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The causes of extinction

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A species may go extinct either because it is unable to evolve rapidly enough to meet changing circumstances, or because its niche disappears and no capacity for rapid evolution could have saved it. Although recent extinctions can usually be interpreted as resulting from niche disappearance, the taxonomic distribution of parthenogens suggests that inability to evolve may also be important.

A second distinction is between physical and biotic causes of extinction. Fossil evidence for constant taxonomic diversity, combined with species turnover, implies that biotic factors have been important. A similar conclusion emerges from studies of recent introductions of predators, competitors and parasites into new areas.

The term 'species selection' should be confined to cases in which the outcome of selection is determined by properties of the population as a whole, rather than of individuals. The process has been of only trivial importance in producing complex adaptations, but of major importance in determining the distribution of different types of organisms.

An adequate interpretation of the fossil record requires a theory of the coevolution of many interacting species. Such a theory is at present lacking, but various approaches to it are discussed.

1. Palaeontology, ecology and genetics

The relation between population genetics and palaeontology is unsatisfactory. It is not uncommon for palaeontologists to assert that population genetics cannot account for the fossil record, whereas population geneticists hold that there is nothing in the record that they cannot explain. Much misunderstanding would be avoided if it were acknowledged that there is a sense in which both these statements are correct. Consider the matter first from the point of view of a geneticist. Whether the pattern of evolution is punctuational or gradualistic, it is compatible with genetic theory. Stasis can be explained by stabilizing selection, and punctuational change by directional selection; even if the changes are rapid by geological standards, they are slow compared to the changes that occur under artificial selection, and occasionally in the wild. There is no need to invoke Goldschmidtian systemic mutations to account for punctuation, or developmental constraints to account for stasis.

Such a reply, quite properly, would not satisfy a palaeontologist, who wants to know why evolution shows the patterns that it does. Why should there sometimes be normalizing selection for millions of years? What causes punctuational events? The answer to such questions cannot be supplied by population genetics, whose theories typically take the form 'IF the following genotypes have the following fitnesses, THEN the population will change in the following way'. It is in this sense that palaeontologists are correct to claim that population genetics cannot account for evolution.

How can this gap between theory and observation be bridged? Anatomists tend to turn to development. I think that this can provide only partial answers. It is certainly true that developmental constraints may determine the way in which a population responds to selection. For example, Vrba (1984*a*) points out that herbivorous primates respond to hard-vegetation diets by evolving thickened tooth enamel, whereas perissodactyls and artiodactyls, faced with similar environments, have repeatedly evolved extreme hypsodonty. In some cases, developmental constraints may altogether preclude a taxon from evolving in a particular direction. For example, mammals seem to be unable to evolve parthenogenesis, perhaps because of differential gene imprinting from the two parents.

What we most need, however, is a theory that says something about the nature of the selective forces operating. Experimental evidence shows that most populations will respond rapidly to directional selection for most characteristics. Although many experiments in artificial selection lead rather rapidly to a plateau, beyond which further response is difficult, it seems that this happens because experimental populations are usually small, and therefore soon run out of genetic variance. Experience with domesticated plants and animals, and experiments (see, for example, Yoo 1980), show that long-continued responses are possible in larger populations. We therefore need a theory of selective forces, which can only come from ecology. For most animals, the major selective forces come from their competitors, their predators or prey, and their parasites.

Unfortunately, we lack a satisfactory theory of the coevolution of many interacting species. I return to this problem in the last section, but, to illustrate the point, consider two very general questions to which theory cannot at present provide an answer. First, imagine a set of interacting species in a physical environment that does not change in time. Each species may nevertheless evolve; for example, to escape from its parasites or to become better at catching its prey. As each species evolves, this will constitute a change in the biotic environment of at least some other species. Hence there will ensue an evolutionary dance, called by Van Valen (1973) the 'Red Queen', in which each species evolves because the others do. The unanswered question is this: will such a dance continue indefinitely, even in an unchanging physical environment, or will it slow down and stop? More realistically, what features would favour continued evolution, and what stasis? A second unanswered question is this. Does the continued existence of many species of plants, herbivores, carnivores, etc., require a physical environment that varies in space and/or time, or is it possible in a uniform environment? Again, more realistically, what features would favour species diversity, and what features would favour the elimination of all but one species at each trophic level?

