

# THE MACROEVOLUTIONARY CONSEQUENCES OF ECOLOGICAL DIFFERENCES AMONG SPECIES

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**Abstract:** In this paper, I examine the dynamics of species richness in a model system in which multiple species compete in a metacommunity (multiple patches linked by dispersal). Patches lie along an environmental gradient, and new species are introduced into the system by speciation of existing species. This model is used to explore how the ecological similarity of species influences the patterns in community structure that result and to determine whether patterns in fossil and systematics data may be signatures for different types of community structure. Making species more similar overall along the entire gradient or making new species that have more similar optimal positions along the gradient to their progenitor both increase the time required to drive species extinction. As a result, making species more similar ecologically to one another

increases overall species richness because of an increased frequency of transient species in the system. Having more transient species in systems shifted the longevity distributions of species in the fossil record towards having a greater frequency of shorter duration species, and the age distribution of extant species that would be estimated from molecular phylogenies also had a higher frequency of younger aged species. Comparisons of these results with species longevity distributions extracted from two data sets and with species ages derived from species-level molecular phylogenies strongly suggest that transient species are an important component of real biological communities.

**Key words:** metacommunity, coexistence, fossils, molecular phylogenies, species richness.

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EXPLAINING patterns of species richness and diversity is the ultimate goal of scientists working in a number of disciplines. In particular, community ecologists, palaeontologists and molecular systematists are all trying in one way or another to understand the processes by which species are made, interact with one another and eventually are lost from the Earth's biota. Each discipline necessarily focuses on different processes because of the vantages afforded by the data that each can amass. This gives each discipline unique insights into the processes that have shaped the world around us. However, at the same time each discipline can become blinkered to the vantages afforded by the other disciplines. Community ecologists tend to ignore that myriad processes can create new species and tend to assume that ecological processes operate to perpetuate the indefinite existence and coexistence of species. Systematists tend to forget that the processes driving speciation and extinction are often generated by the web of interactions in which component species are embedded and not simply by processes internal to the clade. Although palaeontologists in many ways have the best view, they sometimes become more enamoured with the patterns that emerge and are unwilling to pursue or speculate about the ecological processes that may have generated those patterns. Obviously, these are only

caricatures of each field. Moreover, these assumptions and self-imposed limitations are not made from ignorance or hubris. Rather, they are based on the unavoidable empirical limitations of each field and on the theoretical assumptions that must be made in each to progress.

Because we are all studying different features of the same biota, findings from one discipline should, however, be reconcilable across them all. Obviously, some processes may be more or less important to each discipline, and each may have some processes that uniquely operate in their sphere. For example, Gould (1985) argued that punctuated equilibrium is a macroevolutionary process that sets apart palaeontology from community ecology and evolutionary biology. However, the resolution of the fossil record may make this distinction more apparent than real. For example, from my empirical work on the adaptive speciation of damselflies living with different predators, I calculated that 100–500 years would be required for natural selection to transform key morphological traits of one species that lives with fish predators into those of another that faces dragonfly predators: these calculations are based on field measures of selection differentials that damselfly populations experience today and extremely pessimistic assumptions about the heritabilities of these traits (McPeck 1997). If these damselflies had a

fossil record, this key ecological change in morphology would appear decidedly punctuated, even though it was driven by an unremarkable phenotypic response to natural selection. Also, periods of stasis between punctuational events in the fossil record are probably best explained by population structure and optimizing selection imposed by the ecological interactions experienced by a species (Eldredge *et al.* 2005). Attempts to reconcile the disciplines with one another may thus make them stand closer together and not further apart.

Moving concepts and theories across intellectual boundaries are not the only contributions that the disciplines can make to one another. Patterns in the types of data one discipline gathers may also inform critical theoretical issues in other disciplines. As a community ecologist and evolutionary biologist, I am most interested in understanding the causes of contemporary patterns of species richness and diversity. One of the major issues currently being debated within community ecology is the degree to which coexistence mechanisms structure species assemblages. This debate has been ongoing in various guises since the inception of the field, and the latest variation was rekindled by Hubbell's (2001) unified neutral theory of biodiversity. Although not directly testing Hubbell's model, here I explore the consequences of some issues raised by the premise of the unified neutral theory. Specifically, I explore the dynamics of species richness in a model system in which speciation does not necessarily introduce species that can coexist with existing species and extinction is caused by species interactions. I use this model to determine whether characteristic signatures are apparent in data from the fossil record and molecular phylogenies that would allow us to evaluate the role that coexistence vs. neutral processes play in structuring present-day communities. These model predictions are then compared with real data.

## A CONTEMPORARY ECOLOGICAL VANTAGE

Ecologists try to understand patterns of species richness and diversity primarily through understanding the processes that promote or inhibit the coexistence of species. Species 'coexist' in the ecological sense when the outcomes of ecological processes promote their indefinite persistence together (MacArthur 1972; Tilman and Pacala 1993; Chesson 2000; Chase and Leibold 2003): if the ecological regime does not change, coexisting species will never become extinct. Myriad processes can promote species' coexistence on both local and regional spatial scales (see reviews by Tilman and Pacala 1993; Chesson and Huntly 1997; Chesson 2000), and most result from trade-offs in ecological performance caused by interactions with

other species [e.g. intraspecific vs. interspecific competition (Vandemeer 1975), predation vs. competition (Levin 1974; Holt *et al.* 1994; McPeck 1996), competitive vs. dispersal ability (Tilman 1994)]. The ecological regime can include both spatial and temporal ecological variation, and in fact some processes that promote species coexistence are based on spatial or temporal ecological variation (Chesson 2000; Amarasekare 2003). If a species cannot coexist with other members of the community, it will be driven extinct because of its interactions with those that are better adapted to interacting with the abiotic conditions and other community members. Throughout this paper, I will identify these as 'transient' species to distinguish them from 'coexisting' species. Thus, communities can be mixtures of transient and coexisting species (i.e. species that are and are not, respectively, being driven extinct by ecological interactions), and any given species may change categories as new species enter the system and as others exit.

Although ecologists clearly recognize that speciation and extinction are ultimately responsible for the gain and loss of species, the proximate dynamics of speciation and extinction are often assumed not to influence the species richness patterns that result. Ecologists tend to see speciation as a by-product of the processes through which lineages adapt to fill different ecological roles in a community (i.e. fill different 'niches') and thus promote their coexistence (e.g. Rosenzweig 1978, 1995; Pimm 1979; Brown 1995; Schluter 2000). This has been called 'ecological speciation' (Schluter 1996, 2000). Therefore, speciation need only be considered in explaining diversity patterns when all the available niches are not filled: '... if the areas being compared are not saturated with species, an historical answer involving rates of speciation and length of time available will be appropriate; if the areas are saturated with species then the answer must be expressed in terms of the size of the niche space ... and the limiting similarity of coexisting species' (MacArthur 1965, p. 510). Likewise, interactions among species should drive to extinction those species that cannot coexist in the system. This reasoning implies that only coexisting species should be present, and thus understanding species richness becomes a matter of understanding the processes that promote coexistence.

