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Modelling Biological Invasions: Chance, Explanation, Prediction [and Discussion]

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Modelling biological invasions: chance, explanation, prediction

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Biological invasions have their epidemic and endemic aspects: the former include ability to invade, competitive ability to succeed initially, and (if successful) rate and manner of spread; the latter, competitiveness to persist, and (if successful) level and pattern of persistence.

There have been successes, at least in qualitative explanatory terms, in modelling all these aspects. For some, the stochastic element, which is intrinsic to populations of discrete individuals, is crucial. Other aspects, at least at the aggregate level, can usefully be analysed deterministically, with the stochastic element treated as an optional refinement.

The lack of corresponding successes in prediction shows the quantitative weakness of simple models, which in their details are commonly more arbitrary than models in the physical sciences. Careful examination of the sensitivity of predictions to the detailed form of model components can reveal which of these need more accurate formulation, and any corresponding requirement for better data.

1. INTRODUCTION

In this paper, I shall look at the successive stages of invasions (arrival, establishment, spread and persistence) and discuss some of the possible mathematical models and the extent to which they have been successful. Two main themes emerge. The first is the need to incorporate the effects of chance, even at later stages where population numbers are large: comparisons of stochastic with deterministic models show that substantial differences can exist both in quantitative values (e.g. velocities, conditions for persistence), and in qualitative behaviour (e.g. patterns of spread, oscillations about equilibrium). These differences are especially marked when we take account of heterogeneous mixing of populations.

The second theme is the importance of defining models in terms of parameters with clear ecological meanings, and of keeping the structure of models as clear and simple as possible, so that the dependence of conclusions on assumptions is plain. Conclusions are sometimes very sensitive to details of assumptions, and the latter are usually necessarily somewhat arbitrary, because models in the biological sciences are seldom prescribed quantitatively in the precise way that is common in the physical sciences. For the same reason, quantitative predictions outwith the range of observations are seldom reliable; most successes have been in explanation or in qualitative prediction.

Some of the most sophisticated models for ecological invasions have arisen in the context of epidemics. From the theoretical standpoint, there is obviously much overlap. The spread of a disease is essentially an ecological invasion by a microorganism that is a predator of a larger species; thus rabies can be regarded as an invasive species whose ‘food’ is foxes. Conversely, ecological invasion by any species can be viewed as a disease of its food supply; thus sheep may be viewed as a disease of hill grasslands, the ospreys we welcome back to Scotland as a disease of salmon and trout.

Another useful class of models is that of *interacting particle systems* (Spitzer 1970; Liggett 1985; see §3), which were constructed largely for applications in physics: there is an analogy between the change of an ecosystem from one stable equilibrium to another, with the addition of a new invader species, and the phenomenon of 'phase transition', as when a material jumps from one state of magnetization to another.

Potentially, we have to consider invasions in relation to the whole ecosystem; however, it usually seems adequate, as I shall for the most part assume here, to analyse them in terms of a single species, which either does or does not significantly depress its food supply. Alternatively, its main relationship may be competition with an established species, rather than predation. I shall touch only briefly on environmental stochasticity, and on the adaptation of an invader and its environment to each other, aspects that are vital when considering the long-term persistence of an invasion.

Types of model

Populations consist of individuals that are subject to chance (at any reasonable level of detail), so a stochastic model with discrete individuals is inherently more realistic than one that is deterministic or that treats the population as a continuous mass. A detailed stochastic description is also often helpful in specifying a model clearly, even if a deterministic approximation proves adequate for subsequent analysis; examples of deterministic models whose exact derivation is unclear abound, including the classic KPP/Fisher equation (Kolmogorov *et al.* 1937; Fisher 1937) for the advance of an advantageous gene (see Mollison (1977)).

A stochastic model is essential when numbers are small, and thus certainly for consideration of the arrival and establishment of invasions. Some of the most useful analysis has been with simple 'back-of-envelope' stochastic models, as in the pioneering work of MacArthur & Wilson (1967). If I criticize some minor details (§4), this is not intended as an attack on their work, but rather as a tribute to its continuing relevance.

Stochasticity is also important in many cases for spread and persistence, because the relative number with which an individual interacts will be small in many species, for instance in territorial animals. Such species require a stochastic model that takes proper account of their kind of heterogeneous mixing, which may be of several broad types. I shall concentrate on the spatial case (see §3), which seems most appropriate for a consideration of the spread of species.

Theoretical results showing closeness of deterministic and stochastic models exist; however, these are usually of the form 'stochastic approximates deterministic' (see, for example, Barbour 1980, Kurtz 1980), whereas to justify the use of deterministic models we really need results the other way round. For the spatial case, deterministic models certainly appear inadequate. Even if of nonlinear form, such as the KPP–Fisher equation, they do not adequately model the nonlinearity of the population (Mollison 1981; see §3).

Robustness of models

For biological models to be of use they need to be clear and robust. We should be able to identify the model components on which a particular conclusion depends (Drake & Williamson 1986). Preferably these model components should have a straightforward ecological interpretation (e.g. net population growth rate, dispersal distribution). Also the sensitivity of conclusions to the details of our assumptions should be clear. A traditional 'sensitivity analysis', in which numerical parameters are varied, is not really adequate; we also need to know whether our result is sensitive to the form of components (e.g. the shape of a dispersal distribution), or indeed to the inclusion of some further component in our model (see §6).

We should, however, beware of models with too many parameters. Usually these either include a few basic components, which dictate their general behaviour, or, if they genuinely have a large number of degrees of freedom, they have minimal predictive value, and can be used to fit almost any data: as Euler reputedly said, 'give me five parameters and I will draw you an elephant; six, and I will have him wave his trunk'.

2. Arrival

Arrival is the stage where chance is most obviously involved. A single propagule of a species (for instance a seed, a pair of animals or a pregnant female) can start an invasion. Further, we need to take seriously extremely small individual probabilities of success, because the number of propagules 'attempting' to invade may be very large.

This is especially so on an evolutionary timescale, when, for example, an arrival rate of one species per 350000 years is sufficient to account for the present avifauna of Hawaii (Gorman 1979). The problems here have been much clarified by our understanding of the details of continental drift (Jardine & McKenzie 1972; Jardine 1972).

MacArthur & Wilson (1967) presented a number of simple and sensible calculations as to how a species' invasive potential depends not only on its mean dispersal distance, but also on the shape of the probability distribution for the distance of dispersal. For a given mean value, much greater occasional extreme distances will be achieved if this distribution is approximately exponential rather than a short-tailed distribution, such as uniform or normal. They deduced that 'stepping stone' islands should be especially important for the spread of species whose dispersal distribution combines a low mean with short-tailed shape, and suggested that the mixed biota of New Guinea might be explained by the relative superiority of insect and plant species over vertebrates in respect of (a) mean dispersal distance, or (b) longer-tailed shape of dispersal distribution (or (c) greater probability of establishment, see §4).

