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Natural Extinction on Islands [and Discussion]

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Natural extinction on islands

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Almost all recent extinction of species or subspecies on islands comes from human activities. On the other hand, in local populations there is much natural extinction and immigration, i.e. turnover, on small islands. Most of this turnover occurs in locally rare species, and attests to the phenomenon of minimum viable population size. The MacArthur–Wilson theory is based on this turnover which, from an ecological point of view, is generally trivial. More useful theories of minimum viable population size are being developed. Rarity is the precursor of extinction, and species can be rare in several ways. Models of these phenomena are still primitive, particularly those that relate habitat availability to population density. Models of interactive communities show phenomena that may be relevant to the understanding of extinction in the geological record. Lotka–Volterra equations indicate considerable sensitivity to invasions, sometimes producing a cascade of extinction. Chemostat equations show that the behaviour of food chains can change dramatically with small changes in parameters, suggesting that small environmental effects can sometimes cause large ecological changes, including extinctions, in interactive biotic communities.

DATA ON RECENT EXTINCTIONS

Neontological data should provide the background for interpreting palaeontological phenomena. It is often convenient and interesting to study ecological processes on islands or other more or less isolated systems (Williamson 1981). Unfortunately, almost all modern island ecosystems are strongly influenced by human activities (Diamond, this symposium). For birds, the best-known group, all recent extinctions of a species or subspecies were caused by humans, with one exception (King 1985). The exception is a bullfinch, *Loxigilla portoricensis grandis*, a subspecies confined to the island of St Kitts in the Lesser Antilles, last seen in 1880, which may have become extinct after two hurricanes in 1899 (Raffaele 1977). As its name implies, it was an unusually large form of bullfinch, and St Kitts was the only island in the Lesser Antilles where two species of *Loxigilla* coexisted (Lack 1976). So this one exception may possibly be an instance of evolutionary events leading to rarity.

Even though natural extinctions of species may be hard to find, natural extinctions of local populations are still common. So I shall discuss what is known about extinction of island populations, as opposed to island species, then consider the phenomenon of rarity, and finally discuss some ways in which mathematical models may help in the understanding of these modern data, and by extension the understanding of the palaeontological data.

Species are often rare at the edge of their range, and it may be that statistically the single most important cause of being rare is being at the edge of the range (Schoener 1987). Extinction in marginal populations in birds is well known. *Turdus philomelos*, the song thrush, established itself in Shetland in 1906, and increased to about 24 pairs over the next decades. However, the population crashed in the hard winter of 1947, and died out soon after (Williamson 1981), even though it continued to breed in the neighbouring archipelago of

Orkney (Sharrock 1976). In fact there were always a few wintering birds in Shetland, but these may have come from Scandinavia (Lack 1986), and a Shetland breeding population was re-established in 1976 (Berry & Johnston 1980). Another example is shown in figure 1. Remarkably full counts of the breeding birds of Skokholm Island, Wales, were made from 1928 to 1979, except for the war years. This data set shows many local extinctions and immigrations, mostly relating to casual breeding by single pairs (Williamson 1981, 1983). A few slightly more common species, such as *Prunella modularis*, the dunnock, also show turnover. In figure 1 it can be seen that a population of about five pairs went extinct on the island in the early 1940s, and that a population was not re-established until the 1960s. Dunnocks are primarily birds of scrubland and hedgerows; the bleak island of Skokholm is a distinctly marginal habitat for them. The island is almost exactly 1 km^2 in area, so the density of five pairs per square kilometre can be compared with the figure of 28 pairs per square kilometre for English farmland in general and 52 pairs per square kilometre in favourable habitats (Sharrock 1976) to show how unfavourable Skokholm is for this particular species. Indeed, there may be a lack of genetic adaptation as a result of this sort of turnover. Some permanently established dunnock populations in Skokholm-like habitats are in the subspecies *P.m. hebridium* (Sharrock 1976).