These inferences are based on two assumptions: (1) ecological speciation is the primary speciation mode and (2) extinction occurs quite rapidly. Ecological speciation is surely one important mode of creating new species, but it is not the only or even necessarily the primary mode. Speciation occurs by myriad processes, many of which involve no necessary adaptive ecological differentiation at all. For example, 70–80 per cent of angiosperm species are thought to have originated via hybridization and polyploidy (Goldblatt 1980; Lewis 1980; Masterson 1994;

see reviews by Barrett 1989; Rieseberg 1997). In these cases, ecology may play some role in the speciation process (e.g. as a pure consequence of encounter probabilities, plant species that do hybridize may be more likely to live in similar environments), but ecological diversification is not the proximate mechanism creating new species. In animals, hybridization and polyploidy as speciation mechanisms are rare, but other non-ecological speciation mechanisms may be common. Chromosomal rearrangements are the proximate reproductive isolating mechanisms and thus probably the cause of speciation in many animal taxa (reviewed by King 1993). Sexual selection has also been implicated in the radiations of many animal groups [e.g. Hawaiian *Drosophila* (Kaneshiro 1988; Boake 2002), African lake cichlids (McKaye 1991; Seehausen *et al.* 1997; Kornfield and Smith 2000; Turner *et al.* 2001)], and recent reviews have suggested that clades in which sexual selection should be more prevalent are more diverse than sister clades [e.g. birds (Barraclough *et al.* 1995; Møller and Cuervo 1998), insects (Arnqvist *et al.* 2000), lizards (Stuart-Fox and Owens 2003)]. In all of these, speciation is not a by-product of generating ecological differentiation, and so no necessary relationship exists between the degree of ecological differentiation among resulting species and the mechanisms generating reproductive isolation. In fact, in many of these mechanisms, the resulting species may be ecologically quite similar, if not identical, to one another. Moreover, the prevalence of cryptic, sympatric species that are being identified by molecular studies (e.g. Henry *et al.* 1999; Witt and Hebert 2000; Gomez *et al.* 2002) also suggests that significant phenotypic and ecological differentiation is not a necessary outcome of speciation.

Assumptions about the dynamics of extinction must also be more sophisticated. Extinction is not always the result of 'bad luck' on the part of some subset of coexisting species (Raup 1991). Extinctions also occur because of interactions with abiotic features of the environment and with other species (reviewed in Raup 1991; Lawton and May 1995). Moreover, species that will ultimately be driven extinct do not simply realize immediately that they are goners, give up and throw themselves on their swords (metaphorically speaking); ecological and evolutionary winners and losers may co-occur for some time, possibly a very long time. The time to extinction caused by species interactions depends critically on the ecological similarity of competing species (Hubbell 1979, 2001; Shmida and Ellner 1984; Shmida and Wilson 1985; Hubbell and Foster 1986; see review by Chave 2004). The more similar the species are in their ecological performances, the longer it will take for the poorer competitor at a given food web position to be driven extinct; and this time to extinction can be quite long, even in a simple system. Moreover, the time to extinction for the poorer competitor may be

greatly extended if the community exists in multiple patches that are linked by dispersal of the component species (i.e. a metacommunity), and ecological conditions vary both spatially and temporally (e.g. Shmida and Ellner 1984; Tilman 1994; Chesson and Huntly 1997). As a consequence, when we examine real biological systems it is simply foolish to assume that all the species found together are in fact coexisting on local or regional scales (Shmida and Ellner 1984; Shmida and Wilson 1985; Pulliam 1988). Local communities and regional metacommunities are all most likely to be complicated mixtures of transient species on their way to extinction and coexisting species.

The importance of transient species and the role that ecological similarity plays in generating community structure is at the heart of the current debate over Hubbell's (2001) unified neutral theory of biodiversity (see also Bell 2001). This theory addresses the following question: What dynamics result in a system when all species are ecologically identical to one another? Although the ultimate equilibrium of this model had only one species present, the transient dynamics in reaching this ultimate ecological equilibrium may be very long. Moreover, patterns in rank species abundance and diversity predicted in this transient phase fit data from real communities extremely well (Hubbell 2001). This model has been extremely controversial, mainly because it postulates no coexistence mechanisms that would promote the maintenance of species richness (Chesson 2000; Chave 2004). However, it has been extremely stimulating as a counterpoint to the examination of coexistence mechanisms. Specifically, it has focused attention on the role of transient species in ecological systems, and brought to the fore the important roles that speciation and extinction dynamics can play on setting patterns of community structure (McPeck and Gomulkiewicz 2005; Leibold and McPeck 2006).

The coexistence and neutral perspectives on community structure represent the endpoints of a continuum along which ecological systems lie. Most systems probably are not at either of these extremes, but rather are complicated mixtures of coexisting and transient species. Shifts in the relative frequencies of transient and coexisting species may be largely driven by the types of species introduced by speciation and the dynamics of extinction. In the next section, I explore these issues using a simple model of competing species that occupy a system of patches connected by dispersal (i.e. a metacommunity). Species are introduced into the system via speciation, and are lost from the system through the extinction dynamics generated by species interactions. I vary the degree of ecological similarity among species in two ways to explore how these parameters influence the relative frequencies of coexisting and transient species over long time scales. Moreover, I use this model to generate predictions for

the patterns that various ecological scenarios leave in the fossil record and in molecular phylogenies. These predictions are then compared with real fossil and molecular phylogenetic data.

## MACROEVOLUTION IN A METACOMMUNITY MODEL

No local community exists in complete isolation. Patches are always demographically connected to one another via dispersal to some degree, and thus each local community will be imbedded in a larger metacommunity (Shmida and Ellner 1984; Shmida and Wilson 1985; Pulliam 1988; Hubbell 2001; Leibold *et al.* 2004, 2005). To explore how the degree of ecological differentiation among new and existing species may influence patterns in fossil and molecular systematic data, I explore the ecological and evolutionary dynamics of a simulation model of a simple metacommunity [all simulations used in this paper were written in JAVA™ v.1.5 (Sun Microsystems, Inc., Palo Alto, CA, USA, <http://www.javasoft.com/>)].

The metacommunity consists of some number of patches, each of which has a unique local environment. The environmental condition for patch  $i$ ,  $E_j$ , is determined by drawing a random number from a uniform distribution between 0.0 and 1.0; each patch receives a unique environmental value and maintains this value throughout a simulation run (i.e. the model has spatial but no temporal environmental variance). The population size of each species in a patch is regulated according to a discrete logistic equation,

$$N_{ij}(t+1) = N_{ij}(t)e^{\left(1 - \frac{\sum_i N_{ij}(t)}{K_{ij}}\right)}, \quad (1)$$

where  $N_{ij}(t)$  and  $K_{ij}$  are the abundance and carrying capacity, respectively, of the  $i$ th species in the  $j$ th patch at time  $t$ .  $K_{ij}$  is determined by the value of the environmental variable in that patch. The size of each population is regulated according to the total number of individuals of all species in a patch, but the species differ in carrying capacities. In this model, the species are symmetrical competitors (i.e. competition coefficients in the standard Lotka–Volterra competition equations are all equal to 1.0), and if only one patch exists, the species with the largest carrying capacity will eventually drive all others extinct (Charlesworth 1994).