Long-distance wind dispersal

As a contribution to this tradition of simple stochastic models, I present here an attempt to estimate the limits on long-distance wind dispersal of organisms. This is of interest in determining the origins of the biota of remote islands, including in that term both real oceanic islands and habitat islands (Jardine & McKenzie 1972; Carlquist 1967; Wickens 1976, 1979, Sugden 1982); though of course for particular species other means of transport may be plausible, for instance floating logs and the feet and digestive systems of birds (Darwin 1859; Praeger 1911; Ridley 1930; Bisby 1943; Fridriksson 1975; Wickens 1979).

A simple calculation shows that organisms whose terminal velocity of fall in still air, v, is not more than about 1 cm s^{-1} could be carried across the widest ocean gaps in a smooth airflow. Observations of Saharan dust in the Caribbean (Prospero *et al.* 1970) show that somewhat heavier particles can cross when substantial vertical air mixing exists, as in the trade winds. To examine the potential of vertical air movements for enhancing a heavier organism's chances of success, I use a simple stochastic model. (The details are given in an Appendix.) The conclusion is that if, as here, success probabilities of the order of 10^{-10} to 10^{-30} are of interest, then the limit on v is 20 or more times that calculated for smooth airflow. Thus organisms with terminal velocities in the range 3–30 cm s^{-1} (on an evolutionary time scale, possibly up to 1 m s^{-1}), although they are too heavy to form part of the usual 'air spora' (Gregory 1971), are capable of crossing ocean gaps of 1000 km or more in favourable conditions. (The theory, which gives a limit on the terminal velocity inversely proportional to the distance to be crossed, can be applied to distances less than 1000 km. However, because optimal conditions require increasing vertical mixing velocities, it becomes increasingly unrealistic for shorter distances: for instance, it allows that an elephant might remain airborne for about ten minutes.)

3. Interlude: spatial models

As a basis for the discussion of establishment, spread and persistence, I here introduce some models for a population of individuals mixing heterogeneously. One of the simplest forms of heterogeneous mixing arises when individuals are distributed spatially, and interact principally with their near neighbours. This spatial case is a natural one to consider when modelling the spread of species.

As discussed earlier, stochastic models have a certain logical primacy, in that deterministic models can usually be regarded as approximating a more detailed stochastic model; for heterogeneously mixing populations in particular, deterministic models may be inadequate in important respects. Although considerable progress in stochastic spatial models has been made over the last 20 years, they unfortunately remain largely unknown in applied fields. This is partly because of their difficulty, but also partly due to the purist attitude of their originators. It therefore seems worthwhile to take the present opportunity to advertise them more widely. However, this digression is not essential for an understanding of later sections.

The contact process

Possibly the simplest stochastic model showing establishment, spatial spread and persistence is the 'contact process' introduced by Harris (1974). In this model, space is represented by a regular pattern of territories or 'sites', for instance the two-dimensional square lattice, and sites can be in just two states, occupied or unoccupied. Occupied sites become unoccupied at unit rate, and occupied sites colonize unoccupied neighbours at rate λ. (Formally, here a process at rate x means a Poisson process $\text{PP}(x)$, with the probability of a change in a short time interval $\mathrm{d}t$ being $x\mathrm{d}t + o(\mathrm{d}t)$; all these processes are assumed independent. For a rigorous treatment, see Liggett (1985).)

One way of defining a detailed probability structure with these properties is the following 'graphical representation' (Mollison 1972; Harris 1978), which is illustrated in figure 1. In this we draw a vertical line, representing time, through each site. On each line we make marks at unit rate, and between each pair of neighbouring sites we draw arrows at rate λ in each direction. Let A denote the set of occupied sites at time 0. Then we define a site as occupied at time t if there exists a route (called a contact chain) to it from a that goes up lines and along arrows without passing through any marks. If the marks are interpreted as indicating that a site becomes vacant, and the arrows as colonizations, the set of occupied sites $I_A(t)$ clearly has the properties required above.

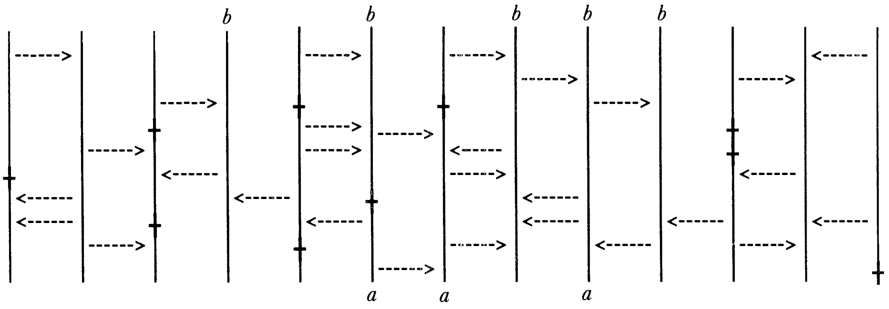

FIGURE 1. The graphical representation of a one-dimensional contact process: a sample realization, showing the set of occupied sites at time t, $I_A(t)$, for one particular choice of the initial occupied set A. a indicates sites of A, b sites of $I_A(t)$.

This probability structure has a number of elegant features. First, it is immediate from the characterization of occupancy in terms of contact chains that the set of occupied sites at time t depends additively on the initial set, i.e. $I_{a \cup b}(t) = I_a(t) \cup I_b(t)$. Secondly, if we reverse time and the direction of each arrow, we get a dual process which is statistically identical, and which has the property that b is in $I_a(t)$ if and only if for the dual process a is in $I_b(t)$.

We can use the same probability structure to define a basic competition model (Clifford & Sudbury 1973). In this model each site is initially assigned to one of two species, and an arrow from a to b indicates the colonization of b by the species currently occupying a (note that we only use the arrows; the marks are not needed).

For this process, the dual, where we reverse time and the direction of each arrow, consists of coalescing random walks; going back in time we are tracing a site's ancestry, and whenever two sites' ancestry traces meet they coalesce, that is to say their ancestors at each earlier time are the same. This observation yields a simple proof that the two species cannot be in stochastic equilibrium. It is easy to show that (in one or two dimensions) any two such random walks must eventually meet. Interpreted for the original (forward time) process, this tells us that, no matter how far apart two sites are, the probability that they are of different species tends to zero as time increases.

Returning to the contact process, the graphical representation gives a natural way of *coupling* (i.e. defining on the same probability space) the process starting with just one site occupied, $I_0(t)$, and the process starting with all sites occupied, $I_\Omega(t)$. If for $I_0(t)$ we define the area of influence of the one site at time t, $J(t)$, as the set of sites that are in $I_0(s)$ for some $s \leqslant t$, and are not in $I_\Omega(u)\backslash I_0(u)$ for $s < u \leqslant t$, then on $J(t)$ the processes $I_0(t)$ and $I_\Omega(t)$ have exactly the same occupied sites (see figure 2). Now $I_\Omega(t)$ is known to tend to a unique stochastic equilibrium, provided λ is greater than a critical value λ_c. It is a natural conjecture that for $\lambda > \lambda_c$ there is non-zero probability that $J(t)$ will eventually spread throughout space, so that $I_0(t)$ will tend to the same stochastic equilibrium, but this has only been proved for the one-dimensional process (see §6).