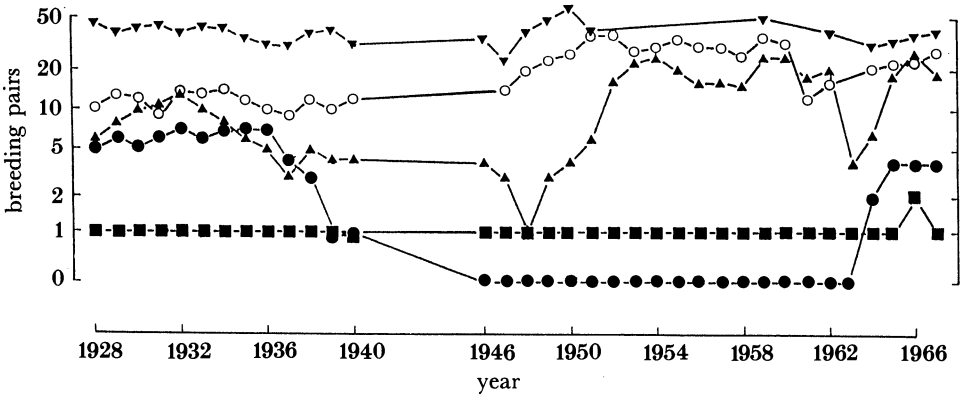

Figure 1. Numbers of breeding pairs for five species of land birds on Skokholm Island, Wales. The ordinate is scaled by arcsinh y, essentially the same as a logarithmic transformation for numbers greater than two. Counts for these species up to 1979 are in Williamson (1983). (▼) *Anthus pratensis*, meadow pipit; (○) *Oenanthe oenanthe*, wheatear; (▲) *Vanellus vanellus*, lapwing; (●) *Prunella modularis*, dunnock; (■) *Corvus corax*, raven. Modified from Williamson (1981).

That most of the local extinctions associated with turnover occur in thin, marginal populations can be seen in another bird community, that in the 16 ha† oak wood at Bookham Common, Surrey, England. Figure 2 is a diagram of the breeding records over 29 years. The species are ordered by their arithmetical mean over the period. About one third of them have an average of less than one pair a year, which means they are, in this survey, normally locally extinct. It is evident that in this relatively small patch of habitat most species occur at so low a density that they are not recorded as breeding in every year, i.e. they regularly become extinct locally. This sort of extinction can be called demographic extinction. There is also environmental extinction, as shown by two warblers that became extinct in the wood in 1971.

† 1 ha = 10^4 m^2.

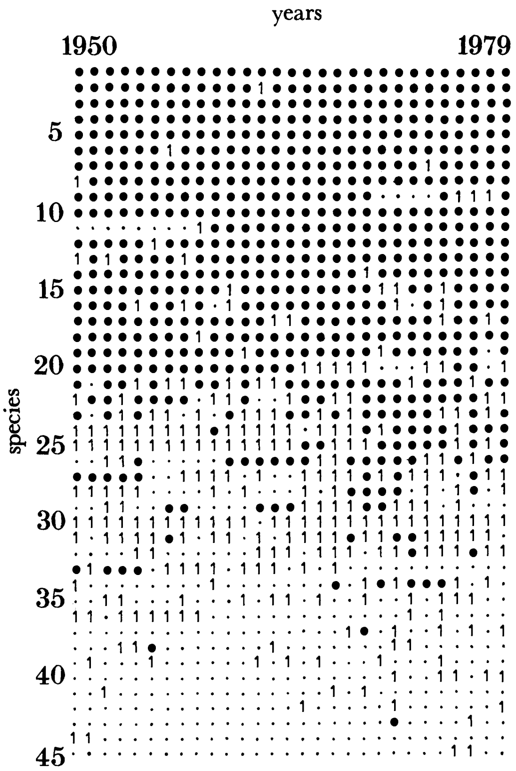

FIGURE 2. A diagram of the breeding community of birds at Eastern Wood, Bookham Common, England. The columns are years. There was no count in 1957. Each row is a species. (●) Two or more breeding pairs; (1) one breeding pair; (·) not breeding. The full data can be found in Williamson (1981, 1987). Modified from Williamson (1987).

These are the ninth species, *Phylloscopus trochilus*, the willow warbler, and the twentieth species, *Sylvia borin*, the garden warbler. Both were affected by the management policy of allowing the rides through the wood to become more overgrown, changing the habitat to their disadvantage (Williamson 1981).