After regulation, individuals of all species are dispersed among patches at the same propensity; a specified fraction of individuals of each species is removed from each patch and evenly distributed among all the other patches in the metacommunity. I assume no fitness costs to

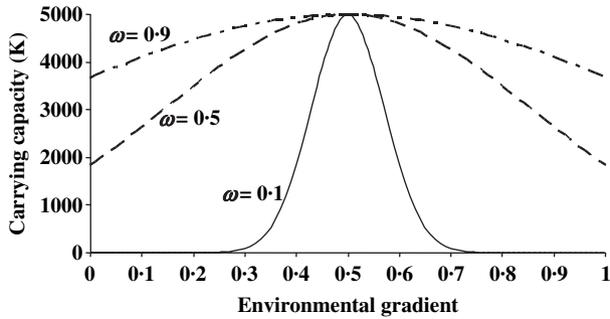
dispersal other than moving to a new patch with a different environmental value.

Species differ in how their carrying capacities ( $K_{ij}$ ) change along the gradient. I assume that the relationship between the environmental value and the carrying capacity of a species has a Gaussian form to permit each species the potential to have the highest carrying capacity on one portion of the environmental gradient. The relationship between  $E_j$  and  $K_{ij}$  used is

$$K_{ij} = K_{\text{opt}}e^{-\left(\frac{E_j - E_i^*}{\omega}\right)^2}, \quad (2)$$

where  $E_i^*$  is the point along the gradient where species  $i$  has its highest carrying capacity,  $K_{\text{opt}}$  is the carrying capacity at  $E_i^*$ , and  $\omega$  is the parameter determining the steepness with which the carrying capacity decreases away from the optimum (Text-fig. 1). With larger  $\omega$ , species with different  $E_i^*$  values would have greater overlap in their utilization of the environmental gradient, and their carrying capacities within any given patch would be more similar. Thus, the steepness of the change in carrying capacity along the environmental gradient influences the degree of ecological similarity among species within a patch.  $K_{\text{opt}}$  and  $\omega$  are assumed to be the same for all species, so species within replicates in these simulations differ only in the position of their optima along the gradient. Each species would be able to persist indefinitely and every patch would be a source (i.e. a place in which the species can maintain a population without continual immigration; Pulliam 1988) if it were the only species in the system. When multiple species are present, whether a particular patch is a sink (i.e. a patch in which the species can maintain a population only through continual immigration from other patches; Pulliam 1988) or source for a particular species, is determined by the properties of the other species present and the density-dependent interactions among them. Thus, in this model, species are driven to extinction solely by the ecological dynamics generated by interactions with the other species present in the system. I defined a species to have become extinct when its abundance in every patch was  $< 1.0$  [ $N_{ij}(t)$  was coded as a double precision real number].

Each simulation began by establishing one species at its carrying capacity in each patch, and a second species was started in only one randomly chosen patch at  $K_{ij}/100$ . Speciation events occurred at random with a specified probability for each iteration. At the beginning of each iteration, a random number was drawn from a uniform distribution. If a speciation event was deemed to have occurred, I randomly chose one of the extant species to be the progenitor of the new species. The new species was then created by drawing a random deviate from a normal distribution with zero mean and a specified standard deviation ( $\sigma_{E^*}$ ), adding this normal deviate to the



**TEXT-FIG. 1.** Representative shapes of the Gaussian function used to characterize the relationship between carrying capacity and the environmental gradient in simulations. Three curves are shown:  $\omega = 0.9$  (long and short dashed line),  $\omega = 0.5$  (dashed line) and  $\omega = 0.1$  (solid line). All three curves have  $K_{\text{opt}} = 5000$  and  $E^*_i = 0.5$  on the gradient.

progenitor's  $E^*_i$ , and establishing this new species in a randomly chosen patch at  $K_{ij}/100$ . This mode of speciation can be thought of as either sympatric speciation or allopatric speciation followed by secondary contact that is initiated by a single migration event into the metacommunity. (I also modelled other scenarios for speciation probabilities, e.g. defining speciation probability as a per-lineage parameter, and similar results were obtained.) The degree of phenotypic differentiation between progenitor and new species was manipulated by altering  $\sigma_{E^*}$ ; larger  $\sigma_{E^*}$  values permit greater differences in environmental optima between progenitors and new species. Thus, manipulating  $\sigma_{E^*}$  also influences the degree of ecological similarity among species by influencing their potential for colonizing areas, through speciation, along the environmental gradient that are better matches to their ecological capabilities.

I recorded a complete 'fossil' record of each replicate by recording the iteration of first appearance and extinction for all species in a replicate. The longevity of each extinct species was then calculated from these 'dates'. I also maintained a record of the phylogenetic relationships among extant species including ancestral splitting dates. This record is comparable with the phylogeny estimated from molecular data assuming a molecular clock. From this phylogeny I also estimated the 'ages' of all extant species as the date to the length of the external branch leading to each species. This crude estimate of a species' 'age' is routinely made from molecular phylogenies (see de Queiroz and Donoghue 1988). I recorded both of these historical records to determine whether characteristic patterns could be discerned from either or both that may provide some insight into the ecological conditions of the system.

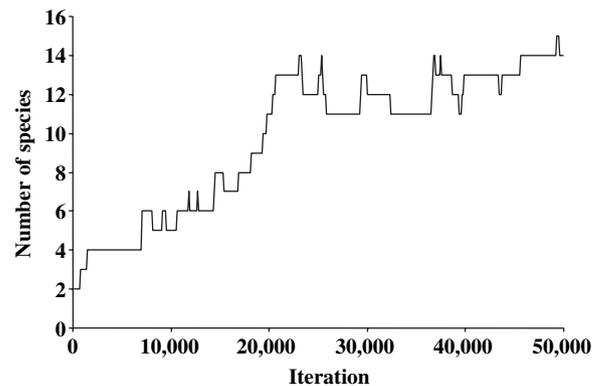
Because new species are continually being introduced via speciation and existing species are being lost via extinction, I ran each simulation for a fixed number of

iterations (50 000). Five hundred replicates of each unique parameter combination were performed. I simulated many parameter combinations, but for brevity, I present the results from only a limited set. In particular, I focus on manipulating two parameters:  $\omega$ , the steepness of the carrying capacity gradient around a species' optimal position; and  $\sigma_{E^*}$ , the parameter scaling the potential amount of differentiation of new species from their progenitor (see eq. 2). The results presented here are characteristic of those seen across the much larger set of parameter combinations I studied.

### Ecological patterns

Text-figure 2 shows the dynamics of a typical run. Initially, species richness increases as new species arise that can better utilize different areas of the gradient. Typically, somewhere in the 5000–20,000 iteration range, the system comes to a dynamic macroevolutionary equilibrium where species richness stabilized but species turnover continued (Text-fig. 2). This dynamic equilibrium is analogous to that described by island biogeography theory (MacArthur and Wilson 1967), but here speciation adds new species and the ecological interactions among species drive some to extinction.