Of course, most evolutionary biologists have some idea of the answer to these questions. But our ideas depend more on casual observation and guesswork than they do on theory, and the ideas of different biologists do not coincide. In this paper I shall attack the gap between population genetics theory and palaeontological observation from two sides. First, I shall discuss some qualitative questions that arise from the fossil record, and ask how ecological considerations might help to answer them. Second, I shall discuss the state of ecological theory, and suggest how it might be developed to be of greater relevance to macroevolutionary problems.

2. The causes of extinction

(*a*) *Lack of evolvability, or running out of niche?*

If a species goes extinct, this is probably caused by a change in its circumstances, biotic or physical. (I say 'probably' because a rare species might go extinct by chance, without any change in its environment; but there remains the question why it was rare in the first place.) One question we can ask is the following: would the species have survived if it had been able to evolve more rapidly? Sometimes the answer is clearly no. If a species died out because its members could not survive the immediate consequences of a meteorite impact, or because the island to which it was confined sank beneath the sea, no capacity for rapid evolution would have saved it. Such unavoidable extinctions can be caused by biotic changes also: an example is G. C. Williams's (imaginary) flea confined to the passenger pigeon. We can say that such a species 'runs out of niche'.

Are all extinctions unavoidable in this sense? One body of evidence suggests that they are not. When discussing the forces responsible for the maintenance of sexual reproduction (Maynard Smith 1978), I pointed out that the taxonomic distribution of parthenogens suggests that parthenogenetic populations (I prefer not to use the term 'species' in the absence of sex) are short-lived in evolutionary time. With few exceptions, there are no high-ranking taxa (genera, families) consisting solely of parthenogens; instead, almost all parthenogens have close sexual relatives. In contrast, the haplodiploid sexual system has arisen rather seldom, but has given rise to large taxonomic groups (e.g. the hymenoptera, the monogonont rotifers). A plausible explanation (although not the only possible one) for the short evolutionary lifespan of parthenogenetic populations is that such populations evolve more slowly to meet changed circumstances than do sexual ones. If so, an inability to evolve rapidly predisposes such populations to extinction.

There is no reason why this method should not be used to identify other characteristics that predispose species to extinction. For example, I have the impression (not checked by serious analysis) that, in flowering plants, dioecy has a taxonomic distribution similar to, but far less extreme than, parthenogenesis.

(*b*) *Physical or biotic causes of extinction?*

Are the changes causing extinctions typically biotic or abiotic? I am not competent to discuss the relative importance of meteorite impacts, volcanic activity, climatic change and changes of sea level. Certainly I do not wish to argue that such events have been unimportant. But I think that palaeontologists should bear in mind that biological events, acting alone or in conjunction with physical change, may have been of equal importance. Indeed, I see no reason why extinctions – even mass extinctions – should not take place in the absence of any change in the physical environment, although it would be hard to account for a mass-extinction event affecting both terrestrial and marine organisms in this way.