An extinction rate can be calculated from the organisms present originally, and those at some later time. Figure 2 shows how surprisingly difficult it can be to define what is meant by being present in an area. For the whole arbitrary period of 29 years, 45 species are recorded as breeding. In any one year, the number varies between 28 and 36 species (Williamson 1987). Only 16 species bred in all 29 years, and a mere five of these had more than one pair each year. So if the wood by some geological process became isolated and only these last five species survived, would the extinction rate be 89, 86, 82, 69 or 0%? Apparent high extinction rates on small islands (Richman *et al.* 1988) show the importance both of immigration and minimum viable populations in the study of community dynamics.

My final example of natural extinction on real islands is the human disease measles. This is caused by a virus closely related to rinderpest and canine distemper and well known for producing lethal epidemics in primitive peoples. In its present genetic form it is widely regarded as having evolved recently, as it requires large urban populations to sustain it. Even more than the bird data, it demonstrates how a species will become extinct if its population size falls too low.

The stochastic population dynamics of measles are probably as well understood as that of any organism. The virus requires a continual supply of new susceptibles, that is a constant supply of children old enough to catch the disease who have not been infected. Infection leads to an almost universal life-long immunity. From an early computer simulation, Bartlett (1957) deduced that an urban population of 200000 would be the minimum needed to provide a sufficient supply of susceptibles to keep the disease going. In populations smaller than that measles would go extinct. He was able to show (Bartlett 1957, 1960) empirically that his estimate was a little low; a figure of 250000–300000 was indicated from public health returns from both sides of the Atlantic. In a more recent simulation, Anderson & May (1986) found that in a population of less than 6500 an epidemic would fail to start. Such communities would, of course, still have occasional cases of measles, from the disease being brought in from outside, but the chain reaction of an epidemic would not start.

The relation between population size and the frequency and strength of measles epidemics is bound to be fuzzy, because there are other factors, such as the reproductive rate of the human population and the frequency of virus introductions, that affect the dynamics. However, figure 3, which shows the frequency of epidemics in island communities of various sizes, shows how accurate the two predictions are. Note that this result can only be brought out graphically with a suitable scale on the abscissa, and that plotted this way the location and uncertainty of the rate of increase of probability of epidemics is brought out neatly.

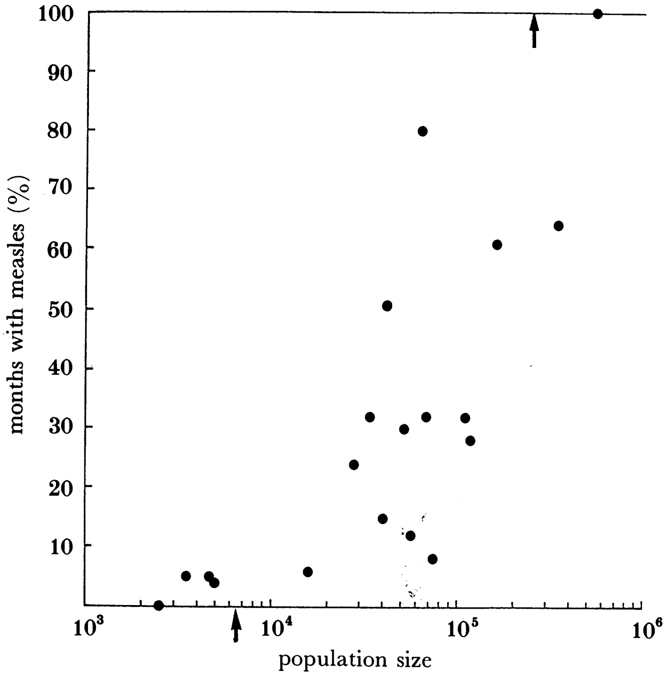

FIGURE 3. Extinction of measles in small island communities. Data from Black (1966). The upper arrow is Bartlett's (1957) estimate of the minimum population size for endemic measles, i.e. for no extinction. The lower arrow is Anderson & May's (1986) estimate of the minimum population size for measles to invade. Modified from Williamson (1981).