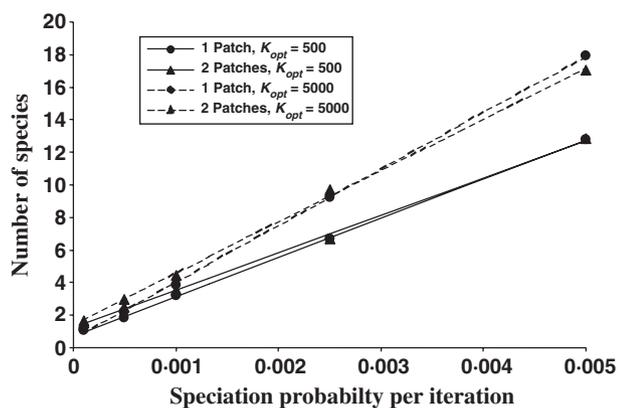
As expected, increasing speciation probability increases species richness (Text-fig. 3). Also, increasing population size at a species' optimal position on the gradient ( $E^*_i$ ) increases species richness (Text-fig. 3). Dispersal rate had no effect on species richness for almost all parameter combinations considered. In addition, consistent patterns in the relationship between species richness and the number of patches in the metacommunity are apparent, but the form on the relationship critically depends on  $\omega$  and



**TEXT-FIG. 2.** The dynamics in the number of species over 50,000 iterations of the model for one replicate. For this replicate, the metacommunity consisted of 20 patches, with  $\omega = 0.5$  and  $\sigma_{E^*} = 0.1$ , a speciation rate of 0.001 and a dispersal probability of 0.05.

$\sigma_E^*$  (Text-fig. 4). The effects of speciation probability and population size may seem intuitive, but from an ecological perspective, they are not necessarily so. First, if the ecological system defined by the species already present can support a given number of species, why should increasing the input rate of new species increase species richness (cf. MacArthur 1965)? Species that cannot coexist with others in the system should be driven extinct. And second, why should a system that can support more individuals have more species?

To explore the explanations for these results, I first consider the situation in which species' carrying capacities fall off sharply away from their optimum (e.g. when  $\omega = 0.1$  in the parameter combinations presented in this paper). Three outcomes can occur following the introduction of a new species: this new species can coexist with the species already present, it may be driven extinct, or it may persist and other species may become extinct. When new species can be quite differentiated from their progenitors along the gradient (e.g.  $\sigma_E^* = 0.1$ ), new species are more likely to colonize underused areas of the gradient (Text-fig. 4C). More patches mean that more of the gradient will be available for species to occupy, new species are more likely to have a patch in which they have the highest carrying capacity (i.e. a source patch) and thus more species can coexist (Text-fig. 4C). In addition, species that are destined to become extinct do so very quickly (Text-fig. 5), because species generally have relatively large differences in carrying capacities in all patches. With these parameters ( $\omega = 0.1$ ,  $\sigma_E^* = 0.1$ ), few species are transients at any one time. The frequency of transients is most easily demonstrated by following species richness after stopping the input of new species via speciation; species richness will drop as transients become extinct (Text-fig. 6). With  $\omega = 0.1$  and  $\sigma_E^* = 0.1$ ,



**TEXT-FIG. 3.** The average number of species after 50,000 iterations when speciation rate and  $K_{opt}$  are varied, and when the metacommunity consists of one or two patches. Each point is the mean of 500 replicates for that combination of parameters. In all replicates,  $\omega = 0.5$  and  $\sigma_E^* = 0.1$ , and species had a dispersal probability of 0.05.

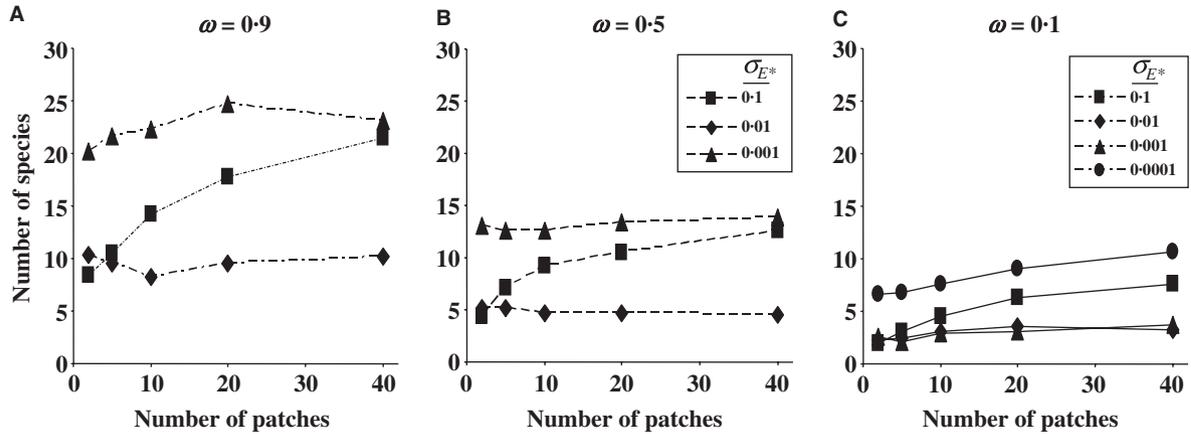
species richness decreases very little when speciation is stopped (Text-fig. 6C), because almost all species present in the system at any time are coexisting with one another.

Still focusing on  $\omega = 0.1$ , decreasing  $\sigma_E^*$  causes new species to be more similar to their progenitors. This has two consequences: (1) it decreases the likelihood that the new and progenitor species will be able to coexist but (2) it increases the time required for species to be driven extinct (Text-fig. 5). The interaction of these effects causes species richness to be a U-shaped function of  $\sigma_E^*$  (Text-fig. 4C). Initial decreases in  $\sigma_E^*$  from relatively large values (e.g.  $\sigma_E^* = 0.1$ ) primarily decrease the chances of coexisting, and so species richness initially decreases. At these intermediate values of  $\sigma_E^*$ , species richness increases little with patch number, because new species cannot differentiate enough to exploit relatively underused areas of the available gradient (Text-fig. 4C). As  $\sigma_E^*$  is decreased further to very small values, the chances of coexistence are at a minimum, but transient species persist longer because species are ecologically very similar (Text-fig. 6). As a result, species richness then increases as  $\sigma_E^* \rightarrow 0.0$ . Moreover, because coexistence by differentiating along the gradient is unimportant at extremely low values of  $\sigma_E^*$ , species richness is relatively high regardless of the number of patches (Text-fig. 4C).

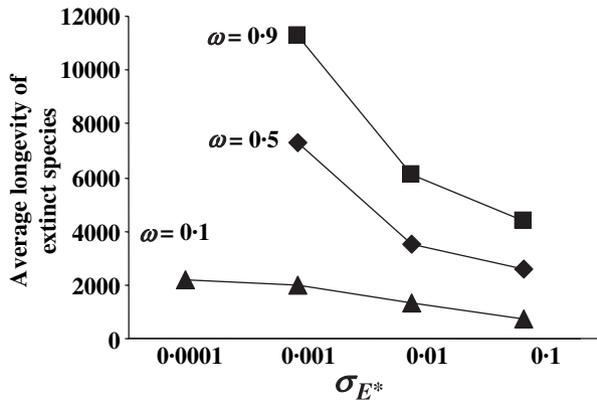
Altering the steepness of the carrying capacity gradient (i.e. changing  $\omega$ ) also strongly influences species richness through the dynamics of transients (Text-fig. 4). Making the carrying capacity gradient less steep (i.e. increasing  $\omega$ ; Text-fig. 1) causes the carrying capacities of species to be more similar within patches, and as a result more time is required for transient species to be driven extinct (Text-fig. 5). Consequently, transient species are more frequent at any time in systems with larger  $\omega$  values (Text-fig. 6). The consequences of changing  $\sigma_E^*$  described above are similar across all values of  $\omega$ , and in particular the U-shaped relationship of species richness with  $\sigma_E^*$  is apparent at all  $\omega$  values (Text-fig. 4). At relatively large values of  $\sigma_E^*$ , new species can colonize under-exploited areas of the gradient, and so species richness increases as the number of patches increases. As  $\sigma_E^*$  is decreased, species richness initially declines and becomes independent of the number of patches, but then increases as  $\sigma_E^*$  is further decreased towards 0.0. Thus, both smaller values of  $\sigma_E^*$  and larger values of  $\omega$  increase the frequency of transients in the system by lengthening the time required to drive them to extinction.

