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Data from palaeontology and biodiversity suggest that the global biota should produce an average of three new species per year. However, the fossil record shows large variation around this mean. Rates of origination have declined through the Phanerozoic. This appears to have been largely a function of sorting among higher taxa (especially classes), which exhibit characteristic rates of speciation (and extinction) that differ among them by nearly an order of magnitude. Secular decline of origination rates is hardly constant, however; many positive deviations reflect accelerated speciation during rebounds from mass extinctions. There has also been general decline in rates of speciation within major taxa through their histories, although rates have tended to remain higher among members in tropical regions. Finally, pulses of speciation appear sometimes to be associated with climate change, although moderate oscillations of climate do not necessarily promote speciation despite forcing changes in species' geographical ranges.

Keywords: speciation; extinction; biodiversity; mass extinction; biotic history; recovery from extinction

1. INTRODUCTION

A rate of speciation is a measurement of how many new species appear in an interval of time within a given taxon and a given habitat, region, or ecosystem. A rate of speciation can also be a comparative measure, less dependent on time, relating to how one taxon seems to diversify relative to another.

The principal processes of speciation remain inadequately understood, despite a huge literature of field, laboratory, and theoretical studies. Still, this does not preclude empirical studies of the magnitude of speciation and the variation of rates observed in historical records. In this contribution, I briefly examine empirical rates of speciation, and of origination of taxa above the species level, from a palaeontological perspective. I first consider the average global rate of speciation and then discuss several sources of variation in rate at scales ranging from the whole of the Phanerozoic down to individual taxa and climatic fluctuations.

2. IS THERE A CANONICAL SPECIATION RATE?

Is there an average speciation rate for the biota as a whole? If there is, this might provide a benchmark rate when considering specific taxa or evolutionary situations. A canonical rate might also provide insight into processes of diversification through study of deviations from this average and the forcing factors involved.

A mean rate of global speciation can be calculated on the back of the envelope by considering the opposite process: extinction. Raup (1991*a*) noted that more than 99% of species that have ever lived are now extinct; May *et al.* (1995) calculated a slightly smaller percentage, but using an older estimate of the average duration of a species. In either case, the vast diversity of the modern biota must reflect only a slight excess of speciations over extinctions. Therefore, if we can estimate a historical extinction rate, we know the approximate speciation rate.

Raup (1991*b*) calculated that the average species among marine animals has a duration of about 4 million years (Ma). This translates into approximately 25% of species becoming extinct per million years. If we assume that the biota has a diversity in the order of 10^7 species (May 1988; Hammond 1995), then approximately 2.5 species should become extinct each year. Assuming a slight excess of speciation, and rounding, this means that the canonical rate of speciation is three species per year.

A rate of three new species per year suggests one reason why processes of speciation are so difficult to study: speciation is a rare event. Of the estimated 10^7 living species, fewer than 20% are known to science and, of the approximately 1.5×10^6 described species, a trivial number is monitored annually. In fact, the discovery of any newly formed species might suggest that the calculated canonical rate is too low. Raup (1991*b*) calculated the average duration of a fossil species by using an assumption of exponential decay of species with increasing longevity (see, also, Raup 1985), akin to Van Valen's (1973) law of extinction. The observation of numerous endemic species in ephemeral environments, such as lakes, might suggest there have been excess numbers of very short-lived species (for examples, see Foster *et al.*, this volume; for fossil examples, see Geary 1990; McCune 1996). But even if the true average duration of species is halved to 2 Ma, the canonical rate grows only to about six new species per year, or roughly one daughter for all species now known. (It is doubtful that the average species longevity could fall much lower than 2 Ma; species of insects seem to have long geological durations; see Labandeira & Sepkoski 1993; Coope 1995.)

Now, there are any number of reasons to believe calculation of a canonical speciation rate is absurd. Extinction is a discrete event, defined by the death of the last individual of a species. Speciation is more nebulous, having to do with relative reproductive isolation and degrees of genetic, morphological, ecological, and behavioural differentiation, as reviewed in this volume. Mayr's (1963) classic *Animal species and evolution* summarizes numerous examples of hybrid zones, ring species, introgression in disturbed habitats etc. which reflect differentiation short of speciation. Other workers have expanded on these observations, and students of plant species have added numerous examples of ambiguous speciation in the modern world (see, for example, Grant 1981; Niklas 1997). So, perhaps the time-scale for a canonical speciation rate should not be 1 yr, but maybe more like a century or even a millennium. This merely involves multiplying the calculation by the appropriate order of magnitude.

From a palaeontological perspective, what is interesting in not the mean speciation rate but the variance about it. I suspect that if we had good historical data, we would find that most years, or even decades, witnessed no new species (absent of human disturbance) and that a few witnessed bursts of new species (see, for example, Bennett 1997). In other words, even a canonical speciation rate calculated over an appropriate time-scale may have limited meaning. Throughout the rest of this paper, I will consider some of the components of variance in speciation rates seen in the fossil record.

3. METHODOLOGICAL NOTE

Much of the numerical information gleaned from knowledge of the fossil record on rates of 'speciation' and extinction is not for species, but for taxa higher in the Linnean hierarchy, usually genera and families. Species are not used for several reasons.

1. Palaeontological species are morphospecies recognized on limited aspects of anatomy, specifically hardparts. The relationship between fossil morphospecies and extant biospecies is not always certain (although, see Jackson & Cheetham 1990; Budd *et al.* 1994). In older parts of the Phanerozoic record, criteria used to define fossil species have varied among generations, cultures, and individual researchers (perhaps not unheard of in neontology).
2. Sampling of fossil species is very uneven in time and space. Many rock formations are disappointingly unfossiliferous whereas a few are spectacularly rich in fossils. This includes not only such renowned examples as the Burgess Shale and Solnhofen Kalkenschiefer but also units rich in 'normal' fossils, such as the Triassic St Cassian beds of the Alps and the Cretaceous Coon Creek deposits of the southern USA. These fossil faunas have received appropriate but still special monographcal attention at the expense of less yielding rock formations.
3. Species of particular interest for economic use and stratigraphic correlation have received much more attention than less useful fossils. Thus, species in groups such as planktonic foraminifera, ammonoids, graptolites, and conodonts have an integrity that is not comparable to other taxa such as benthic foraminifera or sponges.

Palaeontological genera and families, as a whole, have greater taxonomic stability and, because they represent collections of fossil morphospecies, are less subject to the to the vicissitudes of preservation, sampling, and study (Raup 1979*a*). It is true that most genera and families erected in the palaeontologcal literature have not been scrutinized by modern phylogenetic analysis. Nonetheless, when large samples are used, this does not seem to be a significant impediment.