Measles shows most clearly that rare populations are in danger of extinction, because they may by chance fall below a minimum viable population density. So I next consider some features of rarity.

RARITY

As Darwin said (1859, p. 109) 'Rarity, as geology tells us, is the precursor of extinction', though we might nowadays wish to rest this conclusion on ecological studies as well. Because of its importance in conservation in work aiming to avoid extinction, rarity has been much studied recently. One major conclusion is that there are many ways in which an organism can be rare. Perhaps the neatest classification of these is by Rabinowitz (1981), though she notes the other classifications put forward in the same symposium. Her seven forms of rarity come from a dichotomous contrast in three characters. These are the geographical range, which may be either large or small, the habitat specificity, which may be wide or narrow, and the local population size, which may be large or small. Her classification, of course, produces eight categories, but the eighth is the set of common species. In her view, a rare species may have any or all of the three characters of restricted range, restricted habitat or restricted population density.

Earlier, I distinguished environmental extinction from demographic extinction. Rabinowitz, unlike Harper (1981), was not concerned with the change of species characters in time, or indeed in space (Schoener 1987). However, environmental extinction in general implies that there has been a loss of habitat, which will have been reflected, depending on circumstances, in a loss of geographical range or an apparent increase in habitat specificity or both. The characters of environments, as geologists well know, are changing all the time. In figure 4 I have shown an indirect measure of this. Figure 4 is an ordination of the land-bird community of Skokholm (Williamson 1983), and the track of the community looks remarkably like a random walk. The first axis of the ordination is related to the total number of pairs (of all species) breeding, the second to the number of species breeding (Williamson 1987). It can be seen that the total number of pairs has been increasing fairly steadily since records began, whereas the number of species first declined and then increased again. If the course of community change is a reflection of environmental change, and the details of the changes in the individual species that give rise to the ordination strongly suggest that it is, then figure 4 is also related to the important phenomenon that environmental heterogeneity has a reddened

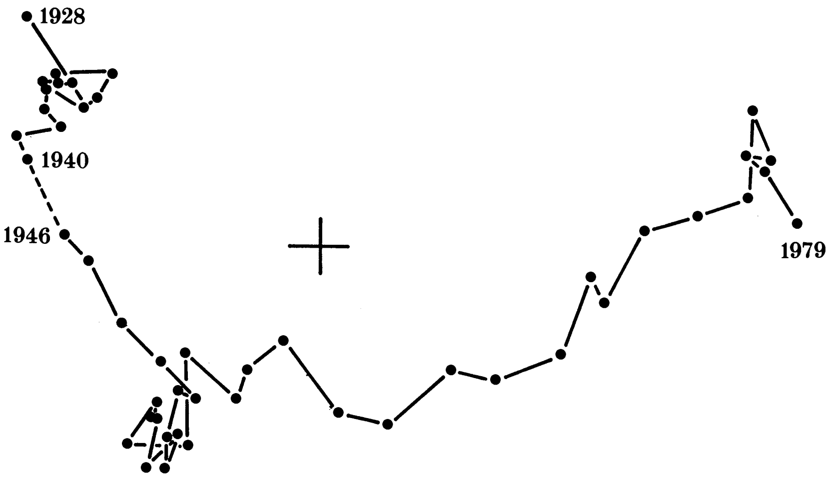

FIGURE 4. A 'step-along' ordination of the land-bird community of Skokholm Island, Wales. The points are connected in time sequence. There were no counts between 1940 and 1946. Modified from Williamson (1983).

spectrum (Williamson 1981, 1983, 1987). Over time, environments will become more and more different from the way they were, and this in itself will lead to the environmental extinction of populations. The fate of the species as a whole will depend on the distribution of its populations, and on its ability to adapt by genetic change to the environmental changes.

Another point that Rabinowitz (1981) brought out is that a population can adapt to the state of being rare. This additional genetic dimension of the problem of understanding demographic extinction certainly makes prediction more difficult. But again, as Darwin (1859, p. 110) was the first to say, rare species will usually evolve more slowly than common ones.