Various other spatial stochastic models can be defined similarly to the contact process. I shall refer in later sections to some slightly more complex models for endemic disease (§4, §6) (Mollison & Kuulasmaa 1985), and to basic models for spatial spread, which are simpler except that they incorporate an arbitrary dispersal distribution (§5) (Mollison 1972, 1977).

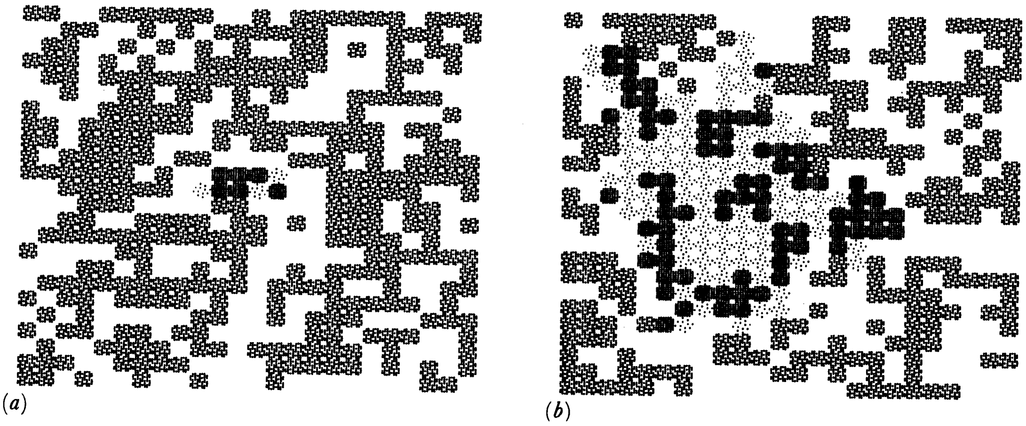

FIGURE 2. Coupled simulations of $I_0(t)$ and $I_\Omega(t)$ for a two-dimensional contact process: (*a*) at time $t = 5$; (*b*), at $t = 60$. Shading indicates: dark, sites in $I_0(t)$ and $I_\Omega(t)$; intermediate, sites in $I_\Omega(t)$ only; pale, vacant sites in $J(t)$ (vacant sites outwith $J(t)$ are left blank). Here $\lambda = 0.6$ ($\lambda > \lambda_c$, which $\lambda_c \doteqdot 0.412$ for the two-dimensional process (Brower *et al.* 1978)).

Linear and nonlinear models

The contact process and other models described above are nonlinear, having a simple form of density-dependence in that each site can accommodate only one individual (this can of course be generalized to any finite group size (Mollison 1972, Ball 1985*a*)). We can obtain a linear stochastic process by removing this restriction and allowing an arbitrary number of individuals at each site. The result is a spatial birth-and-death process, with birth rate $\alpha = 4\lambda$ (in two dimensions; $\alpha = 2\lambda$ in one dimension) and unit death rate.

For the birth-and-death process, the expected numbers $y(s,t)$ at site s at time t are easily seen to satisfy the linear differential equation

$$dy/dt = \alpha\bar{y} - y, \tag{3.1}$$

where $\bar{y}(s,t)$ denotes the average value of y over s's neighbours. It can hence be shown that this process, when it persists, spreads with higher velocity than the contact process, at least $2\sqrt{2}$ times as great in the one-dimensional case.

We can also write down a deterministic version of the contact process, the nonlinear differential equation

$$dy/dt = \alpha\bar{y}\,(1-y) - y. \tag{3.2}$$

(The factor $(1-y)$ here represents the probability of failure to colonize due to a neighbouring site's already being occupied.) However, this equation does not have any (known) close relation to the contact process. Instead, it can be shown that it describes the distribution of the furthest occupied site S_t (in any fixed direction) in the birth-and-death process: precisely, $y(s,t) = p(S_t > s)$ satisfies equation (3.2), where p represents probability. So the result, that both (3.1) and (3.2) give the same velocity, tells us that two different definitions of velocity for the birth-and-death process give the same value.

Thus the linear and nonlinear differential equations have close connections with each other and with the linear stochastic process, but not with the original nonlinear stochastic model, the contact process. This parallels results of McKean (1975) on the KPP/Fisher equation, and of myself and Professor H. E. Daniels (Mollison 1977) on the simple epidemic. The conclusion is that the nonlinear form of these basic differential equations for spatial spread does not, in fact, capture the nonlinearity (i.e. density-dependence) of the population process.

4. ESTABLISHMENT

Stochastic considerations are again important when considering whether the arrival of a small number, N, of propagules will lead to successful establishment of an invading species. In deterministic models the population survives if and only if the reproductive ratio, R_0, is greater than 1, where R_0 is defined as the mean number of offspring per individual when there is no competition from other members of the same species. In the simple stochastic birth-and-death process with constant per capita birth and death rates, the population survives with probability $1-(1/R_0)^N$, provided $R_0 > 1$. In that model, the number of offspring per individual, R say, has a geometric distribution; more generally, for given mean R_0, the probability of survival is greater if variability in R is low.

The condition for probability of establishment to be high (approximately, that R_0 should be large in initial conditions) is thus different from the condition for successful competition (of one species or genotype against another) which is that the net population growth rate r should be high. MacArthur & Wilson's pioneering work (1967) suffers from slight confusion in this area; for instance, it is not exactly correct that a propagule of maximal reproductive value stands the best chance of success (MacArthur & Wilson 1967, pp. 89–92), as is easily shown by an example.

In simple models, it is common to assume that competition within the species is minimal while the population is small, so that the minimum value, R_c, of the reproductive ratio for which the population has a chance of survival is simply 1 (e.g. in stochastic models with homogeneous mixing, and in most deterministic models). This is not necessarily true for stochastic models with heterogeneous mixing, especially spatial models with short dispersal distances, where there can be significant crowding effects even in very small populations. For instance, threshold values, R_c, vary between 2 and approximately 2.4 for the nearest-neighbour epidemic with removal (Mollison & Kuulasmaa 1985) (with the lower value corresponding to the least variability in R). Thus wide dispersal (*pace* MacArthur & Wilson 1967, p. 78) facilitates establishment, provided of course that it is dispersal of a breeding unit.

Whatever the critical value of R_0, the major problem of estimating whether it will be exceeded in a new environment resists any general quantitative approach. Species do not have an absolute value of R_0, only a value relative to a particular habitat or ecosystem.

5. SPREAD

Models for the rate and manner of spatial spread of population processes are reviewed, mostly in the context of epidemics, by Mollison (1977) and Mollison & Kuulasmaa (1985). The main aspects can be summarized briefly as follows.

Deterministic continuous time models typically give velocities of the order of $\alpha\sigma$, where α is the per capita birth rate of the species and σ is the standard deviation of the dispersal distribution (called the 'contact distribution' in the epidemic context, Mollison 1972), provided that this distribution has exponentially bounded tails. If not, the velocity is unbounded.