#### Macroevolutionary patterns

Altering the steepness of the carrying capacity gradient ( $\omega$ ) and the degree of differentiation of new species from their progenitors ( $\sigma_E^*$ ) changes the shapes of frequency distributions in macroevolutionary data. When the

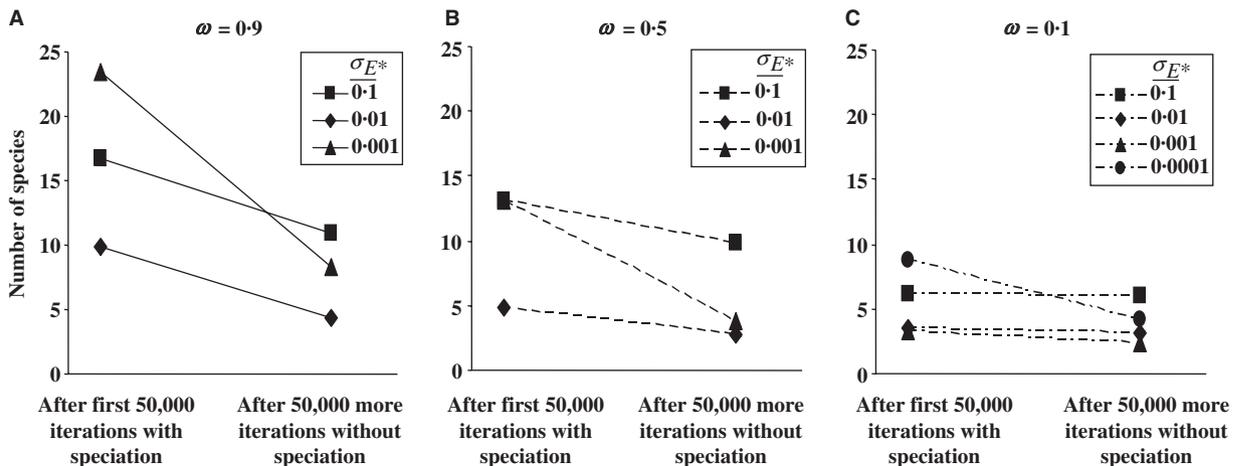


**TEXT-FIG. 4.** The average number of species present after 50,000 iterations under various combinations of number of patches,  $\omega$  and  $\sigma_{E^*}$ . The three panels show the results for different values of  $\omega$ . In each panel, lines connect symbols having the same value of  $\sigma_{E^*}$  for replicates having different numbers of patches. Symbols identifying  $\sigma_{E^*}$  are the same for panels A and B.



**TEXT-FIG. 5.** The average longevity for species that became extinct in 500 replicates of various parameter combinations of  $\omega$  and  $\sigma_{E^*}$ . All data shown here are for metacommunities having 20 patches, speciation probabilities of 0.001 and dispersal probability of 0.05.

carrying capacity gradient is steep (e.g.  $\omega = 0.1$ ), most species are rapidly driven extinct. The distribution of species durations recorded in the ‘fossil’ records of these systems has most species with very short durations, and the rest of the frequency distribution is relatively flat (see inset in panel for  $\omega = 0.1$ ,  $\sigma_{E^*} = 0.1$  in Text-fig. 7). The shapes of these distributions can be roughly characterized by the coefficient of variation [ $CV = \text{variance}/(\text{mean})^2$ ] for the data. If longevity in the fossil record or age of a taxon is not different from random, these data should show a negative exponential distribution with  $CV \approx 1.0$  (Cox and Lewis 1966). Frequency distributions that are more uniform have  $CV < 1.0$  (a uniform distribution has  $CV \approx 0.33$ ), and distributions with a greater frequency of younger age classes have  $CV > 1.0$ . With a steep carrying capacity gradient (e.g.  $\omega = 0.1$ ), all distributions have  $CV > 1.0$ . As the system is moved into areas of parameter



**TEXT-FIG. 6.** The average number of species after 50,000 iterations of simulations with speciation followed by 50,000 iterations without speciation. Other parameters are as in Text-figure 5. This figure shows the same parameter combinations as in Text-figure 4. The drop in species numbers is owing to the extinction of transient species during the second 50,000 iterations of simulations.

space where transient species become more common (increasing  $\omega$  or decreasing  $\sigma_E^*$ ), the longer duration of each transient in the system is reflected in the shift of the distribution for species having greater longevities, and a smoother decline in frequency with duration (e.g. panel showing results for  $\omega = 0.9$ ,  $\sigma_E^* = 0.001$  in Text-fig. 7). This is clearly seen in the change in distribution shapes and the decline of the CV towards 1.0 as  $\omega$  is increased and  $\sigma_E^*$  is decreased (Text-fig. 7).

These same features also influence the distribution of external branch lengths in phylogenies of the species extant at the end of simulations (Text-fig. 8). The distribution of external branch lengths is nearly uniform with  $\omega = 0.1$  and  $\sigma_E^* = 0.1$  (Text-fig. 8). As  $\omega$  is increased and  $\sigma_E^*$  is decreased, the distribution shifts to a greater frequency of younger species with the CV increasing towards 1.0. This shift in the distribution reflects the increasing prevalence of transient species in these areas of parameter space. Moreover, this shift towards the form of a negative exponential distribution suggests that the apparent speciation and extinction rates are becoming relatively constant over time (see review in Nee 2001).

## REAL FOSSILS AND PHYLOGENIES

These modelling results suggest that macroevolutionary data from real systems may reveal clues about the prevalence and importance of transient species and thus the positions of real systems along the coexistence/neutralism continuum (Text-figs 7–8). If so, what do real data of species longevities in the fossil record and extant species age distributions estimated from molecular phylogenies look like?