Perhaps the most interesting, and most puzzling, of Rabinowitz' seven types is that of species that have, for their life-form, low population densities yet quite wide geographical ranges and that occur in a variety of habitats. Salisbury (1942) suggested that some such cases could be related to demographic features, particularly to low reproductive output. Whatever the cause, those species are both those most likely to be adapted genetically to rarity and to be most at risk of demographic extinction. Can mathematical models be developed that allow us to quantify this risk?

Mathematical models with extinction

The most famous theory involving extinction is the MacArthur & Wilson (1967) equilibrium theory of the number of species on an island. This theory postulates a balance between immigration and local extinction, leading to an equilibrium maintained by turnover. Data such as those in figures 1 and 2 show that the central part of the theory is true but ecologically trivial (Williamson 1989*b*). There is turnover, but most of the species turning over are marginal, casual species. Schoener & Spiller (1987) make the same point for spiders on Bahamian islands. The species turning over are rare, and it is often the same species that re-immigrates after going locally extinct. Schoener (1987), working with data for Australian birds, shows that most such species are at the edge of their habitat and geographical range, pseudo-rare in Rabinowitz's (1981) phrase, and common somewhere else, in habitats more favourable to them.

As well as dealing with an essentially trivial ecological phenomenon, the relation of local extinction and of immigration to species number postulated by MacArthur & Wilson is much fuzzier than they assumed (Williamson 1981, 1983), and developments of the theory to predict species–area relations give unsatisfactory answers (Williamson 1988, 1989*b*). More seriously, the theory fails to catch the main features of the change in communities with time, as shown in figures 2 and 4, or to predict or explain which species will form the bulk of the ecological community.

Another related weakness in the MacArthur–Wilson theory is that it is purely a phenomenological theory. It does not 'incorporate detailed demographic mechanisms permitting the calculation of rates of local extinction and colonization from the life history parameters of individuals' (Lande 1987). Nor does it include the environmental variation that drives some immigrations and some extinctions.

Recently there have been several attempts to remedy this, by building models of minimum viable population size that incorporate both demographic and environmental extinction and extinction that involves an interaction between these two processes (Belovsky 1987; Lande 1987). Theories involving purely stochastic change in demographic variables, that is assuming a constant environment, can be remarkably successful. Measles, discussed above, is an example. Incorporating environmental change, which will act by altering the mean and possibly the variance of demographic parameters, is much more difficult. One problem is knowing how to relate environmental change to biological change. A very great deal is known about the pattern of some environmental variables; practically nothing is known about how such changes work through to produce changes in schedules of birth and death rates.

At the end of the Pleistocene, many real and habitat islands were formed as climates changed and sea levels rose. The populations isolated on such patches could, in some cases, no longer be reinforced by immigration. Brown (1971) and Patterson (1984) for mammals on habitat islands in the Rocky Mountains, and Richman *et al.* (1988) for lizards on real islands near Baja California and in South Australia, have estimated local extinction rates, having first estimated the original number of species present from species–area curves. It is unfortunately true, as was shown with the birds of Bookham Common, that the species recorded in a patch of more or less continuous habitat, from range maps and the like, will include many that are not maintaining viable populations in that patch. So it could be said that many of the species apparently going extinct were not there, in the sense of not maintaining permanent populations, in the first place. This reinforces the current conservationist view that reserves will need to be appreciably larger than was thought a few years ago if extinction is to be prevented. Newmark (1987) presents historical records that support this.

Times to extinction are much shorter in minimum viable population models with environmental variation than in purely demographic ones. They are shorter still if catastrophes are included (Shaffer 1987). By making some bold assumptions, Belovsky (1987) calculates extinction rates for relic populations of mammals in the Rocky Mountains, and finds that his environmental extinction models predict too low a rate. He has to assume a rather precise relation between size and demographic parameters to get his result. It is well known, for instance, that the intrinsic rate of natural increase, r, decreases with increasing size across orders. It is less well known that the relation is the other way round within genera and families (Williamson 1989*a*) and even sometimes between families (Stemberger & Gilbert 1985). What is undoubtedly true is that small, rather random, environmental fluctuations increase the chances of small populations going extinct.