1. Most studies of diversity patterns have found that genera and families correlate reasonably well with underlying species patterns, both in the fossil record (see, for example, Sepkoski *et al.* 1981) and in the Recent (see, for example, Gaston & Williams 1993; Flessa & Jablonski 1995; Roy *et al.* 1996*a*). Differences do exist but are often predictable from the behaviour of collections versus individuals (for example, dampening of the magnitudes of mass extinctions).
2. Modelling studies of the efficacy of paraphyletic versus monophyletic taxa (Sepkoski & Kendrick 1993) suggest that traditionally defined paraphyletic taxa can track species' patterns in the fossil record. In fact, if palaeontologcal sampling of species is poor, traditional higher taxa can reflect patterns of diversity and underlying rates of lineage speciation and extinction better than the poorly sampled species themselves.

The last point is important: use of higher taxa in palaeontologcal studies of origination and extinction is not about higher taxa as ontologically real biological entities. Rather, these palaeontological taxa are proxies, standing in where fossil species fail.

4. VARIATION IN ORIGINATION RATES OVER PHANEROZOIC TIME

The idea that there is a canonical speciation rate is compromised by the vast variation in rate observed over geologcal time. Figure 1 illustrates a time series of magnitude of marine originations over the Phanerozoic, measured as the per cent of new genera relative to standing diversity per interval of time. Intervals of geological time have been variously amalgamated and subdivided to provide as equal intervals as possible, given present understanding of the chronometric timescale.

Figure 1 shows that there are two intervals of high rates of origination in the Phanerozoic oceans. The first includes the initial radiation of animals during the Cambrian Period (figure 2) which exceeds most subsequent rates by at least a factor of two. This probably reflects rapid speciation as animals exploited the ecological roles available to large motile organisms capable of capturing water currents laden with food, processing algae and microbial mats, burrowing through sediment to ingest bacteria and other food items, and preying on animals successful in the other three endeavours.

Subsequent to the 'Cambrian explosion', origination rates decline in a general manner. This is exhibited in figure 1 by the exponential fit to the data. There is no reason to believe that origination rates should decay exponentially; the fitted curve is presented merely to draw one's eye to the general declines.

The end-Permian mass extinction (figure 2) disrupted the secular decline of the Palaeozoic Era at the genus level (more so than at the family level; see Sepkoski 1993).

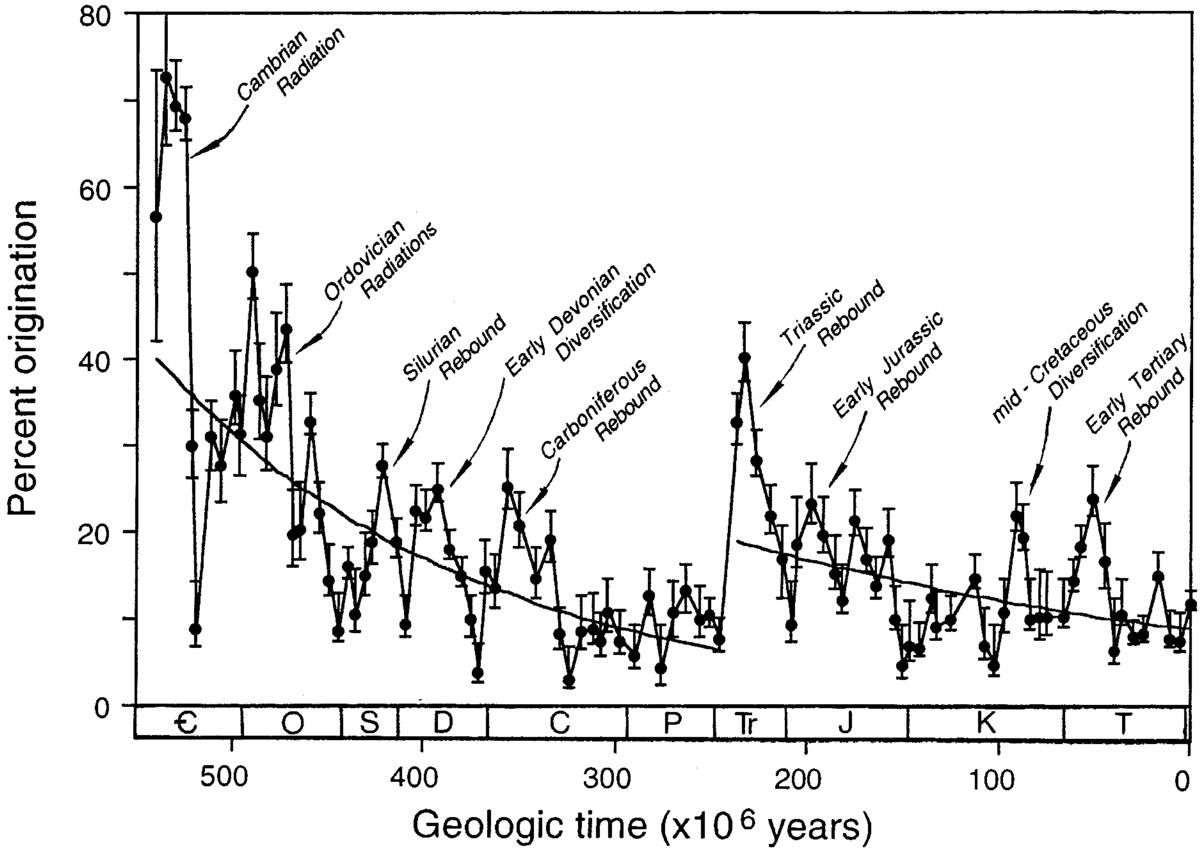

Figure 1. Per cent origination (100 × number of originations/standing diversity) for marine animal genera in 100 time intervals (stratigraphcal stages and substages). A total of 19 291 fossil genera spanning two or more of these intervals were used (for discussion of the database and rationale for excluding genera known only from a single interval, see Sepkoski (1996)). Error bars were calculated by the method of Sepkoski & Koch (1996). The two curves are least-squares exponentials fitted to emphasize long-term secular declines in magnitudes of origination. Main peaks above the curves are labelled. The geological time-scale is indicated along the abscissa (Є, Cambrian; O, Ordovician; S, Silurian; D, Devonian, C, Carboniferous; P, Permian; Tr, Triassic; J, Jurassic; K, Cretaceous; T, Tertiary).