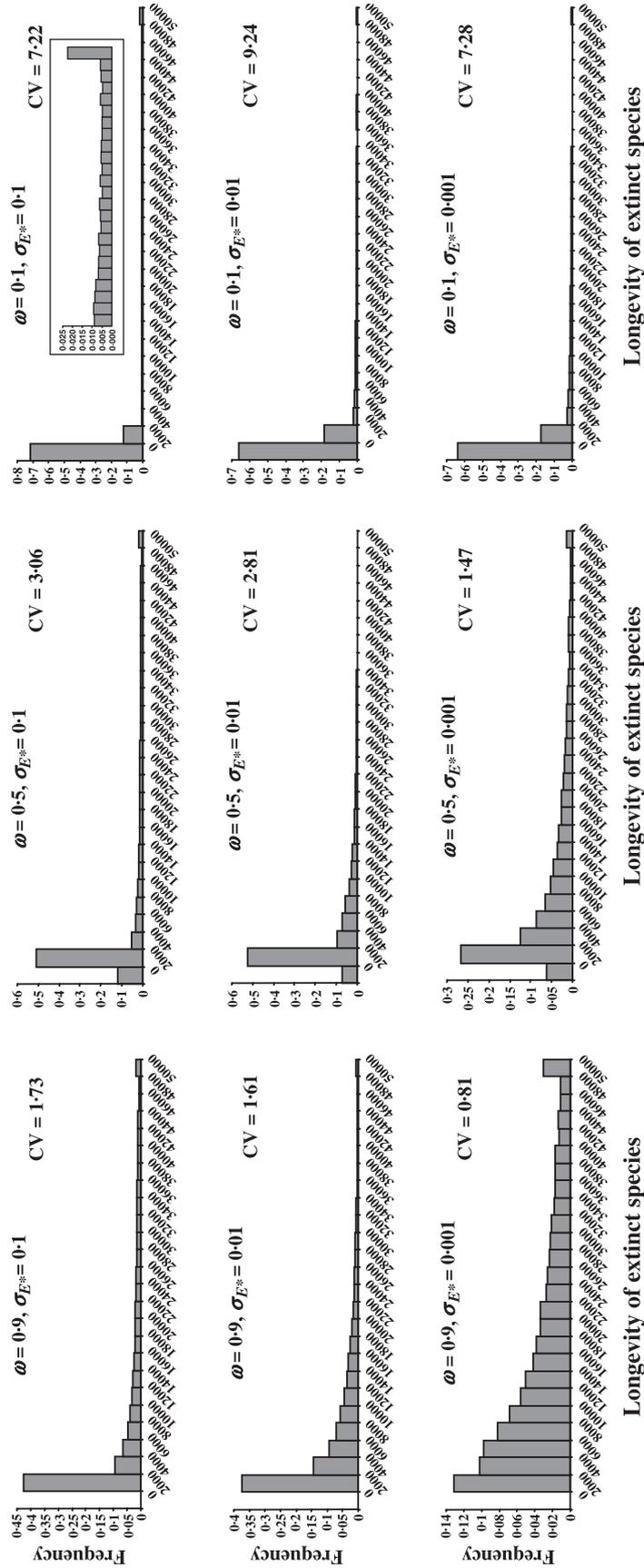
*Fossils.* I examined the distributions of taxon longevities in the fossil record using data from two public data sets. The first was the Sepkoski compilation for marine genera over the Phanerozoic (Sepkoski 2002). For this data set, I extracted first and last appearance dates for each genus, and then examined the frequency distributions for all genera in each of six diverse classes: Echinoidea, Crinoidea, Bivalva, Anthozoa, Gastropoda and Rhizopoda (primarily Foraminifera). The second data set I analysed was the Neptune public database of marine plankton from the Deep Sea Drilling Project and the Ocean Drilling Program. This database extends back *c.* 144 myr and contains species records from *c.* 250 drill holes scattered across the world's oceans. I accessed the Neptune data through the Paleobiology database portal (<http://paleodb.org/cgi-bin/bridge.pl?user=Guest&action=displayDownloadNeptuneForm>). Again, I downloaded first and last appearances for all species listed in the four major groups in the database: Radiolaria, diatoms, nannoplankton and Foraminifera. These two data-

bases have two major groups in common (Radiolaria and Foraminifera) and so comparing the results for these groups can help calibrate interpretations drawn from the two: note that the Sepkoski data set is coarser in both time and taxonomic resolutions.

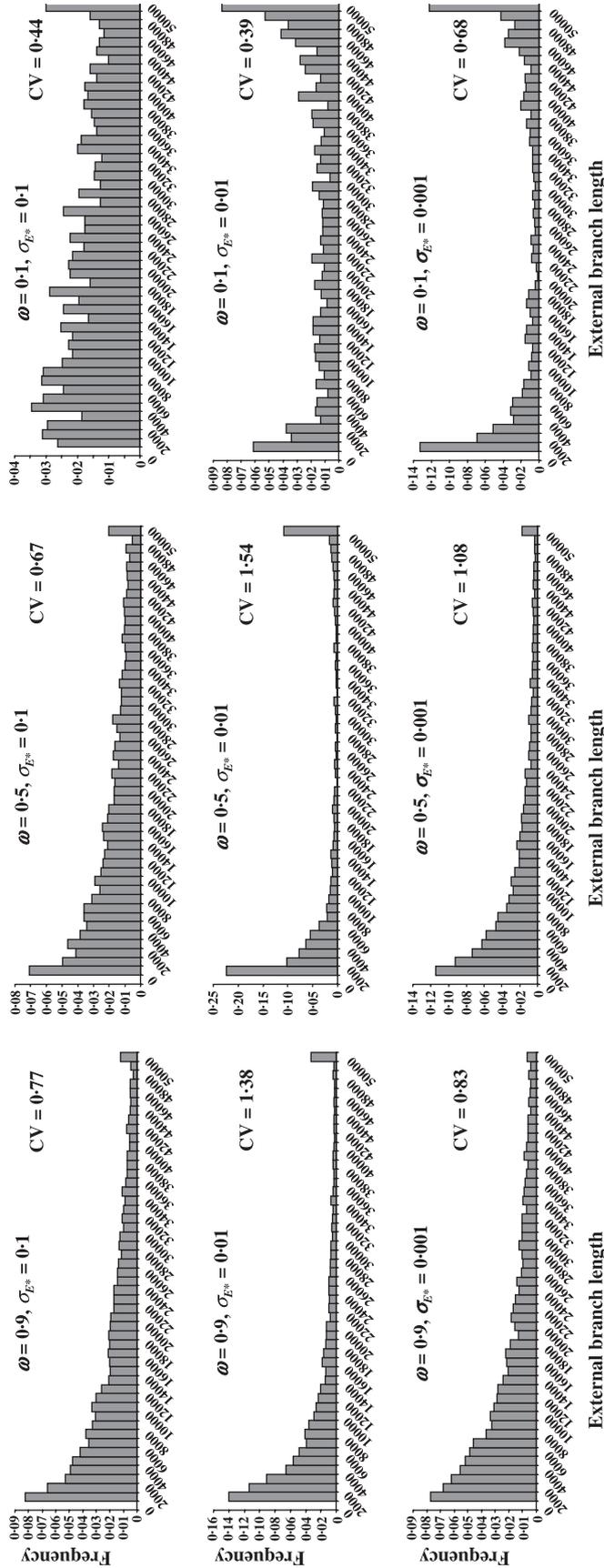
The frequency histograms resulting from both the Sepkoski and the Neptune database analyses showed decreasing frequencies with taxon longevity (Text-figs 9–10). For each major group examined, the Sepkoski database had the shortest longevity class with a frequency that was usually at least twice the size of the next highest frequency class (Text-fig. 9). As a result, the CVs for all taxa were substantially greater than 1.0 (all tests for CV = 1.0 had  $P < 0.0001$ ). By contrast, in the Neptune data set, the Radiolaria and Foraminifera had CVs  $< 1.0$  (Radiolaria,  $\chi_{630}^2 = 551.6$ ,  $P < 0.05$ ; Foraminifera,  $\chi_{604}^2 = 477.98$ ,  $P < 0.001$ ), the diatoms had a CV value  $> 1.0$  ( $\chi_{611}^2 = 829.7$ ,  $P < 0.05$ ), and the nannoplankton had a CV not different from 1.0 ( $\chi_{801}^2 = 826.5$ ,  $P > 0.20$ ). The disparity in the CV values for Radiolaria and the Foraminifera between these two data sets suggests that the coarser taxonomic and time sampling of the Sepkoski data set may cause a greater frequency of single occurrence in these data and thus inflate the CV (see Foote and Raup 1996).