One important conclusion to come from these rather gloomy studies of conservation problems is that closely related species may have quite different minimal area requirements. Thomas (1984) from field studies of the persistence of populations, gives the data in table 1 for the minimal breeding area of non-migratory British butterflies. There are a further 12 migratory species, and 12 species where minimal area is not known, but it is mildly encouraging that so many require such small areas.

TABLE 1. MINIMUM AREA OF VIABLE COLONIES OF BRITISH BUTTERFLIES

(Simplified from Thomas (1984).)

area/ha[a]	0.5–1	1–2	2–5	5–10	10–50	> 50
no. of species of butterflies	15	11	2	2	4	1

[a] 1 ha = 10^4 m^2

Interactive and community models

If a general theory of extinction is to be developed, a general theory of rarity is needed. One point that comes through strongly from the SCOPE programme on the Ecology of Biological Invasions, is that there is no general theory that allows us to predict which species can invade and which cannot (Williamson 1989*a*), and part of the reason for this is that there is no general theory of the distribution of commonness and rarity between species in the same trophic level.

The fact that some species are common and some rare could be due either to some habitats or environments being commoner than others, or to interactions between species leading to different equilibrium population densities. It has certainly long been a general view that subtle biological interactions are involved in many extinctions. For instance Darwin (1859, p. 319) said that 'unperceived injurious agencies... are amply sufficient to cause rarity, and finally extinction'. What some models of species interactions show is that quite simple, fairly strong, ecological interactions may lead to quite surprising results. I shall give two examples.

The first is a large computer-simulation model developed by Drake (1985). This is a Lotka–Volterra type model, which means that the equations are the simplest and most linear that can be reasonably postulated. He modelled only feeding relations as between carnivore and herbivore; all competitive effects were indirect through share resources or shared predators. He had a pool of 100 species, some primary producers, some herbivores and so on, each with fixed parameters. He started each run with two producers and one herbivore, and then introduced other species randomly from his pool. He calculated the stability of the system after each introduction and considered that species went extinct if the system was unstable. These simulations require much computer time, and he only completed ten runs, ending with ten different communities.

One of Drake's runs is shown in figure 5; I have chosen it because it has the largest extinction of any of his runs. After rather more than 1100 introductions, which means that each species has already been introduced about 11 times, one particular introduction produces a mass extinction, reducing the number of species present in stable equilibrium from 19 to nine. Other cascades of extinction can be seen in the graph, and Drake was unable to find any general rules about when such cascades would occur and what species would be involved.

It is possible that Drake's results come from using over-simplified dynamical models, or from using an unnatural distribution of interaction strengths between species. Opinions differ, relevant data are rare. My second example is more widely agreed to be realistic. Equations that govern continuous culture systems, otherwise known as chemostats, incorporate equations and functional forms that have been established experimentally by microbiologists (Williamson 1972).

The simplest chemostat involves one species of bacterium limited by one particular substrate, such as a carbon source. Such a system is stable at all dilution rates almost up to the maximum growth rate of the bacterium. Adding a predator, a ciliate protozoan, produces quite a different result. Figure 6 summarizes the pattern found by a simulation study of such a system.

The parameters used in this simulation system are those of Curds (1971) and are based on those found experimentally for real species of bacteria and ciliates. The parameters are a maximum specific growth rate, a saturation constant and a yield coefficient for each of the two simulated species. As is natural, the maximum growth rate of the bacterium is set at a greater value than that of the ciliate. Consequently on the right of figure 6 the ciliate becomes extinct,