In the wake of the end-Permian event, the Triassic witnessed levels of origination comparable to the Ordovician, a few tens of millions of years after the Cambrian explosion. The Triassic burst of genus origination reflects the phenomenon of rebound: rapid diversification in the aftermath of mass extinctions, as will be discussed below. The exceptional magnitude of the Triassic burst of origination reflects mostly the extreme magnitude of the end-Permian mass extinction: approximately half of marine families, 80% of genera and perhaps 96% of species were extinguished (Raup 1979*b*; Sepkoski 1989), leaving vacant ecospace available for survivors to radiate into during the subsequent Triassic (Erwin *et al*. 1987).

The fitted curve over the Mesozoic and Cenozoic in figure 1 simply draws one's eye to the continuing decline in origination rates, which will be discussed below. Note, however, that magnitudes of origination in most recent geologcal times are comparable to rates seen during similar icehouse intervals of the late Palaeozoic.

5. VARIATION IN SPECIATION AND ORIGINATION AMONG MAJOR TAXA

The two phases of secular decline in average rates of genus origination is not unlike what Van Valen (1974) found for rates of extinction among families: per-family extinction rates appear to decline through the Palaeozoic, accelerate in the wake of the end-Permian mass extinction, and then decline again through the Mesozoic and Cenozoic Eras. Raup & Sepkoski (1982) had previously analysed total rates of extinction and argued that there was a steady deceleration of extinction that encompassed the whole of the Phanerozoic, except when punctuated by events of mass extinction.

Both sets of authors explained secular declines in terms of continuous processes, either taxa slowly evolving resistance to extinction-causing perturbations (Raup & Sepkoski 1982), or evolution and reorganization of community-level interactions (Van Valen 1974) (see review in Gilinsky (1994)).

An alternative hypothesis is that secular changes in Phanerozoic origination and extinction rates reflect sorting of higher taxa. If higher taxa with rapid rates of origination and extinction (that is, are volatile in the sense of Raup & Boyajian (1988)) dominate early ecosystems and are replaced by clades with relatively low rates, then secular declines in both origination and extinction become, in effect, epiphenomena. Testing this hypothesis with rates of extinction is actually easier than with rates of origination for several reasons.

1. Rates of extinction within major taxa through the Phanerozoic appear much more constant than rates of origination. Origination rates tend to decline somewhat over the history of major taxa, as will be discussed

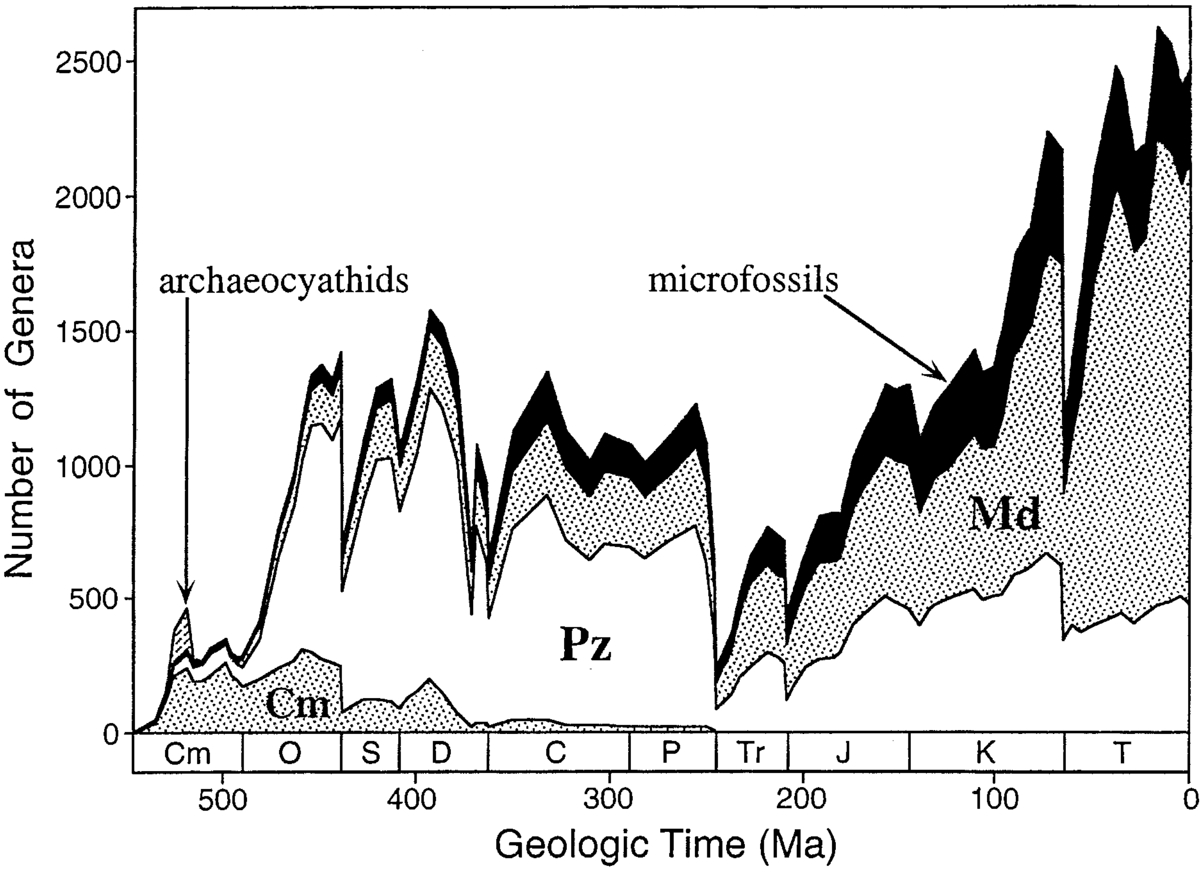

Figure 2. Standing diversity of marine animal genera through the Phanerozoic, using the same data on genera as in figure 1. The three great evolutionary faunas (Sepkoski 1984) are indicated by the fields (Cm, Cambrian fauna; Pz, Palaeozoic fauna; Md, Modern fauna). 'Microfossils' indicates the diversity of animal-like protists (Radiolaria and Foraminifera). 'Archaeocyathids' indicates the enigmatic diversity of the Archaeocyatha, which are mostly considered as sponges. From Sepkoski (1997).

below; in contrast, rates of extinction tend to be more stable (Van Valen 1985*a*). Thus, a characteristic rate of extinction has more meaning than an average rate of origination.

2. Analytical models for calculating taxic rates of evolution are more fully developed for extinction than for origination. These models vary from the simple methods of Stanley (1979) to the branching models of Raup (1985) and Gilinsky & Good (1991).
3. Extinction in the fossil record has received much more empirical study since the K/T hypothesis of Alvarez *et al.* (1980). Thus, data on times of extinction in any synoptic database have probably received more scrutiny from the community than have times of origination.