More realistic stochastic models have lower velocities, typically around 0.5 $\alpha\sigma$. Two technical points concerning deterministic models are of interest: (1) they have other solutions with arbitrary high velocity, of no practical interest because of their dependence on the population's being assumed continuous instead of discrete, and (2) nonlinear models superficially appear to model populations better, but have much closer connections with linear deterministic and stochastic models than with the most interesting nonlinear stochastic case (see §3).

Stochastic models can show an interesting mixture of steady progress and 'great leaps forward', though still with finite velocity, when the dispersal distribution has long tails (Mollison 1972). Qualitatively, stochastic models explain well the range of observed velocities of population processes. This includes the slow march north of oaks into northern Europe after the last Ice Age (approximately 0.3 km a^{-1}; (Skellam 1951; Bennett, this symposium)).

At this meeting, we have also heard of the spread of coypu, mink and muskrats in Britain and Europe (2–20 km a^{-1}; (Usher, this symposium; Williamson & Brown, this symposium)), and of fox rabies in Europe (up to about 50 km a^{-1}, with some higher values over short periods (Sayers *et al.* 1985; Ball 1985*b*)). A wide variety of examples, mostly with velocities of 10–100 km a^{-1}, is described by Elton (1958), including, for instance, the spread of chestnut blight and of starlings in the U.S., each at about 50 km a^{-1}.

As in our consideration of arrival (§2), occasional long dispersal distances have a disproportionate importance for spread, and thus for attempts to control it. The comparison of mink and coypu in Britain (Usher, this symposium) suggests that the occasional long dispersal distances of the former pose a more difficult problem for control than the greater fecundity of the latter. Similarly, the autumn dispersal of young male foxes has a significant role in the advance of rabies.

The highest estimates of velocity mostly relate to windborne organisms, for instance the invasion of the Americas by African bees (up to 500 km a^{-1} (Taylor 1977)), and the annual invasions of North America by stem rust, which has been known to travel at over 500 km per month in favourable spring weather (Stakman & Harrar 1957). Pedgley (1983) surveys the windborne spread of insect diseases, including ephemeral fever, which spread among Australian cattle in 1967–68 at up to 300 km per week.

When using models for quantitative estimates, the assumptions of the basic continuous time models need careful scrutiny. For instance, for a species such as oak, with a substantial minimum generation gap and a very high production of potential offspring (here acorns), a discrete-time model is probably more appropriate. In such a model, the velocity is still proportional to σ, but its dependence on α varies with the shape of the dispersal distribution. Thus an observed velocity of 0.3 km a^{-1} could correspond to values of σ ranging roughly between 0.3 and 5 km for dispersal distributions ranging from exponential to uniform (Mollison 1977) (even at $\sigma = 0.3$ km, it would appear that the acorns received substantial assistance in their dispersal!).

Control by barriers

When we wish to prevent the spread of a species, we may create a control zone in which conditions for its survival are depressed to sub-endemic levels. To date, models for control zones have been largely inadequate, for two main reasons. First, it is difficult to predict how far conditions will be depressed by a given control strategy, or even whether it will make spread more difficult as intended (see §7). Secondly, deterministic models for control zones (see for example, Thieme 1980, Källen *et al.* 1985) fail to capture the individual nature of the problem.

The importance of the form of the dispersal distribution is also often ignored, especially when a diffusion equation is used to model spatial spread, as this essentially assumes that individual dispersal movements are infinitesimal. A more promising stochastic approach to control zones is described by Ball (1985*a*).

A further elementary, but real, problem of control zones is that of the information base. Bacon (1981) demonstrates this problem with respect to official U.K. proposals for rabies control by a simple calculation showing that determinations as to how far the disease has spread in wildlife could well be in error by a distance several times as large as the depth of the proposed control zone.

6. PERSISTENCE

We have already discussed (in §4) the threshold value, R_c, of the reproductive ratio, above which there is a chance that an invading species will become established. Whether a species can persist in the long term is a rather different question: a trivial example showing the difference is given by the epidemic with removal, where there is no regrowth of the 'food supply' (i.e. susceptibles), so that, although the epidemic may spread widely if $R_0 > R_c$, it cannot persist anywhere. However, when the remainder of the ecosystem retains the capacity to regrow to its original level as the invader's population falls, it is a natural conjecture that the threshold for persistence, R'_c say, will be the same as that for establishment, R_c.

Some simple deterministic models for persistent disease are dissected by Mollison (1984, 1985), and their sensitivity to underlying assumptions examined. It transpires that some results are relatively robust (for instance concerning the threshold for endemicity, and the proportion of infected cases at equilibrium), but have alternative simpler, almost 'model-free' derivations. Other results (for instance concerning the stability of the endemic equilibrium) do require the full model, but are very sensitive to its exact form.

The kind of theoretical results that may reasonably be conjectured for more complex systems can be exemplified by what has been proved for the one-dimensional contact process (see §3). For this it is known that: (*a*) there is a critical value, λ_c, of the parameter λ (roughly, $R_0 \doteqdot 2\lambda/(1+\lambda)$) such that persistent stochastic equilibrium is possible just for $\lambda > \lambda_c$ (λ_c is estimated to be *ca.* 1.649 (Brower *et al.* 1978)); (*b*) for an initial population of one individual, there is positive probability of spread throughout the environment precisely when $\lambda > \lambda_c$; when that happens, (*c*) spread of both left and right edges, l_t and r_t, is asymptotically at a velocity known to lie between $\lambda - \lambda_c$ and $\lambda - 1$; and (*d*) between l_t and r_t conditions tend to the unique persistent stochastic equilibrium distribution.

The contact process can be regarded as an epidemic with recovery. Mollison & Kuulasmaa (1985) simulated a slightly more realistic endemic model, and compared its qualitative behaviour with the non-spatial endemic model of Anderson *et al.* (1981). They found that, in the spatial model, the equilibrium proportions are radically altered; the food supply is much less depressed, and the 'population' (i.e. infected cases) considerably smaller than in the non-spatial model.

The spatial model's behaviour is roughly described in terms of 'wandering patches' of population, whose scale of pattern is relatively large, considering that individuals only interact with their nearest neighbours, and is reminiscent of actual data on the spread of fox rabies in Europe (figure 3). It does not, and cannot be expected to, have periodic behaviour of the kind associated with the non-spatial model. However, if we consider the sequence of states a site