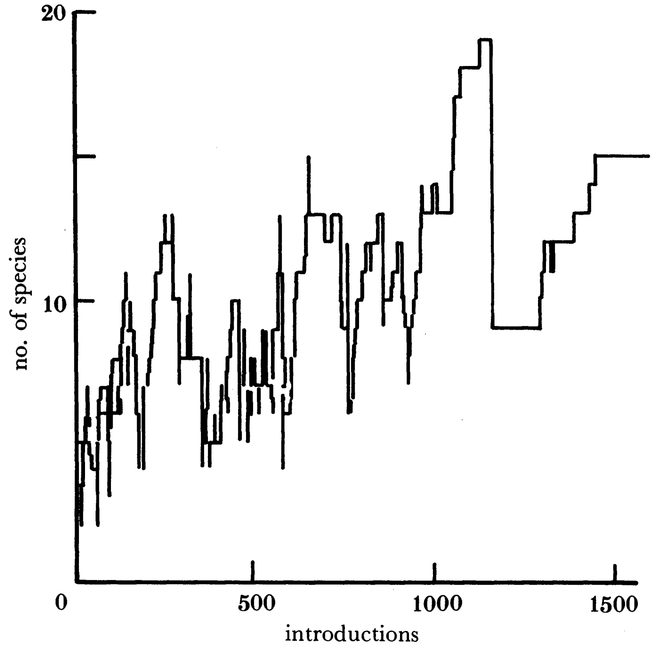

FIGURE 5. Immigration and extinction in a theoretical Lotka–Volterra community. The species are drawn from 100 species defined by their parameters. There is extinction of over 50% of the community after 1150 invasions. The community stabilises after 1500 invasions. From Drake (1985), with permission.

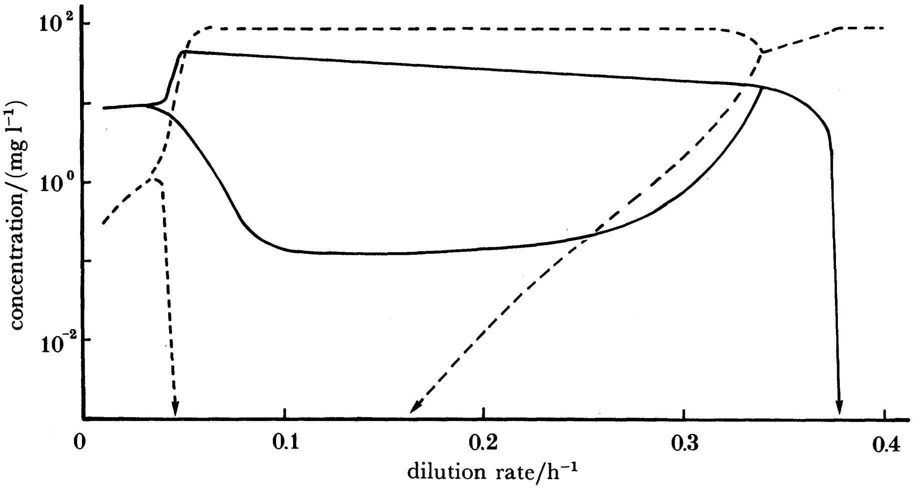

FIGURE 6. The theoretical behaviour of a bacterium–ciliate chemostat system. The lines show the maximum and minimum of the limit cycle oscillations at different dilution rates. Parameters of the system as in Curds (1971). Ciliates go extinct at high dilution rates. There are stable states at very low dilution rates and at dilution rates just less than the critical point for ciliate extinction. The oscillations in the middle range of dilution are so large that extinction of the bacterium, followed by extinction of the ciliate, would be expected.

or cannot invade, because the dilution rate is more than its growth rate can cope with. The transition from a stable community of predator and prey to the extinction of the predator by wash out occurs very rapidly with change of dilution, as can be seen by the almost vertical line in the ciliate graph at the right-hand side.

Below the critical dilution rate for ciliates, about 0.38 h^{-1}, there is a small range of dilution rates in which both the simulated bacterium and the simulated ciliate come to stable equilibrium points. At 0.34 there is a bifurcation, and at dilutions less than this the system goes into limit cycles. That is, both the bacterium and ciliate numbers converge to stable oscillations, oscillations that repeat indefinitely with the same amplitude and wavelength. Figure 6 shows the maximum and minimum of the oscillations at each dilution. Drake's rules would regard the system as unstable below a dilution rate of 0.34, and record an extinction. Certainly for dilutions around 0.1 the size of the oscillations on the bacterial population are so vast, six to eight orders of magnitude, that in a real situation the population would almost certainly go extinct. The ciliate would inevitably go extinct afterwards. Taking three orders of magnitude as the limit of a feasible cycle that would persist in a real chemostat, extinction of both species would occur at all dilution rates between 0.23 and 0.045.