Despite these problems with calculating characteristic rates of origination, I have proceeded to compute rates for genera in 16 large taxonomic classes of marine animals. The rates were calculated as per-taxon rates of origination (that is originations per genus per million years) for geological stages variously subdivided and amalgamated to provide as even as possible a 5.5 million-year sampling interval (based on a modified version of the time-scale in Harland *et al.* (1990)).

Figure 3 illustrates the average rates of genus origination with the taxa divided into the three great evolutionary faunas of the Phanerozoic marine fossil record (figure 2). The rates of origination appear to vary substantially, as found at the family level for orders and classes by Holman (1989). The Cambrian evolutionary fauna encompasses the main taxa that radiated rapidly during the Cambrian explosion and dominated diversity throughout that period. Their average rates of origination tend to be higher than taxonomic groups that subsequently became important (although not without overlap). Thus, the huge peak in origination rates over the Cambrian in figure 1 is a function of the dominance of groups in this fauna.

The taxonomic groups of the Palaeozoic evolutionary fauna illustrated in figure 2 diversified during the Ordovician radiation and dominated the world ocean through the remainder of the Palaeozoic Era. Their average rates of origination tend to be lower than taxa of the Cambrian fauna, which is reflected in the smaller magnitude of per cent origination over the Ordovician Period in figure 1, despite the fact that three times more diversity was emplaced than during the Cambrian explosion. The waning origination rates through the post-Ordovician reflect two factors: (i) continuing decline of members of the Cambrian evolutionary fauna (see figure 2), with their very high rates of origination; and (ii) growing importance of the slowly originating Modern evolutionary fauna, especially during the late Palaeozoic Era (that is, Carboniferous and Permian).

The major groups of the Modern evolutionary fauna tend to have the lowest rates of origination in figure 3 and certainly have the lowest among-group variance.

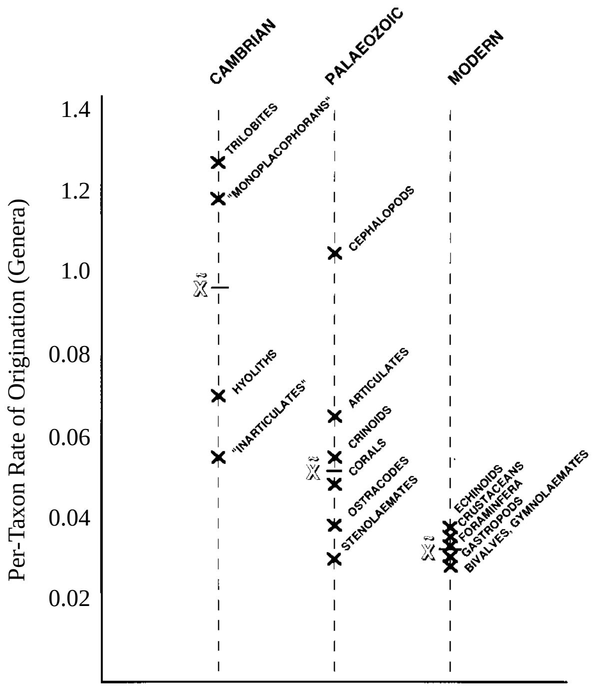

Figure 3. Average rates of origination for main classes in the three evolutionary faunas. Rates were calculated as the per-taxon rate of origination (number of originations/standing diversity × interval duration). Averages are arithmetic means of rates weighted by standing diversity in each interval such that intervals with low diversity of a class get low weight. Median values ($\tilde{X}$) of the rates within each fauna are illustrated, showing the general decline in magnitude of origination rates from the Cambrian to the Modern fauna.

These are the groups that came to dominate global diversity in the wake of the end-Permian extinction event. The high rates of origination over the Triassic are partly a function of their accelerated diversification during the rebound from the Permian mass extinction. The high rates are also partly a function of a huge radiation of ammonoid cephalopods: a group more characteristic of the Palaeozoic evolutionary fauna which exhibits average origination rates rivalling members of the Cambrian fauna (figure 3). Ammonoids were a main component of marine diversity in the Triassic fossil record, but later became proportionally less important as members characteristic of the Modern fauna diversified.

This explanation for secular decline in rates of genus origination is actually quite similar to mathematical treatments of decline in the extinction rates of families presented by Sepkoski (1984, 1991*c*) and Gilinsky (1994). But if origination rates tend to be variable over time, why should there be a correspondence? It is a palaeontologcal observation that rates of origination and extinction tend to be correlated, over nearly an order of magnitude of differences in rates. Stanley (1979, p. 258) formalized this observation as his first rule of macroevolution: the 'rate of speciation in adaptive radiation and rate of extinction are strongly correlated in the animal world' (see, also, Van Valen 1985*b*; Stanley 1990; Gilinsky 1994). Figure 4 illustrates Stanley's (1979) data, which are measured for species, by using indirect calculations of extinction and diversification rates.

Stanley (1979, 1990) presented several explanations for the correlation between speciation and extinction rates. The first is almost trivial, but still important: a taxon with high extinction but low speciation will not survive long enough to be considered important. More substantively, Stanley argued that species' characteristics that might promote speciation, such as numerous small, geographically isolated populations, might also leave species prone to extinction (see, also, Stanley 1986*a*). For example, species with low dispersal ability should tend to be endemic, with comparatively small population sizes more subject to extinction than widespread species, but low-dispersing species should also have more subdivided populations prone to speciation. Jablonski (1986, 1995) expanded upon this with statistical studies of North American molluscs of the Late Cretaceous (see, also, Hansen (1978, 1982) for early Tertiary molluscs). Jablonski demonstrated that molluscs with planktotrophic larvae—larvae that spend weeks to months feeding in marine surface waters—have wider geographical distributions, longer geological durations, and lower speciation rates than nonplanktotrophic species. Molluscs that reproduce by either direct development, or non-feeding, short-duration planktonic larvae have opposite characteristics: narrower geographical distributions and higher speciation rates (although, see Lieberman *et al.* 1993).