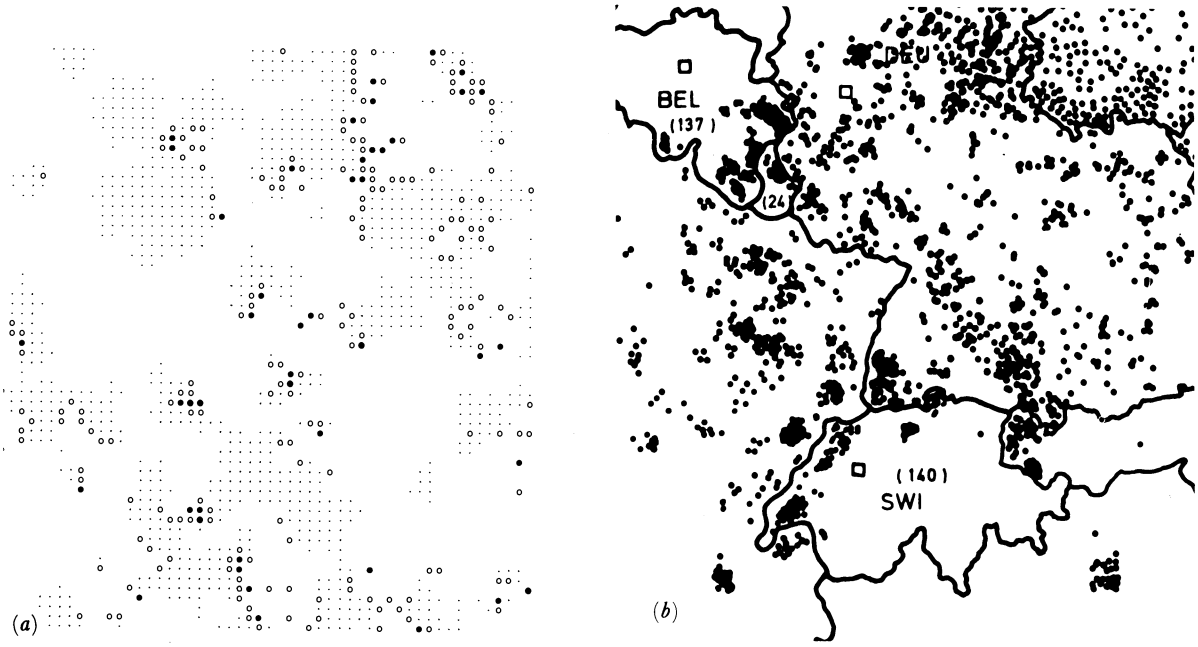

FIGURE 3. (*a*) Simulation of stochastic spatial endemic model (from Mollison & Kuulasmaa 1985). Filled circles, infectious sites; open circles, incubating sites; dots, susceptible sites; vacant sites are left blank. (*b*) Rabies cases in central Europe, July–September (from Schneider *et al.* 1985).

goes through (susceptible to infected to vacant to susceptible), we might expect any apparent oscillations to be related to the 'turnover' period, τ/p_I, where τ is the mean time for which an individual is infected and p_I the equilibrium proportion of infected sites. Coincidentally, for fox rabies this turnover period is about three years, roughly the same as the period predicted by the non-spatial model $(2\pi\tau/\sqrt{p_I})$.

These simulations show how it may be difficult to distinguish between chance inhomogeneities of the population in a homogeneous habitat, and inhomogeneities that reflect variation in the habitat, when a population (or disease) may be genuinely above its threshold for persistence only in particular habitat 'islands' (see, for example, Gorman 1979). It would be interesting to look at similar models with a number of interacting species in a homogeneous habitat and see how much the stochastic and spatial aspects facilitate coexistence.

The distinction between heterogeneous mixing and heterogeneity of population parameters also applies to certain human diseases, where the 'habitat islands' consist of subgroups of the population, which for one reason or another have much higher contact rates. Models incorporating contact rates varying with age (Dietz & Schenzle 1986) or sexual habits (Hethcote & Yorke 1984; Anderson & May, this symposium) have been studied deterministically, but these do not capture the heterogeneous mixing associated with the network of contacts made by individuals, an aspect which may be equally important and deserves attention; this would seem to require stochastic models.

So far, I have referred implicitly only to persistence in a large habitat. MacArthur & Wilson (1967) discussed the balance of invasions and extinctions in a small island habitat, linking the probability of persistence to the carrying capacity, K, for the species. An interesting refinement would be to examine various behavioural patterns that may assist persistence of small populations, for instance different types of territorial behaviour.

Fluctuations in population parameters, either regular or stochastic, will also often be important in determining whether an invasion can persist. For instance, seasonal variation in transmission rates for measles affects the minimum population size required for it to persist (Bartlett 1960; Stirzaker 1975).

Anderson & May (this symposium) suggest that high R_0 makes persistence of a disease difficult. This may well be the case in small habitats. For instance, for the spatial endemic model described above, high R_0 is associated with larger patches moving faster, and this will make extinction more likely if the habitat is so small that it can only support one or two patches; however, in larger habitats, high R_0 would enhance persistence. With the example of influenza they mention, it may be the high turnover rate of the disease, relative to the rate of population growth and annual fluctuations in transmission rates, that causes it to die out locally, rather than a high value of R_0.

The genetic and behavioural characteristics of successful invaders, as discussed by several speakers at this meeting (O'Connor, Lawton & Brown, Gray, and Crawley, this symposium), is for the most part a topic for qualitative rather than quantitative conclusions. Some species have the ability to invade but not persist: for instance the 'supertramp' bird species of Diamond (1974), which have high dispersal ability and rapid breeding but are comparatively inefficient at exploiting resources in the long term. Persistence will also often depend on the adaptation of the invader and its environment to each other, as in the example of the coevolution of myxomatosis and its host (Ross & Tittensor, this symposium).

7. Discussion and conclusions

As we have seen, mathematical models have made useful contributions to our understanding of all stages of biological invasions, explaining their behaviour in terms of simple ecological parameters. For instance, in arrival, not only the mean but also the shape of the dispersal distribution matters; establishment depends on a high reproductive ratio, R_0; the mean velocity of spread depends principally on the population growth rate and the mean dispersal distance, though the variation in rate of spread may depend on the shape of the dispersal distribution; and persistence depends on the carrying capacity, K, and on any stabilizing features of the population dynamics. We can use such models to estimate parameters or for approximate quantitative deductions, for instance for the mean dispersal distance of oaks (§5).

At their best, such models make it clear what ecological aspects are modelled to what accuracy. They have the minimal number of parameters required to model important features correctly (Occam 1488), and the dependence of conclusions on the various assumptions is clear (Bradley 1982). For instance, in models for an endemic population which regulates its food supply, the equilibrium population and cyclical behaviour around equilibrium depend on the net growth rate, r, of the food supply and the mean generation gap, τ (Mollison 1984, 1985), and on the form of heterogeneous mixing in the population (see §6). On the other hand, establishment and persistence depend on the reproductive ratio, R_0 (see §§4, 6), and the difference for a model incorporating heterogeneous mixing seems simply to be that the threshold value of R_0 will be increased.

Even with such a simple condition for endemicity, depending on the one parameter R_0, quantitative predictions outwith the range of observations (as in Anderson *et al.* 1981) are not reasonable. Prediction is especially difficult where ecological conditions are significantly altered; for instance, with control by killing, because this will disrupt the population to an extent that depends on the detailed strategy, and the consequent change in the value of R_0 is more a question of animal behaviour than of mathematics (Mollison 1984, 1985).

The problems of quantitative prediction in general become worse rather than better if we make our model more detailed. For instance, staying with models designed with fox rabies in mind, the apparently much more 'realistic' model of Voigt *et al.* (1985) makes crude quantitative assumptions about basic parameters such as R_0, r and τ, but the crucial effect of these assumptions is easily missed in a model which has over 30 parameters.