A number of authors have reported a surprisingly constant diversity (as measured by numbers of genera or families) within particular taxa over many millions of years, despite continued extinction and speciation (see, for example, Webb (1969) for Cainozoic land mammals in North America and Boucot (1978) for Palaeozoic brachiopods). This implies that either speciation rate or extinction rate, or both, are functions of standing diversity: by analogy, constant population size implies density-dependent birth or death rates (Rosenzweig 1975). This suggests that biotic factors are important in extinction: it does not amount to proof, because regulation may be via speciation rate. In some cases, it is possible to follow changes in diversity resulting from identifiable environmental change. Boucot (1978) reports that in the Silurian, when only a single marine province is recognized, there were 90 genera of articulate brachiopods: this number rose to 350 in the lower Devonian, when there were six marine provinces, and fell again to 93 genera in the Mid-Devonian when there was a reduction in provinciality. These changes can be ascribed to physical changes (i.e. in provinciality), but they were presumably mediated by competition. Marshall *et al.* (1982) analyse the changes in mammalian diversity resulting from the union of North and South America 3 Ma BP. Before the join, there was a rather constant extinction rate of 0.3 genera per genus per million years in the north, and of 0.4 genera per genus per million years in the south. At the time of the junction, the proportions of southern mammals moving north and of northern mammals moving south were approximately equal, although the effect on the standing diversity was greater in South America, which had a smaller number of genera before the junction. In fact, the diversity increased by 50% in the south, and this was followed by a 70% increase in extinction rate. All these observations are consistent with the hypothesis that there was an equilibrium between extinction and speciation, and hence an important role for biotic factors. The final diversity in South America was greater after the junction, but this was caused by speciation of Northern rodent species after they had moved south.

Figure 1 shows an example of long-term constancy in plant diversity. There is a contrast between the approximate constancy before the origin of the angiosperms, and the steady increase since. Knoll (1986) suggests that this can be explained by the fact that rare animal-pollinated plants can persist, but rare wind-pollinated plants cannot. This is plausible, and confirmed by recent experience in plant conservation, but leaves unexplained a similar change from approximate constancy to steady increase in marine invertebrates in the Cainozoic (Sepkoski 1984).

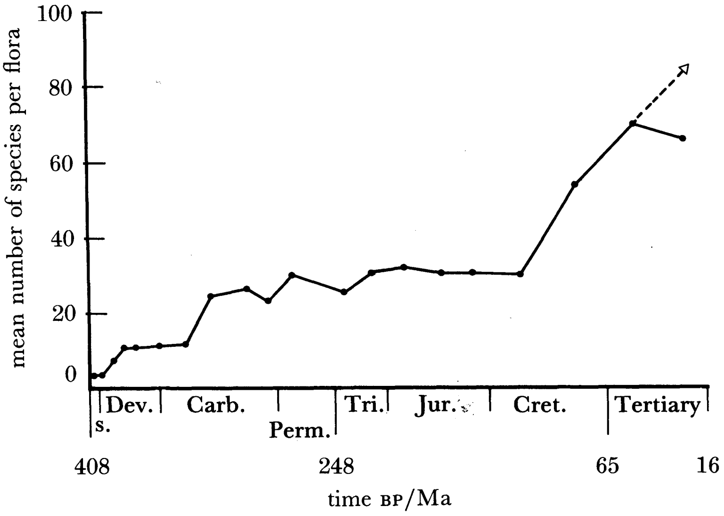

FIGURE 1. Mean number of species per flora during the Phanerozoic. The broken line is an estimate for Neogene floras in moist subtropical to tropical environments, similar to those in which the earlier floras are thought to have grown. (After Knoll 1986.)

What can we learn by looking at recent extinctions? Some, such as that of the passenger pigeon, and perhaps that of the large mammals of North and South America, were the direct result of human overkill. Others, such as the extinction of the large flightless birds of New Zealand, resulted from human overkill combined with destruction of habitat; in that case the burning of forests. In many cases, habitat destruction is probably by itself a sufficient explanation. Typically, habitat destruction results from human actions to which there is no obvious analogue in the past. A change in climate might destroy a particular habitat in one place, but the relevant species have often shifted to higher or lower latitudes or elevations, rather than disappeared. In some cases, however, barriers to migration have prevented such a shift, and climatic change has led to habitat destruction globally, not just locally. Also, climatic change can produce large changes in the total area covered by particular habitat types, and this would result in changes in total diversity. An alternative cause of habitat destruction at the present time is the introduction of foreign species; for example, the native vegetation of New Zealand has been replaced over large areas by the introduced gorse *Ulex*. Comparable habitat destruction may have been caused in the past by plant species that arrived from elsewhere, or which evolved *in situ*. It is illuminating to review the extinctions that have resulted from the introduction, accidental or otherwise, of species into new areas: in particular, onto islands, or, for aquatic organisms, into lakes or rivers. But in comparing these data with those of palaeontology, it is as well to remember that they concern mainly terrestrial and fresh-water vertebrates, whereas the fossil data concern mainly marine invertebrates.