What is perhaps most significant in Jablonski's work is that these different rates of speciation and longevity are heritable at the level of clades; that is, molluscan species with planktotrophic larvae tend to give rise to daughter species with similarly low rates of speciation whereas molluscan species with nonplanktotrophic larvae give rise to species with similarly restricted geographical ranges and high rates of speciation (Jablonski 1986). In Jablonski's analyses, the underlying cause of characteristic speciation rates is evident from modes of reproduction. In other cases, characteristic speciation rates may relate to ecological factors, such as physiology and function, that affect population structure and density and which are shared by common descent within higher taxa (for example, Martin 1992; Lawton *et al.* 1994). But why characteristic rates should remain heritable over 10s to 100s of millions of years within taxa at the level of orders and classes, as in figure 3, remains unclear.

This problem of why evolutionary rates are conserved within disparate taxonomic groups is one of the great unsolved problems of macroevolution. Yet, it is incredibly important because much of the faunal turnover we observe at higher taxonomic levels in the marine fossil record can be attributed to these characteristic and evidently heritable rates of speciation and extinction (Sepkoski 1991*c*).

6. REBOUNDS OF ORIGINATION RATES AFTER MASS EXTINCTIONS

The decay curves plotted in figure 1 fit the data in only the roughest of ways. There are many peaks and troughs in the magnitude of origination that represent much more than random variation about best-fit curves. Some of the peaks reflect acceleration of origination in the aftermath of mass extinctions, as labelled in figure 1. Rebound, discussed with respect to the end-Permian mass extinction, is a general feature of recoveries from all of the larger

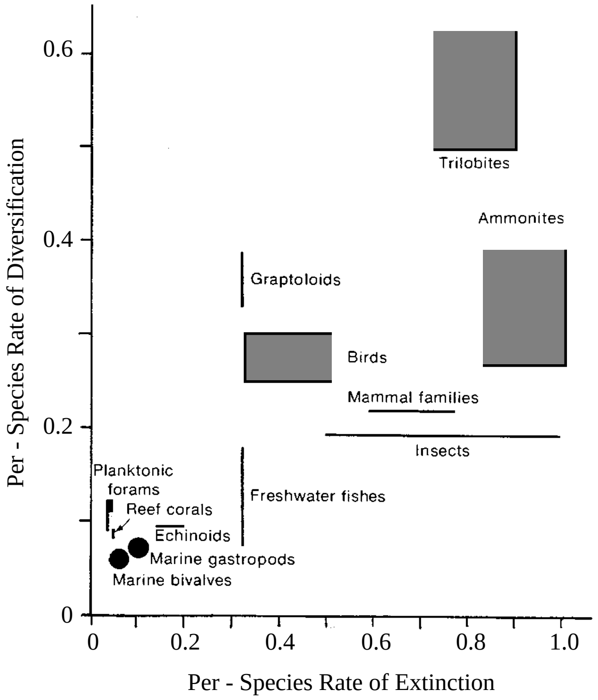

Figure 4. The average rate of diversification plotted against rate of extinction for several major groups of taxa, after Stanley (1979, p. 231). Because diversification rate equals speciation rate minus extinction rate, the positive trend of the points indicates magnitudes of speciation and extinction must be positively correlated. (If not, the graph would show a negative trend.) Lengths of lines and areas of boxes indicate uncertainties in the rates. The per-species rate of extinction was calculated as the reciprocal of mean species durations (in millions of years). See Stanley (1979) for details of the calculation of mean duration and diversification rate.

extinction events. What is surprising, though, is that acceleration of origination is not immediate after mass extinctions (Hallam 1991). Measured on time-scales of geological stages (averaging about 5 Ma duration), there is a lag of several stages between the initial rise of diversity after the mass extinctions and the maximum rate of origination. The end-Ordovician mass extinction and subsequent Silurian rebound provides a typical example, illustrated in figure 5. The mass extinction involves a sharp peak in extinction rate (although distributed over two geologically short intervals of the latest Ordovician; see Brenchley 1990; Brenchley *et al.* 1995). With the start of the Silurian Period, extinction rates drop to levels characteristic of the background rates of earlier times. However, measured magnitudes of origination do not jump immediately; rather, there is a protracted increase over 20 Ma, with maximum rates reached only at the end of the Wenlockian Series. (Note that magnitudes in figure 5 are measured as percentages; the delayed peak of origination is not simply a function of increasing diversity.)

There are various explanations for this recurring pattern.

1. The protracted rise in origination rates after mass extinctions is an artefact of imperfect knowledge of the fossil record. Incomplete preservation of fossil taxa and incomplete sampling of their preserved temporal ranges means that documented first and last occurrences are only minimum estimates of true times of origination and extinction. This problem has received most attention with respect to the often apparent gradual declines of species toward mass extinctions (Signor & Lipps 1982) and is often referred to as the 'Signor–Lipps effect'. The same attenuation of documented times of origination should occur during rebounds from mass extinctions, and this has been referred to as the 'Lipps–Signor' or even 'Sppil–Rongis' phenomenon effect. Erwin (1996) discusses evidence for this phenomenon in data on the recovery from the end-Permian mass extinction.