An approximate summary of quantitative models for invasions might be that they are of great use in clarifying our ideas, for examining the logical consequences of assumptions, and for comparing different assumptions; also for broadly quantitative explanations and estimates of parameters and for qualitative predictions. Quantitative predictions, however, are rarely of use outwith the range of observations. The archetypal result is that an invasion will succeed if R_0 is above its threshold value in the new environment. This leaves us wiser only in the sense that, like Socrates, at least we know that we know nothing.

Appendix 1. Long-distance wind dispersal of organisms

The one means of long-distance dispersal available to all species with sufficiently light propagules is the wind. Here I attempt to determine quantitatively what the restriction 'sufficiently light' means in the context of the transport of particles over hundreds of thousands of kilometres.

Consider first particles crossing under smooth airflow. Provided an organism is viable up to height H^*, and has some probability of being carried up to this height, as, for example, in a convection tower associated with a thunderstorm, and that there is some probability of winds blowing in the desired direction with mean velocity G, then the organism will be able to cross a gap of width D if its terminal velocity in still air, v, is less than $v_0 \equiv GH^*/D$. For example, for the Atlantic under present-day meteorological conditions, $v_0 \sim 1$–$2\ \mathrm{cm\ s^{-1}}$ (taking $G = 10$–$15\ \mathrm{m/sec}$, $D = 4000\ \mathrm{km}$, $H^* = 4$–$6\ \mathrm{km}$). Particles with $v \lesssim 1\ \mathrm{cm\ s^{-1}}$, then, are undoubtedly sufficiently light to travel thousands of kilometres. Such travel is well documented (Darwin 1846; Gregory 1961, 1971; Junge & Jaenicke 1971; Delany *et al.* 1967; Prospero *et al.* 1970; Bowden *et al.* 1971), though to be observable particles must travel in huge numbers: a density of one particle per cubic metre equals about $10^{15}\ \mathrm{d^{-1}}$ for transoceanic transport (taking a particle cloud of cross-section $1200\ \mathrm{km} \times 1\ \mathrm{km}$, $G \approx 10\ \mathrm{m\ s^{-1}}$). When it is a matter of the spread of a disease, or of a species, a single viable particle landing in a favourable spot suffices; if we are concerned with a prolific species for which, over an evolutionary timescale, a probability of long-distance transport as low as 10^{-30} (for a single organism) might be significant, we must consider values of v substantially greater than v_0; taking as lower bound 10^9 seeds $\mathrm{a^{-1}}$ (a single plant of *Acropera* can emit a third of this number (Ridley 1930)), and as upper bound 1000 seeds $\mathrm{s^{-1}\ m^{-2}}$ of the entire African continent, gives a range of 10^{15}–10^{30} per million years for a prolific species.

For $v > v_0$, particles must rely on vertical motions of the air; the greater v is, the more violent this mixing must be. For a given vertical velocity spectrum of the wind and given v, the surviving particles may be expected to settle into a 'quasi-steady' distribution: that is, one in which the profile of their distribution remains the same, though being depleted proportionally all the time;

the rate of convergence to this shape is greater for more violent mixing. Associated with such a quasi-steady distribution will be a constant (proportional) fallout rate, ϕ. Then for large T, the probability of survival to time T will be given by

$$p(T) \approx p_0 \,\mathrm{e}^{-\phi T}, \tag{1}$$

where p_0 is a constant, roughly representing the probability of a particle's being initially carried to a considerable height. (Thus we are not interested in local deposition, a problem to which sophisticated attention has been paid (Sutton 1932; Smith 1962; Pasquill 1971; Chamberlain 1975; Waggoner 1983).)

We shall find a lower bound to the fallout rate that is proportional to v; then, if we define v_ϵ as the greatest value of v for which there is probability at least ϵ of an organism's being carried across a gap D, we can find an upper bound of approximately $v_0 \ln (p_0/\epsilon)$ for v_ϵ ($\approx 46v_0$ when $\epsilon/p_0 = 10^{-20}$, for instance).

Theory

We can prove that (1) holds, and that there is a lower bound proportional to v for the fallout rate, provided that the vertical motions of particles are not correlated over times that are large compared with the characteristic eddy times of the vertical mixing. Consider particles of given terminal velocity v being transported in airflow between an absorbing barrier at 0 (the surface) and a maximum height H, which could be a meteorological barrier (e.g. a temperature inversion), or a limit of viability. Because we wish to calculate a *lower* bound for the fallout rate, we shall make the optimistic assumption that particles are only lost at the surface. We shall, for convenience, approximate the height scale by dividing it into N discrete steps (which may be taken arbitrarily small to improve accuracy). Let τ be such that the correlation of particles over times more than τ apart may be ignored; by assumption τ is comparable to the maximum characteristic time of eddies. Then the vertical mixing of the particles can be described by a transition matrix, Q, such that

$$x_i(t+\tau) = \sum_j Q_{ij}\, x_j(t), \tag{2}$$

where $\boldsymbol{x}(t)$ represents a distribution of particles over the states $i = 1, 2, \ldots, N$ (representing heights iH/N). Q is substochastic, i.e. $\Sigma_j Q_{ij} \leqslant 1$ for all i. If we add the absorbent state 0, corresponding to particles that have fallen out, we get the stochastic matrix Q ($\Sigma_j Q_{ij} = 1$ for all j); the movements of particles between states $0, 1, \ldots, N$ over successive time intervals of length τ form a Markov chain.

Let us make the realistic assumption that it is possible to get from any state, other than 0, to any other state (in a finite number of steps); that is, the states $1, 2, \ldots, N$ form a class, which is transient because all particles will eventually reach the state 0. It can then be shown that, for given Q, there is exactly one possible quasi-steady distribution, i.e. eigenvector of Q. The proof of this runs as follows:

Consider the continuous function $\boldsymbol{x} \rightarrow Q\boldsymbol{x}/|Q\boldsymbol{x}|$ on $P_1 \equiv \{\boldsymbol{x} : x_i \geqslant 0, \Sigma_i x_i = 1\}$, where $|\boldsymbol{z}|$ denotes $\Sigma_i z_i$ (that $|Q\boldsymbol{x}| \neq 0$, for $\boldsymbol{x} \in P_1$, follows from the assumption that the states $1, 2, \ldots, N$ form a single class). P_1 is compact and convex, so that we can apply Tychonoff's fixed point theorem (Dunford & Schwartz 1958) to deduce that there exists $\boldsymbol{x}^*$ such that $Q\boldsymbol{x}^* = \boldsymbol{x}^*/|Q\boldsymbol{x}^*|$; that is, a positive eigenvalue $\boldsymbol{x}^*$ of Q with eigenvalue $\lambda \equiv |Q\boldsymbol{x}^*|$. Now suppose there were two eigenvectors $\boldsymbol{x}^*$, $\boldsymbol{z}^*$ with respective eigenvalues $\lambda \geqslant \mu$. Now $z_i^* > 0$ for all i, because the states $1, 2, \ldots, N$ form a single class; so we can scale $\boldsymbol{z}^*$ such that $\boldsymbol{x}^* \leqslant \boldsymbol{z}^*$, with equality for at least one state, j, say. Then $(Q(\boldsymbol{z}^* - \boldsymbol{x}^*))_j = \mu z_j^* - \lambda x_j^* = (\mu - \lambda)\, x_j^*$, which is less than 0 if $\lambda \neq \mu$; this result is contradictory, as $\boldsymbol{z}^* - \boldsymbol{x}^*$ and Q are both non-negative. Therefore $\lambda = \mu$; then $\boldsymbol{z}^* - \boldsymbol{x}^*$ is another eigenvector, but with a zero entry, which is impossible. So we may deduce that Q has only one positive eigenvector, $\boldsymbol{x}^*$. The corresponding fallout rate, ϕ, is given by $\mathrm{e}^{-\phi\tau} = \lambda$; thus $\phi = \tau^{-1} \ln \lambda^{-1} \approx (1 - \lambda)/\tau$.