Diamond (1984) has argued convincingly that introduced predators have been one of the commonest causes of extinction on islands. Although human predation was the major cause of the extinction of the Moas, many smaller New Zealand birds succumbed to the rats that the humans brought with them. On islands lacking native rats (e.g. Hawaii, Midway, Lord Howe), introduced rats have quickly eliminated native birds. In contrast, introduced rats have had little effect on the birds of islands (e.g. Solomons, Christmas Island, Galapagos) that had native rats. On some islands (e.g. Tonga, Samoa, Marquesas, Aldabra) with no native rats, but with land crabs, native birds have survived the introduction of rats. Thus a taxonomic group can be driven to extinction by a predator of an ecologically unfamiliar type. Other examples are the extinction of many endemic birds on Guam by the brown tree snake, and (particularly infuriating for population geneticists) the extinction of the native snail, *Partula*, on Moorea by a carnivorous snail, introduced to control a herbivorous snail that had itself been introduced to give the natives something to eat. The introduction as a game fish of the peacock bass, *Cichla ocularis*, into Lake Gatun in Panama led to the elimination of eight of the 11 commonest native fish, and had secondary effects on the abundance of other fish species, of the zooplankton, and of herons, terns and kingfishers (Zaret & Paine 1973).

It is harder to find clear examples of extinction caused by the introduction of a competitor. For freshwater fish, there is ample evidence (Werner 1986) that the introduction of a new species can drastically reduce the numbers and growth rate of competitors, and may restrict them to part of their previous ecological range, but outright extinction seems to be unusual. The work of Moulton & Pimm (1986) on introduced birds on the Hawaiian islands is illuminating in this context. They record 18 cases in which closely related species were introduced onto the same island. In three cases both are extinct, in nine cases one is extinct, and in six cases neither is yet extinct. In those cases in which one species is extinct, the difference in beak size was significantly less than in cases in which both survive (a mean of 9% in the former, and 22% in the latter). This suggests that competitive exclusion does occur, but requires very close similarity in resource utilization. Unless two species are very similar, they are likely to share the available resources. This is in line with the conclusion (Lawton 1982) that, in herbivorous insects, many possible ecological niches are vacant in most communities. However, this conclusion should be treated with caution. In particular, it is dangerous to reason as I have just done, jumping from fish to birds, and thence to insects. The role of competition may be different in different taxa, and at different trophic levels. In particular, competition may play an important role in plant extinction.

A cause of extinction that would be particularly difficult to detect in the fossil record, and hard enough in recent communities, is disease. Rinderpest was introduced into Africa towards the end of the last century by Indian bullocks used in Kitchener's army to pull guns. It decimated the native ungulates, and caused the extinction of one of them, Swayne's Hartebeest. In Hawaii, the endemic birds are now confined to altitudes above 3000 feet† by avian malaria, brought by resistant introduced bird species. These examples show that extinction can be caused by disease, but it will be difficult to decide how frequent such events have been.