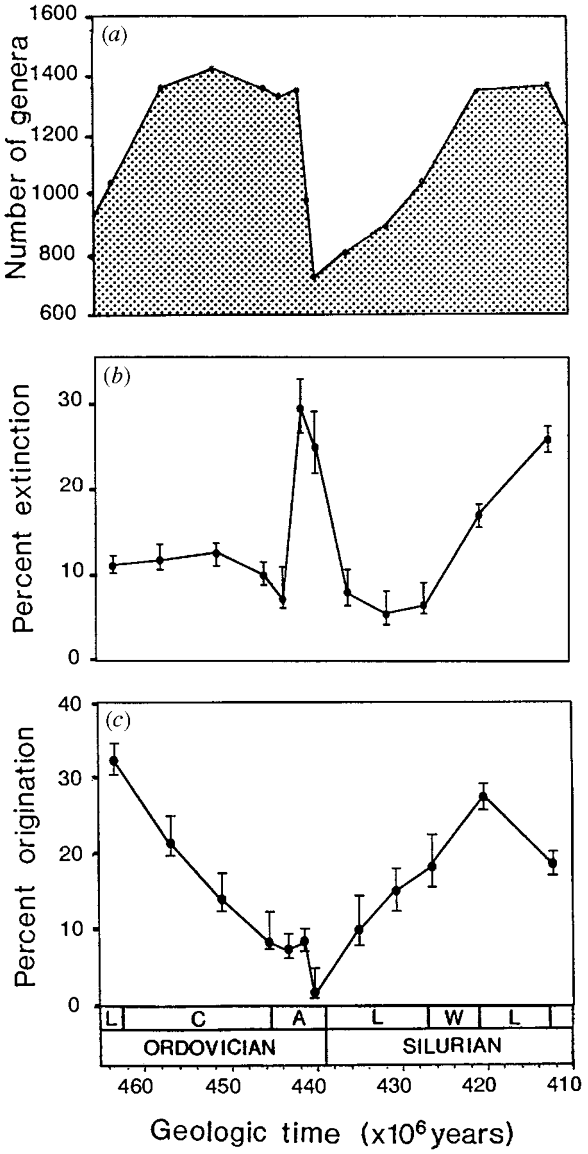

Figure 5. Diversity, extinction, and origination around the end-Ordovician mass extinction and Silurian rebound. (*a*) Illustrates the sharp drop in standing diversity of marine animal genera at the end of the Ordovician Period and then the long recovery of diversity to pre-extinction levels through the first half of the Silurian Period. (*b*) Shows that the peak of extinction at the end of the Ordovician was sharp. (*c*) Shows, in contrast, that originations did not increase abruptly after the pulse of extinction, even though diversity began to recover; rather, origination rates increased to the middle Silurian. Data, calculations, and error bars as in figures 1 and 2. Letters on the abscissa indicate stratigraphic series (from left to right: L, Llandeilo; C, Caradoc; A, Ashgill; L, Llandovery; W, Wenlock; L, Ludlow).

2. The protracted rise in origination is an artefact of mixing data for taxa with very different characteristic rates of origination. Because rates of speciation and extinction are correlated, rapidly speciating taxa should suffer more at mass extinctions than slowly speciating groups (see, for example, Sepkoski 1984). Thus, the aftermath of mass extinction initially will see disproportionate numbers of slowly speciating taxa, with rapidly speciating groups only later recovering and becoming important components of the biota. The data for marine animal genera, however, display no such pattern: when divided into evolutionary faunas, the more slowly speciating Modern fauna exhibits the same prolonged rise in origination rates as the more rapidly speciating Palaeozoic and, especially, Cambrian faunas.
3. The protracted increase in origination could have a biological basis, involving the slow re-establishment of stable ecological communities (see, also, Schindler 1990; Hallam 1991; Harries 1993; Erwin 1996). The immediate aftermaths of mass extinctions are characterized by outbreaks of what have been termed 'disaster species' (Kauffman & Erwin 1995; Hart 1996; Walliser 1996). These are marine species that have nearly cosmopolitan distributions, are hugely abundant in local fossil deposits, and have remarkably short durations, often lasting in the order of 10^5 years. A recurring pattern is that 'disaster species' blossom immediately after a mass extinction and are quickly replaced (on geological time-scales) by subsequent disaster species. Thus, it appears as if the world ecosystem undergoes a turbulence in the wake of mass extinctions before the biological system settles down and rediversification begins in earnest. Increased speciation and rediversification apparently ensues on both geographical scales, with the re-establishment of biogeographical provinciality, and on environmental scales, with the re-establishment of community differentiation (i.e. beta diversity). The latter has best been documented for the Silurian rebound after the end-Ordovician mass extinction (Sheehan 1975), although much more work needs to be done with respect to that rebound and others.

7. VARIATION OF SPECIATION AND ORIGINATION RATES WITHIN TAXA

Most of the considerations above were directed toward large-scale secular variations in rates of origination. Much of this seems to involve either sorting among higher taxa over long intervals of time or response to historical events such as mass extinctions. However, there is variation within major taxonomic groups that can be related to time, geography, climate, and life-history strategies. The last has already been mentioned with respect to studies by Hansen (1982), Jablonski (1986) and others. Below, I discuss several other sources of large-scale variation in speciation rates within major taxa.

(a) *Time*

Few major taxa exhibit constant rates of origination across long intervals of geological time. Gilinsky & Bambach (1987) found that most higher taxa of marine animals exhibit regular decline in magnitudes of origination through their histories. They studied 99 major taxa, both extant and extinct, and used Linnean families as proxies for species-level originations. They subdivided Phanerozoic time into coarse intervals of roughly 20 Ma duration (to avoid small-number variation and to smooth effects of short-termed, unique events), and they calculated several metrics of origination and extinction for each interval.

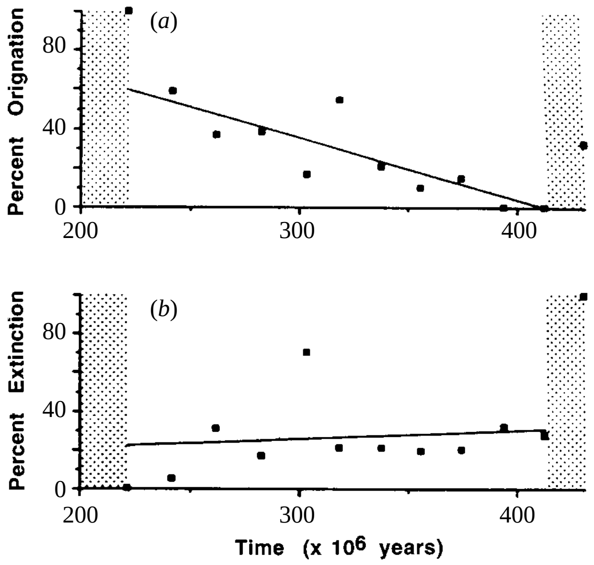

Figure 6. Proportion of originations and extinctions relative to standing diversity through time for families of rugose corals, after Gilinsky & Bambach (1987). The fitted lines show that rate of origination declined rather regularly over time whereas average extinction increased very mildly. Points represent data for stratigraphic series of the Palaeozoic Era. The lines are linear regressions on time (measured from the approximate start of the Vendian Period). First and last points in the stippled fields were excluded from the fits in order to avoid the necessary 100% origination in the first time interval and 100% extinction in the last.

Figure 6 illustrates a typical example from Gilinsky & Bambach's (1987) study. It illustrates per cent origination and extinction for the Rugosa, an extinct clade of Palaeozoic corals. Gilinsky & Bambach found that among most of the 99 taxa analysed, magnitudes of origination declined significantly when regressed on time, but extinction tended to be stationary or, in a minority of taxa, increased only slightly through history.

Gilinsky & Bambach's (1987) results are probably not an artefact of taxonomy. Although studies at lower levels in the Linnean hierarchy are sparse, a few anecdotal examples exhibit similar patterns. For example, Foote (1988) used cohort analysis (Raup 1978, 1985) to estimate species-level rates of origination and extinction from genera of early Palaeozoic trilobites. He found a substantial decline in calculated rates of speciation from the Cambrian to the Ordovician Period. Maurer (1989) examined actual measured rates of speciation for North American horses and found a marked decline with respect to diversity; because diversity of horses expanded through much of the Tertiary, speciation within the group must have declined through time.