It can be proved further that $\lambda^{-n}\boldsymbol{x}(n\tau)$ tends to $p_0 \boldsymbol{x}^*$ as $n \to \infty$, i.e. that (1) holds, provided only that Q is not periodic (another realistic assumption) (Darroch & Seneta 1965). Thus

$$\boldsymbol{x}(T) \approx p_0\, \mathrm{e}^{-\phi T} \boldsymbol{x}^* \quad \text{for large } T.$$

To estimate the minimum possible value of ϕ, suppose first that Q satisfies the following 'drift condition': the expected altitude of a particle decreases by $v\tau$ in time τ, irrespective of its initial altitude. Then it is easily shown that $\theta \approx v/\overline{H}$ where $\overline{H}$ is the mean altitude of particles in the quasi-steady distribution; $\overline{H}$ must of course be less than H, so $\phi \gtrsim v/H$. The drift condition is only an approximation, however; when the vertical mixing becomes fast compared with v, violation of the drift condition in the lower boundary layer may be expected to be increasingly important. To investigate whether ϕ can be less than v/H in this case, let us make the optimistic assumption that the deposition velocity, v_{g}, remains comparable with v as the vertical mixing increases ($v_{\mathrm{g}} \approx v$ for low values of the friction velocity u_*, but increases as u_* increases (Chamberlain 1967)). In the limit, as v_{g} becomes negligible compared with the mixing, we may expect $\boldsymbol{x}^*$ to tend to the uniform distribution; then $\phi = v_{\mathrm{g}}/H \gtrsim v/H$. Thus in either case

$$\phi = kv/H, \quad k \gtrsim k_0 \geqslant 1. \tag{4}$$

To proceed any further, we must make more assumptions about Q. We may expect both k and the speed of convergence to the quasi-steady distribution to depend on the characteristic length h and velocity u of eddies (in the vertical direction), when these can be defined, and on their ratios to H and v respectively ($m \equiv H/h$, $b \equiv v/u$). To examine these dependences, we shall consider here just the simplest possible model, based on the Bernouilli random walk between one reflecting and one absorbing barrier. In this, the states $2, 3, \ldots, N-1$ satisfy the drift condition (probability of a step down $= \frac{1}{2}(1+b)$, of a step up $= \frac{1}{2}(1-b)$), while the boundary conditions are chosen such that the deposition rate $= v$ and that $\boldsymbol{x}^*$ is the uniform distribution when $v = 0$ (when both barriers are reflecting). In this model, $m = N$.

For this model, the constant k depends, to a degree of approximation that is good except when b is close to unity, on the product mb. Now k tends to 1 as mb tends to 0, and increases fairly slowly up to $mb \sim 4$ (when $k \approx 2$). Thus for the random walk model

$$\phi \text{ is near-minimal} \quad \text{if and only if} \quad mb \text{ is small.} \tag{5}$$

Lastly, we return to the question of how fast $p(t)$ approaches its asymptotic value of $p_0\, \mathrm{e}^{-\phi t}$. Let T_δ be the least time such that $|p(t)\, \mathrm{e}^{\phi t} - p_0| \leqslant \delta$ for $t \geqslant T_\delta$. If a mean diffusivity constant K can be defined for Q we may expect $T_\delta = c_Q H^2/K$, where c_Q varies only slightly with Q. For the random walk model, $K = hu$, so that $T_\delta = c_Q (H/u)\, m$; computer simulations show that $c_Q \approx 0.2$ when $\delta = 0.01$, at least for $m \leqslant 100$. Now $\phi = kv/H$, so $\phi T_\delta = kc_Q mb$; when the mixing is sufficient for the fallout rate to be small, mb is small (condition (5)), and hence $\mathrm{e}^{\phi T_\delta} \not\gg 1$.

Therefore

$$p(T) \approx p_0\,\mathrm{e}^{-\phi T}, \text{ provided } \mathrm{e}^{-\phi T} \ll 1. \tag{6}$$

In other words, for the random walk model at least, convergence to the quasi-steady distribution is guaranteed for exactly those conditions that interest us, namely when ϕ is near-minimal and $p(T)/p_0 \ll 1$. If the rate of convergence for this simple model is at all typical of the rate for more general, physically realistic Q, we may conclude that $p(T) \sim p_0\,\mathrm{e}^{-\phi T}$, at least to within an order of magnitude or so; this result enables us to make the following deduction. The terminal velocity, v_ϵ, of a particle whose probability of crossing a gap D is ϵ, has an upper bound given by

$$v_\epsilon \lesssim (GH/k_0 D)\ \ln\,(p_0/\epsilon), \tag{7}$$

where $k_0 \equiv \min\,(\phi H/v) \gtrsim 1$, and $H \geqslant H^*$, so that a simpler, but cruder, bound for v_ϵ is $v_0\ \lg\,(p_0/\epsilon)$.

Conclusions

To refine these results, a more physically detailed analysis, especially of the relation between the vertical mixing and the velocity of deposition, would be needed. It should then be possible to make a better estimate for k_0, and to predict the shape of the quasi-steady distribution in specific conditions for comparison with observed profiles of distant migrants, such as rust spores (Hirst & Hurst 1967; Hirst *et al.* 1967*a*, *b*).

To indicate quantitatively the implications of our results, consider first, as an example, the Saharan air outbreaks of the North Atlantic (Carlson & Prospero 1972), which carry great quantities of dust to the Caribbean (about 10^{11} g d^{-1}, (Prospero & Carlson 1972)), including a fair proportion of particles with $v > v_0$ (Prospero *et al.* 1970). Taking $D = 4000$ km, $G = 7$ m s^{-1} and $H = 5.5$ km (Prospero & Carlson 1972), and $k_0 = 1$, we obtain, for $\epsilon = 10^{-20} p_0$, $v_\epsilon \lesssim 45$ cm s^{-1}. Given that particles with $v \geqslant 3.2$ cm s^{-1} (corresponding to a quartz particle of $\geqslant 20$ µm diameter) can make up as much as 4 % of the Saharan dust collected at Barbados (Prospero *et al.* 1970), it should be possible to estimate the probability of transport for particles up to at least this size, by comparing measurements made on both sides of the Atlantic. Unfortunately, the only measurements to date for the eastern side of the Atlantic have been made at sea level (Chester & Johnson 1971; Chester *et al.* 1971), whereas the majority of dust is transported in a layer at heights between about 1.5 and 6 km. For the present we have rough bounds $3.2 < v_\epsilon < 45$ cm s^{-1}; and may guess that v_ϵ is most likely to be approximately 10–20 cm s^{-1}, so that the vertical mixing is, in this case, quite close to optimal.