The contemporary evidence, then, shows that extinctions can be caused by single introduced predators, competitors or parasites. Is there evidence from the fossil record for comparable biologically caused extinctions? Perhaps the strongest evidence that competition plays an important role in determining either extinction rates or speciation rates, or both, comes from the observation of constant taxonomic diversity despite species turnover, discussed above. What of the evidence for the competitive displacement of one taxon by another in the fossil record; for example, of brachiopods by bivalves, of cynodonts by thecodonts, or of multituberculates by rodents? Confronted by data of the kind illustrated in figure 2, it is natural to suppose that taxon A has been competitively displaced by taxon B, and to seek some adaptive reason for the displacement. In this case any such attempt would be misguided, because the figure has been drawn to represent data generated by a computer program in which the probabilities of speciation and extinction were constant, subject to the constraint that a constant total diversity be maintained. This illustrates the point, first made by Raup *et al.* (1973), that it is fatally easy to read a pattern into stochastically generated data.

The first task, then, is to provide convincing evidence that a pattern really exists. This is not easy. If the available data consist of numbers of genera (or of species, or families) at different time horizons, the first requirement is to subdivide the data by geographical region and ecological function, and not merely by taxonomic criteria. This point is nicely illustrated by Thayer's (1983) criticism of an argument by Gould & Calloway (1980). The latter had argued that there is no evidence that the rise of the bivalves had caused the decline of the brachiopods: the two groups were 'ships that pass in the night'. Their reason was that there is a positive correlation between the levels of diversity of the two groups at different horizons, whereas if competition caused displacement the correlation should be negative. Thayer argued that the observed correlation could arise from factors increasing, or decreasing, taxonomic richness in general, and that, if functional groups are taken into account, the data are more in accord with the competitive hypothesis. For example, a decline in pedunculate brachiopods has been accompanied by a rise in epibyssate bivalves; a comparison of groups living on hard substrates. Although Thayer's point is a good one, however, I have the impression that a more detailed statistical analysis of such cases is needed before firm conclusions are drawn.

A first and difficult task, then, is to show that a pattern calling for a causal explanation really exists. Even if it does, there remain two possible explanations: competitive displacement or vacancy occupation. According to the former, taxon A went extinct because of competition from taxon B: according to the latter, taxon A went extinct for reasons that had little or nothing to do with taxon B, and the latter subsequently evolved to fill the vacant niches. Note that both

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† 1 foot ≈ 30.48 cm.

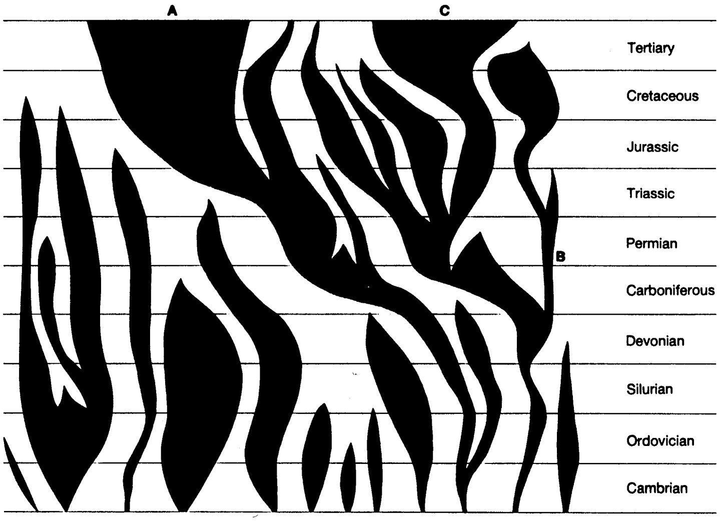

FIGURE 2. A phylogeny in which the horizontal width of a taxon at any time is approximately equal to the number of genera.

explanations imply competition; vacancy occupation supposes that taxon B was prevented by competition from evolving into niches occupied by A. Thus the conventional explanation of the extinction of the dinosaurs and the subsequent radiation of the mammals assumes that the former event owed nothing to the latter, but that the latter was made possible by the former.