*Phylogenies.* I also examined the estimated ages of extant animal species from published molecular phylogenies. I surveyed the literature for papers reporting the results of species-level molecular phylogenies. The criteria for inclusion were the following: (1) the paper must present a figure of a molecular phylogeny constructed using a technique either that applies a molecular clock assumption to the data or in which branch lengths are proportional to genetic distances among taxa; (2) the figure must also present a scale to convert branch lengths into either time or substitutions/site; and (3) at least 50 per cent of the putative members of the clade must be included in the analysis. For papers that only presented a figure giving substitutions/site, I applied the further restriction that the sequences must be from mitochondrial genes, so that I could apply the standard molecular clock estimate of 2.3 per cent divergence/million years to the branch lengths (Brower 1994). I extracted the lengths of all external branches (i.e. the length to the first ancestral node for each species) from trees after converting branch lengths to estimates of time. This project is ongoing, and the results presented here are only a preliminary analysis of the data.

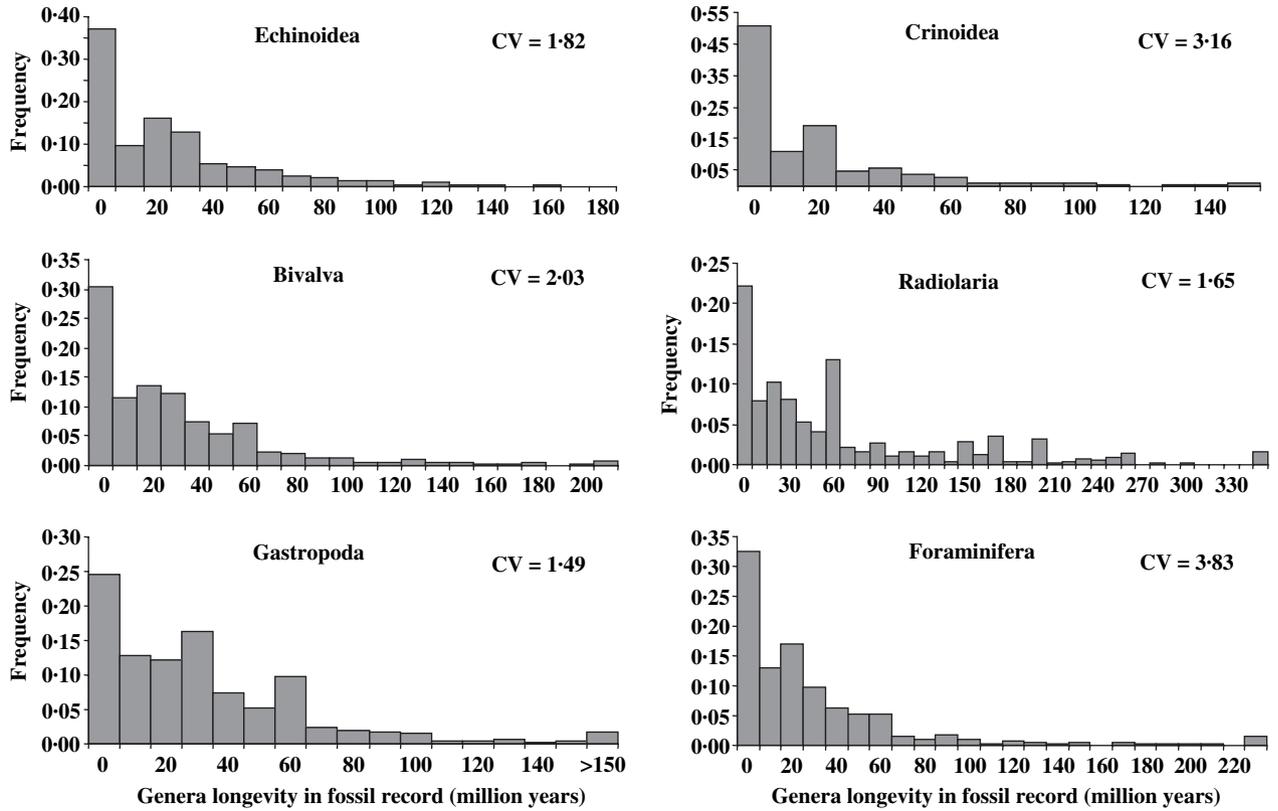
The data presented are based on phylogenies of 46 arthropod clades (including Hexapoda, Chelicerata, Decapoda, Crustacea and Anostraca), 108 chordate clades (including most major Vertebrata groups) and 11 mollusc clades (including Gastropoda and Bivalva). These analyses yielded phylogenetic species-age estimates based on exter-



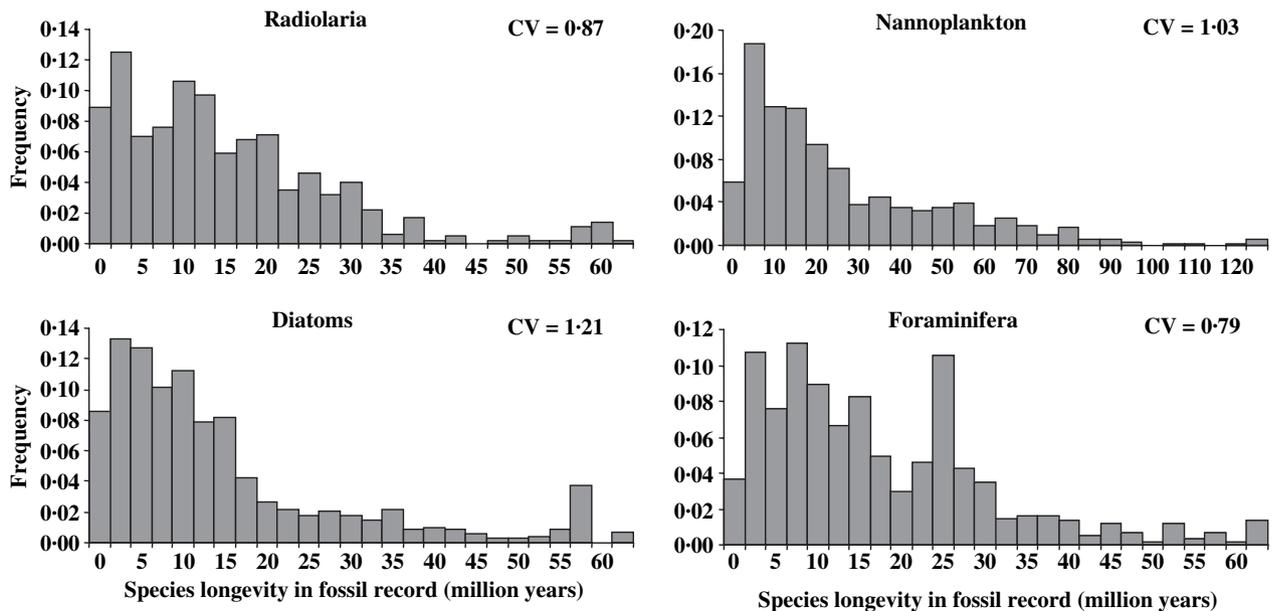
**TEXT-FIG. 7.** The frequency distributions of the longevities of extinct species for 500 iterations of various parameter combinations of  $\omega$  and  $\sigma_{E^*}$ . Other parameters are as in Text-figure 5. The coefficients of variation (CV) for each distribution are given in each panel.