For substantially larger particles to cross such a gap would require larger values of the product GH. The mean velocity, G, will be substantially larger for jetstreams, but these have a smaller vertical extent (1–2 km) so that GH will not be much increased; it is, in any case, doubtful whether they have sufficient vertical mixing to make the fallout rate near-minimal for particles with v up to about 1 m s^{-1}.

We may summarize the position as regards organisms' chances of crossing gaps of $D \gtrsim 1000$ km as follows. If their terminal velocity in still air, v, is $\lesssim v_0$ (where v_0 is inversely proportional to D and ≈ 1 cm s^{-1} when $D = 4000$ km) they will be able to cross subject only to viability and to the wind's being, at least occasionally, in the right direction. Most fungal spores, some pollens, and the pteridophyte *Lycopodium*'s spores, for example, fall into this class

(Gregory 1961; Hirst & Hurst 1967). Larger organisms, with $v \sim 10v_0$, require in addition that effective vertical mixing (with characteristic vertical velocities several times as large as v) should extend over a depth of several kilometres; such conditions may be expected to occur, for example, in trade wind belts. Larger fungal spores and pollens, some plumed fruits and orchid seeds fall into this class (Praeger 1911; Gregory 1961; Hirst & Hurst 1967; Ridley 1930). (For an approximately spherical organism of unit specific gravity, the requirement is roughly that its diameter should be less than 100 μm; an irregularly shaped organism could be considerably larger.) $70v_0$ (in present-day conditions ≈ 1 m s^{-1}) may be considered an absolute upper bound; it corresponds to a probability of crossing of approximately 10^{-30} in conditions of optimal vertical mixing.

Because we are interested in very low values of the probability of crossing, P, say, and because $\ln P$ in given conditions is roughly proportional to v, the most extreme meteorological conditions will be important, almost regardless of their probability; similarly, the smallest possible viable propagule will be important. For example, P (strictly ϵ/p_0) may fall from 10^{-10} to 10^{-20} if either the fallout rate is doubled or the radius of the particle is increased by a factor of $\surd 2$ (because $v \approx r^2$ for particles of roughly unit specific gravity and $v \lesssim 3$ m s^{-1}).

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Discussion

R. M. ANDERSON, F.R.S. (*Department of Pure and Applied Biology, Imperial College, London, U.K.*). Models are used for different purposes. Policy seeking to control diffusion of a disease like rabies needs information about how wide an exclusion barrier must be, how far fox densities must be suppressed, and what the likely rate of population recovery to danger level is. Such details are better provided from deterministic than from stochastic models.

D. MOLLISON. I do not agree. Policy-makers do like quantitative answers, but we should not give them if they are not reliable. Deterministic models are a useful first step in qualitative understanding of the spatial spread of invasions (Skellam 1951) and epidemics (Kendall, in discussion of Bartlett (1957), pp. 64–67; Mollison 1972), but the problems of control zones highlights their shortcomings. The usual differential equation models are not stopped by any depth of control zone at any level of depression short of 100%, and have to be somewhat arbitrarily doctored (as in Thieme 1980; Källen *et al.* 1985) to give a more sensible answer. The stochastic modelling of Ball (1985) is clearly superior in this respect. Even with a stochastic model, there remain the problems I discussed (§§5, 7) of estimating how far conditions for the disease are depressed, and of dispersal distribution. In the absence of quantitative data on such points, simple back-of-envelope calculations, such as those of Bacon (1981) which I cited, at least have the advantage that their assumptions and limitations are clearly visible.

R. M. ANDERSON. Can Professor Mollison give me one example of a situation where stochastic models have influenced policy? There are many where deterministic ones have.

D. MOLLISON. I was here only attacking the use of deterministic models in the specific context of spread across a barrier, where they cannot be expected to give the right answer except by luck.

More generally, I would agree with Bradley (1982) that often it has been simple, almost model-free, points that have been important, and that quantitative details of models for epidemics and invasions, whether deterministic or stochastic, can be unnecessary and misleading (Bradley 1982, p. 320). Certainly, before accepting quantitative estimates it is vital to understand how they depend on the components of the model, so as to have some idea how reliable they may be (Mollison 1984; Bradley 1982, p. 331). Specific examples with stochastic models respecting these points include the wide selection of 'back-of-envelope' calculations of MacArthur & Wilson (1967), the relation between community size and the extinction of measles (Bartlett 1957), and the dependence of the breakpoint concept for schistosomiasis on the distribution of individual worm burdens (May 1977).

M. S. **Bartlett** (*Priory Orchard, Priory Avenue, Totnes, Devon, U.K.*). Dr Mollison has suggested that it is important to consider stochastic, in contrast to deterministic models, in predicting the characteristics of real ecological or epidemiological situations. It would, however, seem helpful to try to classify these situations (as one or two of us have attempted already) into those where a full stochastic treatment is necessary, as, for example, when numbers are small, and those where comparable deterministic formulation is adequate.

Incidentally, perhaps Dr Mollison could say more precisely what he means by 'prediction' from models. He might be concentrating on the narrower interpretation of predicting future consequences or have in mind the wider interpretation which would include any scientific predictions from the model that could help to indicate its value. Sometimes, even if comparatively simple models are not very satisfactory in the narrower predictive sense, they might be quite illuminating in the wider sense.

D. **Mollison**. I would agree with Professor Bartlett's first point, where he modestly understates his own pioneering role in investigating both deterministic and stochastic models. We might go further in distinguishing cases where a stochastic model is essential for even broad qualitative results (as usually when overall numbers are small) and those where a deterministic model provides a good qualitative description but may be wrong quantitatively (as can happen when overall numbers are large but the numbers with whom each individual interacts is small).

As to 'prediction', I hope the written version of my paper (especially §§1 and 7) makes my meaning clearer.

Sir Richard Southwood, F.R.S. (*Department of Zoology, South Parks Road, Oxford, U.K.*). Do Professor Mollison's models for the transport of insects across the sea take differences in aerodynamic mixing over land and sea into account?

D. **Mollison**. No. The model simply gives an upper bound under arbitrary mixing. However, I do point out that vertical mixing over the ocean, for instance in trade winds, can be quite close to optimal for the transport of particles with settlement rates of up to about 30 cm s^{-1}.

Additional references

Bartlett, M. S. 1957 Measles periodicity and community size. (With discussion.) *Jl R. Statist. Soc.* A **120**, 48–70.

May, R. M. 1977 Togetherness among schistosomes: its effects on the dynamics of the infection. *Math. Biosci.* **35**, 301–343.