The evidence of recent extinctions, suggesting that habitat destruction, predators, and perhaps parasites, are more effective agents of extinction than competitors, might seem to suggest that competitive displacement of one taxon by another will be rare. I am not sure we should take this argument seriously. There is plenty of evidence that competition can reduce the abundance and ecological range of a species, and in the long run this must make extinction more likely. One palaeontologist willing to argue for competitive displacement is Knoll (1986). During the Silurian and Devonian, a series of vascular spore-bearing taxa replaced one another. Each taxon appeared first as a minor element in the community, expanded to become dominant, and then dwindled as a new taxon appeared. Knoll argues that the morphological characteristics of the successive dominants would ensure increased capacity for gathering light and absorbing water and nutrients, and so could account for competitive displacement. He can find no evidence for mass extinctions followed by rediversification, or for a significant role for climatic change or of herbivory.

Is there evidence that predators have caused the extinction of major taxonomic groups? One example is worth describing in a little detail, although it should perhaps not come under the heading of predation. Thayer (1983) argues that there has been a steady increase in the abundance and variety of animals that disturb marine mud and sand deposits, for example by swallowing it and digesting any organisms it contains; examples are holothurians, malacostracans, tellinid bivalves, and polychaets such as *Arenicola*. A consequence of the activities of these 'bulldozers', not all of which are predators, is to make life difficult for other organisms, and in particular for immobile filter feeders living on soft substrates. For example, bulldozers may make larval settlement impossible, either by swallowing or accidentally burying the larvae. As a consequence, there has been a decline in the number and variety of immobile organisms on soft substrates; for example, free-lying brachiopods, tabulate and rugose corals, and blastoid echinoderms. Modern representatives of these taxa either live on hard substrates or are themselves mobile.

One interesting feature is that these immobile groups suffered particularly severely in the Permo-Triassic mass extinction. This is a bit puzzling. If Thayer is right, they were on their way out anyway. But why should they have been particularly susceptible to a mass-extinction event? It is reasonable that organisms with different ecologies should be differentially susceptible to a major physical disaster. For example, if the Cretaceous extinction was caused by a meteorite impact, it is reasonable that organisms in the water column should have been more susceptible than benthic forms, and that direct herbivores should have been more susceptible than deposit feeders. But why should organisms that were in decline anyway be particularly susceptible? Of course, if the 'mass extinction' was merely a more intense continuation of processes that were already occurring, the coincidence is no longer puzzling. Nor is there any convincing evidence that different mass extinctions had similar causes. Jablonski (1986*a*, *b*) has reviewed the similarities and differences between the patterns of disappearance during mass extinctions and at other times.

3. The role of species selection

Several authors (Maynard Smith 1983; Vrba & Eldredge 1984; Vrba & Gould 1986) have drawn a distinction between two processes that can lead to the extinction of some species and the survival of others. The distinction is best explained by a hypothetical example. Suppose that two species of lizard, A and B, differ in that A individuals are better at catching insects, and that in consequence species A survives and B goes extinct. Contrast this with a second case in which species B is parthenogenetic; as the biotic environment changes, species A evolves to meet the change, but species B does not, and in consequence goes extinct. In the first of these cases, the 'performance' (Emerson & Arnold 1989) that determines survival is the performance of individuals: in the second, it is the performance of the species as a whole. Thus individuals catch flies, but populations evolve. All the authors listed above have argued that only the second case should be referred to as 'species selection'. According to this view, the criterion for species selection is that the performance that determines survival is one that could be measured only on the species as a whole, and not on an individual (although the performance, rate of evolution, depends on a characteristic of individuals, namely sexual reproduction).

Species selection, in this narrow sense, can also affect traits that influence speciation rate. For example, if marine invertebrates with direct development speciate more frequently than those with planktotrophic larvae, this could lead to an increase in the proportion of species with direct development (Jablonski 1986*c*). In such a case, however, it is well to remember that an increase in number of species does not necessarily imply an increase in number of individuals (Vrba 1984*b*), and that the increased speciation rate may be balanced by increased extinction.