Gilinsky & Bambach (1987) offered several hypotheses for secular declines in origination rates within major taxa. Of these, one was in the flavour of Van Valen's (1973) Red Queen hypothesis: the basic adaptations of a successful group are established early in its history, as seen, *a posteriori*, in its diversification; however, when a group's biotic context changes as a result of continuing evolutionary turnover among surrounding taxa, the initial adaptations become increasingly less beneficial and overall speciation rate declines. A second scenario presented was that 'genetic and developmental systems may become resistant to change as they age' (Gilinsky & Bambach 1987, p. 444). This speculation, bolstered by some reference to genetic studies, was also suggested to reduce possibilities of speciation over the history of a major taxon.

A simpler explanation for secular decline in origination rates is offered in Maurer's (1989) work: as a group radiates, it exerts a crowding effect (or, alternatively, it fills available niches), slowly decreasing opportunities for further speciation (see, also, Rosenzweig 1975; Sepkoski 1978, 1991*a*). This effect in marine higher taxa may be further enhanced by the general succession of evolutionary faunas, during which older faunas are replaced in sequence by faunas with new ecological organizations. This replacement could lead to origination rates actually declining below extinction rates within taxa of the older evolutionary fauna (Sepkoski 1991*b*).

(b) *Geography*

Speciation rates vary in space as well as time. The role of geography in speciation is central to many hypotheses of population differentiation, from the shifting-balance model of Wright (1931, 1982), the peripatric model of Mayr (1963), the vicariance model of Croizat *et al.* (1974), to the clinal model of Endler (1977), among others. However, measurements of variations in speciation rates at grand scales remain limited.

High diversity in equatorial oceans and landmasses suggests that rates of speciation may be higher in tropical than in temperate, boreal, or polar regions. However, high diversity could also result from low rates of extinction in the tropics (Jablonski 1993; Flessa & Jablonski 1996). Stehli *et al.* (1972) calculated mean geological ages of extant species of planktonic foraminifera along a transect from the equatorial Pacific to the Arctic Ocean and found little difference. As mean age of extant species relates to mean duration (Stanley 1979; Pease 1987), and extinction rate is the reciprocal of mean duration (Raup 1985), this would suggest a near constant extinction rate across latitude for this group. Thus, the high diversity of foraminifers near the equator (but not on it; see Rutherford & D'Hondt 1996) would suggest higher rates of speciation, at least at some point in time, at lower latitudes.

At taxonomic levels of genera and families, mean geological ages tend to decrease toward the tropics. This has been shown for marine corals (Stehli & Wells 1971; Veron 1995), bivalves (Stehli *et al.* 1969; Hecht & Agan 1972; Flessa & Jablonski 1996), and barnacles (Newman 1986). Flessa & Jablonski (1996) present a detailed statistical analysis for genera of extant bivalves, and argue compellingly that smaller mean ages of low-latitude (within 30° N–S) marine bivalves relative to higher latitude bivalves reflect higher speciation and not reduced extinction.

At taxonomic levels even above the family, there is evidence that the tropics experience enhanced origination, or at least more frequent appearances, of groups with novel morphologies. Jablonski (1993) analysed the palaeolatitudes of first-documented fossil occurrences of 42 taxonomic orders that originated in the oceans during the Mesozoic and Cenozoic eras. He divided these orders into two sets: 26 that he assessed to have good fossil records (and thus less likely to reflect merely the vagaries of preservation and palaeontologic sampling); and 18 that were lightly sclerotized or otherwise lacked potential to be widely sampled. Jablonski found that first appearances of the former set were significantly more numerous in tropical latitudes than expected at random, whereas the latter set conformed to expectations of palaeontological sampling. Again, the evidence suggests that tropics are cauldrons of evolution, with high rates of evolutionary activity.

(c) *Climate*

It could be hypothesized that latitudinal variation in rates of origination is simply a correlate of climatic variation and the forced responses of effected populations. But even in the tropics, climate has changed considerably over time-scales of 10^5 years (see, for example, Colinvaux 1989, 1996; Guilderson *et al.* 1994). Variation in the Earth's orbit about the Sun affects solar insulation with characteristic periodicities of approximately 2×10^5, 4×10^5, and 10×10^5 years—the Milankovitch cycles. Bennett (1990) was one of the first workers to recognize the effects that climatic oscillations on these time-scales might have for speciation rates (although, see Cronin 1987). Bennett (1990, 1997) argued that disruption and reassembly of terrestrial and marine communities (Coope 1987, 1995; Overpeck *et al.* 1992; Valentine & Jablonski 1993; Elias 1994; FAUNMAP Working Group 1996) on Milankovitch time-scales might cancel microevolutionary processes affecting phyletic evolution, leading to the appearance of widespread evolutionary stasis. On the other hand, disruption of communities during climatic oscillations might also isolate small populations for time periods of 10^5 years, long enough for some surviving isolates to diverge from their ancestral species.

Vrba (1992) expanded upon these ideas in her 'habitat theory' of evolutionary change (see, also, Vrba 1985, 1987). Figure 7 is her illustration of how hypothetical populations might respond to Milankovitch oscillations in climate. Each cell in the figure is meant to represent a map view of a species' geographical range, and differences among columns illustrate different scenarios for the response of geographical range, population structure, and genetic constitution as climate oscillates. Except for 7*a*, in which there is no change, species are shown to respond by range fragmentation and (usually) re-expansion with each oscillation. Figure 7*b* shows what may be the most common case: fragmentation of range into a number of isolated populations, but without genetic differentiation so that the species later re-expands unchanged. The alternative is illustrated in figure 7*d*, in which the isolates are so small and limited that the species becomes extinct.