There is a surprise, only hinted at by Curds (1971), at very low dilutions. The system is once again in a steady state. The transition from enormous oscillations to steady state again occurs over a very small range of dilutions, as can be seen from the almost vertical curve at the left of the graph of the simulated bacterium.

Altogether this simple system of just two species shows remarkably complex behaviour. In two zones, at the lowest and at high dilution rates, there are steady states. Each zone ends abruptly as the dilution rate is increased slightly. Between these zones the system shows a remarkable range in the amplitude of oscillations. With such complexities in an extremely simple system, is it surprising there is still much to learn about real ecosystems?

Conclusions

All these data and models show that with relatively small changes in conditions extinction may suddenly occur, and for reasons that are not obvious. In Drake's model, cascades of extinction can happen. There are at least two large and important gaps in our understanding. The first is being able to say for any particular extinction why it happened, rather than to show a range of reasons that might have caused it. The second is knowing, in almost all communities, why some species are rare in the first place.

I thank Kevin Gaston, Brian McArdle, Moya McCloskey and Charlotte Williamson for much advice, help and discussion. The work on chemostat systems is supported by Department of the Environment contract PECD7/8/107. I am grateful to Jim Drake for permission to use figure 5.

Discussion

C. B. Goodhart (*Gonville and Caius College*, *Cambridge*, *U.K.*). The examples given here of the extinction of island populations are mostly no more than 'pseudo-extinctions', where there are plenty of other flourishing populations living elsewhere apart from the one going extinct. This is quite different from the historical extinction of whole species as discussed in the other contributions to this symposium, and it is important to make a clear distinction between the two.

Nowadays, whenever a much-needed bypass is proposed, for example, conservationists can be relied upon to discover some obscure moth or moss, or whatever, whose only known home in Britain will be destroyed unless the road is diverted, often at a cost of millions of pounds. But it usually turns out that the creature concerned is rare in Britain only because it is here at the edge of its distribution, and it is common enough on the Continent. So its loss from this country, however regrettable, would really only be a pseudo-extinction, and not the irrevocable biological disaster that the word 'extinction' might be thought to imply.

So professional ecologists would be wise not to cry 'wolf' too often in such circumstances, lest they are ignored when there really is something worth saving. Indeed, they have a professional duty to look at each case objectively on its merits, taking into account also the costs involved, in any advice they may feel called upon to offer. However desirable something may be, it is always possible that the cost could be too high, even when it is somebody else who is going to have to pay it.

M. H. WILLIAMSON. In reply to Dr Goodhart's first point, I do indeed discuss the extinction of local populations rather than the extinction of species, but these are real extinctions for the populations concerned, not pseudo-extinctions. Species extinction occurs when all local populations have become extinct, so the study of local extinctions is relevant to the study of species extinction.

Dr Goodhart's second point is valid, though I would have preferred a more objective statement of it.

D. A. WEBB (*Trinity College, Dublin, Republic of Ireland*). I am always rather suspicious of models, and I can't help wondering whether, if Professor Williamson instead of using a chemostat had built a vast vivarium and had introduced owls and mice at recorded rates the curves would have come out the same. I have no doubt that his model would apply well to certain lower organisms, but when you move to higher organisms the differences in behaviour and limitations of habitat and so on are so vast that I am sceptical as to the predictions derived from one field being applicable in the other.

M. H. WILLIAMSON. Many ecologists and field biologists are suspicious of models, and this may have slowed the agreement about valid general statements in ecology. In Professor Webb's example, the curves would be similar but not the same. The detailed mathematical formulation would certainly be different, but almost any predator–prey system would have a tendency to oscillations. Local extinctions following a boom and crash (a single oscillation) are well known for vertebrates.

J. COHEN. Dr Williamson's use of the word 'extinction' seems rather different from that of other speakers at this meeting. For most of us, 'temporary extinction' resembles usage like that on the Vapona packet: 'Kills insects for up to three months'.

M. H. WILLIAMSON. I do not use the phrase 'temporary extinction', but Dr Cohen is perhaps trying to make the point made by Dr Goodhart in his first paragraph.

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