Some taxa may diversify more extensively than others because they have a developmental system that favours diversification. (For a recent discussion of this idea, see the papers by Dawkins, Liem and Vrba in Wake & Roth (1989).) One cannot think of this as a case of individual selection because individuals do not diversify. However, I would prefer the term 'lineage selection' to 'species selection' for such cases, because the process does not require that the lineages be sexual.

Vrba & Eldredge (1984) used the term 'species sorting' to refer to all cases of differential survival and extinction of species, however caused. How important has species sorting been in evolution? I think that it has been of only trivial importance in giving rise to the complex and integrated adaptations that are characteristic of all living organisms, but that it has been of major importance in determining the abundance and distribution of organisms with different structures and adaptations. The reason why it is of trivial importance in giving rise to adaptations is a quantitative one. It is useful to quantify selection in terms of the bits of information that a given selective process can add to the genome. Thus one bit can be added by the selective removal of half the population, two bits by the removal of three quarters of the population, and so on. On this measure, five mass extinctions, each leading to the loss of 97% of the extant species, could add at most 25 bits; equivalent to culling half a population selectively for 25 generations. Thus species sorting, whether the target of selection is the individual or the population, is not a relevant process in the generation of individual adaptation. But as a process influencing the abundance and distribution of organismal types it is crucial. I suspect that most species sorting is a consequence of individual rather than species selection. However, the individual characteristics that prevail need not be those that determined survival. To take a hypothetical example, suppose that the characteristics that enabled many mammalian species to survive the end-Cretaceous extinction were small size and the habit of eating seeds or insects. It would be a consequence of this that the characteristic mammalian gait and jaw mechanism replaced those characteristic of the dinosaurs, but their survival would not be evidence of their selective superiority. It think that much of the disagreement between palaeontologists and neontologists on the role and importance of species sorting has arisen because they want to explain different phenomena. A palaeontologist sees dramatic changes in the kinds of organisms that inhabit the Earth, but is often blind to adaptation; a neontologist sees function everywhere.

4. Models of coevolution

Interpretation of the fossil record would be greatly helped by a theory of the coevolution of many interacting species. Unfortunately, no satisfactory theory exists; indeed, no fully satisfactory theory exists for the stability of ecosystems composed of non-evolving species. It may be that different systems – for example, marine and terrestrial, tropical and temperate – require fundamentally different models. Nevertheless, I now present a brief and contentious account of where we stand. It is convenient to start with the still widespread idea that the stability of an ecosystem (in the sense of approximate constancy of species composition and relative numbers) is a consequence of the large number of species and the complexity of their interactions. Elton (1958) argued for this view, pointing to the relative instability of species-poor subarctic (and to a still greater extent, agricultural) systems. This idea may be correct, but stability is not a necessary mathematical consequence of species richness and complex interactions. Indeed, May (1972) showed that precisely the opposite is the case: in model systems, based on Lotka–Volterra dynamics with randomly chosen parameters, stability becomes less likely as the number of species, and the number of interactions per species, increases. The conclusion from May's work is that complexity itself is not sufficient. One or both of two additional features must be incorporated: the parameters are not random, but are influenced by selection, and there may be structural features common to all ecosystems that favour stability.

A general structural feature of ecosystems is that they are composed of plants, herbivores, carnivores and decomposers (although some species may play more than one role, and a few systems do not depend on plants). Three important suggestions have been made about this structure. Hairston *et al.* (1960) argued that, at least in terrestrial systems, herbivores are usually limited by their predators and parasites, so that they are unable to reduce the level of plant cover substantially below that determined by the resources of light, water and nutrients. If this is correct, it would explain why botanists have been more successful than zoologists in detecting competitive replacement in the fossil record. However, Connell (1970) and Janzen (1970), in a proposed explanation for the diversity of tropical forests, assumed that herbivores are more successful in controlling plants. They proposed that no one tree species can become abundant, because it is kept rare by specialist herbivores and parasites: the resulting tree diversity then supports diversity at higher levels. This model would explain increasing taxonomic diversity by the increasing stenophagy of herbivores, and host specificity and virulence of plant pathogens. A third general point (Pimm 1982) is that food chains will not lengthen indefinitely, because long food chains are dynamically unstable. It follows that any substantial increase in diversity must occur by increasing the number of food chains, and not their length.