Figure 7*c,e,f,g* are variants in which populations isolated by climatic change develop sufficient differentiation to be considered distinct species. In figure 7*c*, the differentiated

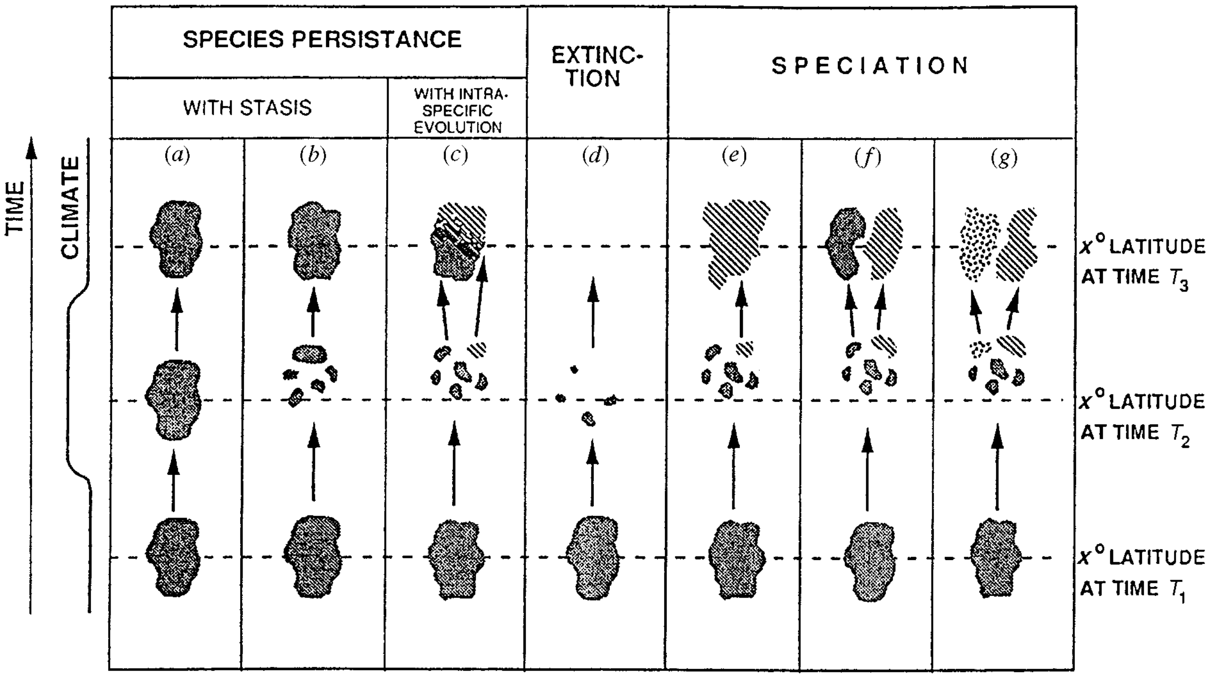

Figure 7. Hypothetical map views of a species range at three time intervals through a climatic oscillation (left-hand side), from Vrba (1992, fig. 4). Different patterns of shading at times T_2 and T_3 indicate evolution of new species from isolates of the parental species. See text for further explanation.

population expands parallel to the merged, undifferentiated isolates of the ancestral species to establish a parapatric pattern; *f* is similar but the species remain allopatric. Figure 7*e* illustrates a situation in which the differentiated population survives the climatic oscillation, but all undifferentiated isolates of the ancestral species do not; the new species expands over the ancestor's original range. Finally, figure 7*g* illustrates a scenario in which more than one isolated population differentiates and survives as remaining populations of the ancestor disappear.

These are hypothetical situations currently with very limited documentation. Vrba (1985) has presented some evidence for clustered speciations and extinctions ('turnover pulses') among diverse groups of Neogene mammals during rapid climatic shifts over Africa. Similar pulses of rapid faunal extinction and speciation have been recorded among marine animals at the onset of important glaciation in high northern latitudes, around 2.5 Ma BP (Stanley 1986*b*; Allmon *et al.* 1993; Jackson *et al.* 1996). Repeated episodes of speciation during Milankovitch fluctuations have yet to be demonstrated, and, in fact, there is some preliminary evidence that rates of speciation may have been slow during the glacial oscillations of the Pleistocene (Jackson 1995; Zink & Slowinski 1995; Roy *et al.* 1996*b*; Bennett 1997).

Even if pulses of speciation are not obvious at timescales of 10^4 to 10^5 years, there is suggestion in the fossil record that pulses such as seen in the Pliocene may have been recurrent, especially in the marine realm. Brett & Baird (1995) documented high levels of persistence of benthic species over intervals in order of 5×10^6 years in mid-Palaeozoic rocks in the northern Appalachian Basin of the USA. These intervals of stability were interrupted by short periods of extinction and appearance of many newly evolved species and immigrant species. This pattern of pulses of speciation followed by prolonged stability of faunas has been termed 'coordinated stasis' (see Brett *et al.* 1996). Miller (1997) presents a very useful review of the phenomenon and concludes that, like the habitat theory, coordinated stasis needs far more empirical scrutiny.

8. PROSPECTUS

This review has examined a few aspects of large-scale patterns of speciation and taxon origination from the perspective of the fossil record. Although it is possible to use palaeontological data to calculate a canonical rate of speciation—three species per year—it is clear that this has limited meaning. There is large variation about this average rate on time-scales of 10^4 to 10^8 years. A variety of explanations have been offered for this variation, but many uncertainties and unsolved problems persist. Below, I re-emphasize three of these.

1. Why do major taxa vary over approximately an order of magnitude in characteristic rates of speciation (and rates of extinction)? And why are these characteristic rates maintained to some extent through the histories of the taxa? Although some insight has been provided by consideration of life-history strategies (for example, Jablonski 1986), differences among taxonomic classes and orders and evident heritability of rates have never been adequately explained. Yet, if difference and heritability are taken as empirical fact, a seemingly disparate variety of palaeontological observations can be modelled, including the succession of evolutionary

faunas (Sepkoski 1984), the secular decline of origination and extinction rates (Sepkoski 1984; Gilinsky 1994), and even the onshore–offshore expansion of diversity seen in so many marine taxa (Sepkoski 1991*c*).

2. Is there a consistent structure to patterns of speciation during rebounds from mass extinctions? The rapid turnover of species in low-diversity communities prevalent after mass extinctions and the delayed onset of rapid rates of speciation also do not have adequate understanding. Here, the solution to the problem may begin with much better palaeontologcal documentation of patterns, investigated with far greater temporal resolution, taxonomic discrimination, and geographical detail than represented in figure 5. Better biological models of speciation in extensive, disturbed habitats may also contribute. Such studies may have relevance reaching far beyond life's past history: they may enhance our understanding of what might happen if present-day biodiversity continues to decline and if humankind is ever able to stop its devastation (Sepkoski 1997).
3. Is most speciation clustered during times of rapid change in climate? The hypotheses of Bennett (1990, 1997), Vrba (1992), and Brett & Baird (1995) remain largely untested. This is, in part, because it is very difficult to resolve spatial patterns, such as conjectured in figure 6, on the necessary time-scales of 10^4 to 10^5 years in the fossil record. Yet, such data are again important for questions about modern biodiversity. If projections of global warming are true, we will need comparative data to predict: (i) consequences for the biota; (ii) how ranges might become fragmented; and (iii) how rates of speciation, as well as extinction, might change.

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