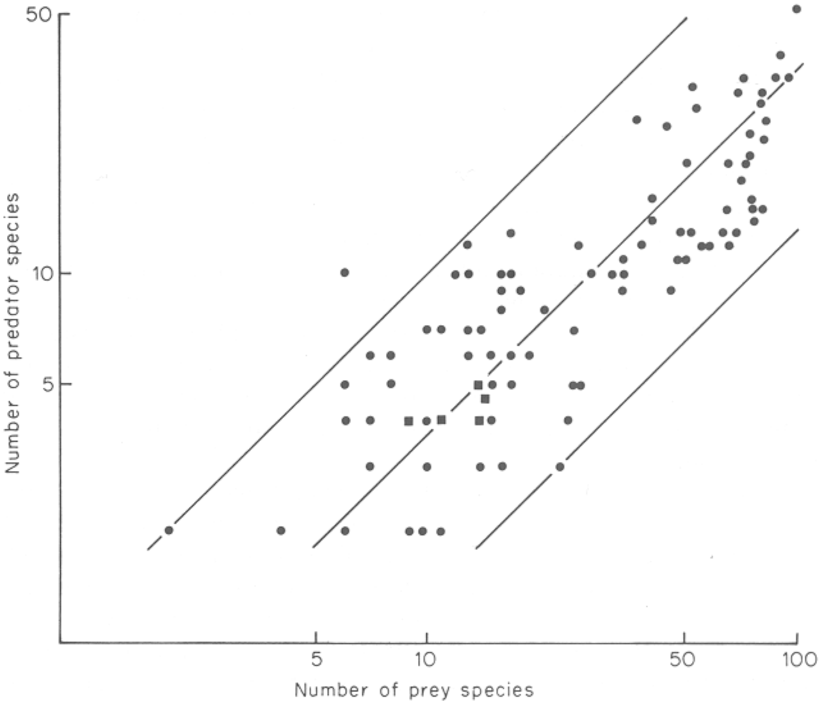

Figure 14.2. Number of predator and prey species in freshwater communities. The central line is 2.7 prey per predator, the mean of the two sets and very close to the reduced major axis. The upper line is the 1:1 ratio, the lower 7.3:1 ($7.3 = 2.7^2$). Square points relate to two identical observations. Modified from Mithen and Lawton (1986), data from Jeffries and Lawton (1985)

possible to be certain what would happen to a new species, though a prey invasion is more likely at the first and a predator one at the second, assuming that predator–prey relationships are important in invasion. In between, more or less anything could happen on the basis of the information in this graph. Even in models that produce qualitatively similar relationships (Mithen and Lawton, 1986), predicting, on the basis of similarity to other members of the web, survival time of species invading the foodweb is impossible.

The predator–prey ratio has also been studied by Cohen and his colleagues, as for instance in Newman and Cohen (1986), marrying ingenious theory with extensive survey. There is a worry, voiced for instance by May (1983), that the studies surveyed are more informative about the way ecological surveys are done than about ecological systems. The predator–prey ratios found in this work differ appreciably from those of Figure 14.2. Until these differences in predator–prey ratios are resolved, there will be even more uncertainty about using them for explanation, let alone prediction.

The other aspect of food webs that I think relevant to the study of invasions is the use of computer models of imaginary species. The most notable of these are by Post and Pimm (1983) and Drake (1985), both using Lotka–Volterra equations, and arbitrarily selected parameters, but giving reasons for their choice of method. The number of parameters is unfortunately large. The possible types of equilibrium were first expounded in an ecological context by Lotka (1924) and are well known. Foa a set of species represented by differential or difference equations, a stability matrix, often called the community matrix, can be formulated, and the stability of the set determined from the eigenvalues of the matrix. The two representations, difference and differential, can be mapped one to one, and so are equally stable as far as this form of stability is concerned (Williamson, 1987). Invasion is only possible if the equilibrium is unstable, but the invader may still go extinct. Many remarkable results can be found in more general models with non-transitive relationships or non-linearities (Gilpin, 1975; May and Leonard, 1975). An example of a non-transitive system is when A beats B beats C beats A.

Different conditions are needed to determine permanent coexistence (Hutson and Moran, 1982; Hutson and Vickers, 1983; Hutson and Law, 1985). These apply to any number of species in a Lotka–Volterra system, but as yet only to systems with three or less species in the more general case. A set of invaders can be represented by an extension to the community matrix, called the invasion matrix (Reed and Stenseth, 1984; Stenseth, 1986). The eigenvalues of this invasion matrix, which are mathematically independent of those of the community matrix, indicate whether an invasion is possible, but not whether it will succeed. These difficulties perhaps indicate some reasons why the computer simulations on the whole did not produce clear-cut results.

Both Post and Pimm (1983) and Drake (1985) found that successful invaders in their models differed only slightly, and on average, from the total set of species considered. The results are in the direction expected. Successful invaders have lower intrinsic mortality, better productivity and are less affected by predators, but, as these are statistical effects, there are plenty of individual exceptions. Note that the models avoided the complications discussed by Hutson and his colleagues by considering only stable and unstable equilibrium points, not trajectories. Bender et al. (1984) and Hastings (1986) using pure competition models, the antithesis of the pure predator–prey models, again found much complexity and surprising results.

One problem with these complex food-chain models is relating them to what is measured in the field. To take the simplest set of modified Lotka–Volterra equations representing a self-limited producer p and a herbivore h (with t time and the other terms all constants),

$$\begin{aligned} \mathrm{d}\ln p/\mathrm{d}t &= r_p - ap - bh \\ \mathrm{d}\ln h/\mathrm{d}t &= cp - e. \end{aligned} \tag{12}$$

In these, r_p is the intrinsic rate of natural increase of the producer, but e is merely a death rate, the rate of decline of the herbivore population under starvation. The value of r for h must be the maximum rate of increase possible in the system, which is at the asymptote for p alone, namely r_p/a so

$$r_h = (cr_p/a) - e. \tag{13}$$

If another producer is now introduced, r_h will increase. The herbivores do better on a mixed diet. It is perhaps not surprising then that polyspecies models have a multitude of possible outcomes.

All these community models are equilibrium models. That is, the starting point as well as the end point is an equilibrium. In contrast, the models of up to three species discussed in Section 14.2 include non-equilibrium behaviour as well, the behaviour of the system in transit between equilibrium points. Real communities are probably never at an equilibrium point, and certainly never stationary (Williamson, 1987a). Disturbance makes invasion easier, and disturbed communities are likely to be further from equilibrium (Rejmanek, 1984). So it is quite possible that non-equilibrium community models, when these are developed, will be more informative than those considered here.

14.5 CONCLUSIONS

There is a very great deal of empirical data about invasions, as the chapters in this book show. There are also very many models that might be of use in understanding invasions. The major deficiency is in connecting the two. Much thought needs to be given to defining parameters, reducing their number where possible, and to testing the validity of equations. A useful way forward would be to get many more measurements in the field of those parameters that have been discussed, such as the intrinsic rate of increase, the reproductive capacity and the diffusivity. Indeed, the models that have been the most successful, for instance those in epidemiology, are those whose development has seen close collaboration between modellers and experimentalists, and this can be expected to be the case in future. Even so, as we are discussing models of real, complex, ecosystems, the best that can be expected for some time will be an improvement in understanding; useful models for prediction will remain rare.

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