A second necessary extension of May's model is to suppose that parameters are selected and not random. There are two ways in which non-randomness can arise in the interactions between species in an ecosystem. First, consider the species on an island not too far distant from the mainland. Those that are actually present are the survivors of the probably much larger number of immigrants. Thus the existence of a stable ecosystem on an island does not prove that any arbitrary set of species will constitute a stable system, but only that some subset of the total set of immigrants will do so. In fact, stability is harder to explain than this might suggest, because, as MacArthur & Wilson (1967) pointed out, the number of species on islands commonly remains rather constant despite continuing turnover of actual composition, owing to immigration and extinction.

What of species on the mainland? The interactions of these species are non-random because they have evolved together. Is there any theoretical reason to expect that coevolution should lead to greater stability? We can answer this question only in part, and only for pairs of interacting species (for reviews see Roughgarden (1983); Slatkin & Maynard Smith (1979)). For competitive interactions, theory does suggest that the typical result will be that competitors will specialize on different resources ('character displacement'), and hence that coexistence will become more stable, although the empirical support for this prediction is by no means overwhelming. For symbiotic interactions, Law & Koptur (1986) have argued that evolution has led to stability, and to low taxonomic diversity of endosymbionts. The real difficulty arises for exploitative interactions: predation, herbivory and parasitism. Here, evolution seems likely to lead to continuing 'arms races', and recurrent extinctions (for a contrary view, see Schaffer & Rosenzweig (1978)).

These models deal only with pairwise interactions. Yet Futuyma (1983) has argued that long-term coevolution of pairs of species is the exception, and that most biotic interactions of evolutionary significance are diffuse and short-lived. His reason is as follows. If, for example, the interaction between a plant species and a herbivorous insect was stable and long-lasting, we would expect to find that the phylogeny of a plant family, and of the herbivorous insects feeding on it, would map closely onto one another. In general this is not what is observed, although it is true that particular insect families often attack one or a few plant families. If, as Futuyma thinks, coevolution is usually diffuse rather than pairwise, we need a theory of the coevolution of many species. Is there anything we can usefully say? Van Valen (1973) proposed the 'Red Queen' model, according to which an evolutionary improvement by one species would be experienced as an environmental deterioration by others, thus leading to a continuing evolutionary dance. He went further, arguing for a 'zero-sum' assumption, according to which a unit improvement in one species is exactly balanced by the summed deteriorations for others, and deduced from this a 'law of constant extinction'. Stenseth & Maynard Smith (1984) accepted his general model, but argued that his zero-sum assumption rested on a confusion between ecological and evolutionary advantage, and was mistaken. They concluded that an ecosystem could behave in one of two ways:

(i) 'Stasis': evolution would slow down and cease, until kicked into motion by changes in the physical environment; or

(ii) 'Red Queen' dynamics: evolution, even in a constant physical environment, would continue indefinitely, with recurrent speciation and extinction.

The obvious weakness of this theory is that it predicts nothing testable. We need a model of coevolution that includes more ecological structure. If May's model leaves out evolution, our model leaves out ecology. We need models which would help to answer such questions as the following.

(i) Which ecological factors favour stasis, and which favour 'Red Queen' dynamics?

(ii) In what circumstances will ecological diversity evolve and be stable? Are spatial and/or temporal diversity necessary?

(iii) Can apparently stable ecosystems collapse because of the invasion of novel species? If so, how different must the invader be from any existing species?

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