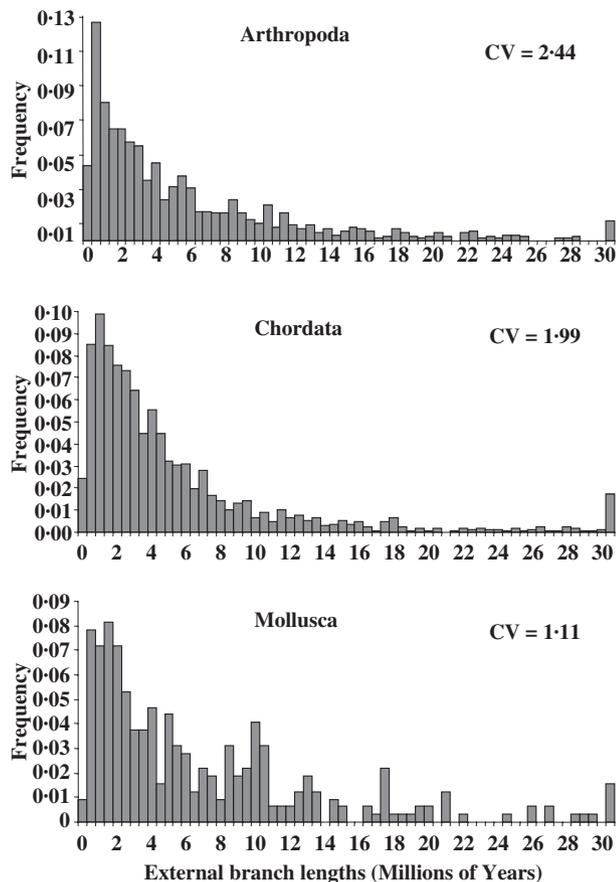
**TEXT-FIG. 8.** The frequency distributions of external branch lengths taken from the phylogenies among the extant species at the end of simulations for 500 iterations of various parameter combinations of  $\omega$  and  $\sigma_{E^*}$ . Other parameters are as in Text-figure 5. The coefficients of variation (CV) for each distribution are given in each panel.



**TEXT-FIG. 9.** Frequency distributions of longevities of genera for six major groups extracted from the Sepkoski compilation of marine fossils (Sepkoski 2002). The coefficients of variation (CV) for each distribution are given in each panel.



**TEXT-FIG. 10.** Frequency distributions of species longevities for four major groups extracted from the Neptune Paleobiology database (<http://paleodb.org/cgi-bin/bridge.pl?user=Guest&action=displayDownloadNeptuneForm>). The coefficients of variation (CV) for each distribution are given in each panel.



**TEXT-FIG. 11.** The frequency distributions of external branch lengths extracted from published species-level phylogenies for clades in three animal phyla. The coefficients of variation (CV) for each distribution are given in each panel.

nal branch lengths for 888 arthropod species, 1667 chordate species and 264 mollusc species (Text-fig. 11). All three phyla had the frequencies declining with increasing species ages (Text-fig. 11), and with arthropods and chordates having CV values significantly greater than 1.0 (Arthropoda,  $\chi^2_{884} = 2161.9$ ,  $P < 0.001$ ; Chordata,  $\chi^2_{1665} = 3325.7$ ,  $P < 0.001$ ) and molluscs having a CV not different from 1.0 ( $\chi^2_{262} = 292.2$ ,  $P > 0.05$ ).

## DISCUSSION

Spatial and temporal variation in ecological conditions across the landscape is the norm (Kolasa and Pickett 1991), and the landscape presents a variegated and shifting mosaic of ecological opportunities and problems for species (Hutchinson 1958; Thompson 2005). New species do not come into existence *ex nihilo*; new species arise in an ecological and evolutionary context. New species will be introduced into any particular ecological mosaic by

immigration of species that have originally diversified and adapted in another biogeographical area, and by range expansions following speciation (sympatric and allopatric) within the biogeographical area defined by the metacommunity under consideration. The model considered in this paper explores the dynamics of the ecological sorting process as species are introduced to a system. Given that these dynamics critically depend on the degree of ecological differentiation among established and new species, it is imperative that we understand whether and how ecological differences among species are generated.

The results presented here suggest that the ecological similarity among species being introduced via speciation can have profound effects on the resulting communities (Text-fig. 4). The major effects of ecological similarity flow from the slowing of times to extinction for transient species (Text-fig. 5). As a result, transient species persist longer and are thus a greater proportion of total species richness at any one time (Text-fig. 6). In this model, two parameters govern the degree of ecological similarity among species:  $\omega$  and  $\sigma_E^*$ . These parameters influence ecological similarity in different ways, and I consider the effects of each in turn here.

The  $\omega$  parameter influences the ecological similarity of species across the entire gradient by scaling the change in carrying capacity along the environmental gradient (Text-fig. 1). When the carrying capacity gradient is steep (i.e.  $\omega$  is small), the carrying capacities of any two species in most patches will be quite different if their optimal positions on the gradient are different. To understand the effect of the carrying capacity gradient on time to extinction, consider a system with only one patch. Here, the species with the higher carrying capacity (call this species 1 in patch 1 with  $K_{11}$ ) will drive the other (species 2 in patch 1 with  $K_{12}$  such that  $K_{11} > K_{12}$ ) extinct, because species 1 can invade and increase in population size even when species 2 is at  $K_{12}$  (Charlesworth 1994). The population of species 1 will stop increasing when the summed abundances of both species equals  $K_{11}$  (eq. 1). At this point, species 2 will decline at a rate proportional to  $r(1 - K_{11}/K_{12})$ . Note that increasing population abundance at the optimal carrying capacity (i.e. the parameter  $K_{opt}$  in eq. 2) increases the time to extinction (Text-fig. 3) by increasing the change in population size required on average to drive a species extinct. As the carrying capacity gradient becomes shallower, the ratio of carrying capacities will decrease, which slows the rate of decline for species 2 and thus increases the time to its extinction. This is the effect that causes greater species richness in multipatch systems by lengthening the persistence time of transients (Text-fig. 4).

With  $\geq 2$  patches in the system, species coexistence is possible because different species can have the highest carrying capacities in different patches. This also necessar-

ily establishes source–sink dynamics as the governing feature of the model, in the sense of the original definitions of a source as a patch in which a species can maintain a population without continual immigration and of a sink as a patch in which a species cannot maintain a population without continual immigration (Pulliam 1988). Two or more species can coexist in this model if patches are available in the system such that (1) each species has at least one source patch in the system (i.e. where it has the highest carrying capacity) and (2) immigration by other species into this source patch does not depress its fitness to a degree where it cannot maintain a population (i.e. the mass effects of Shmida and Ellner 1984; Shmida and Wilson 1985; Pulliam 1988; Loreau and Mouquet 1999; Mouquet and Loreau 2002; Amaresekare 2003). Thus, the number of coexisting species increases with the number of patches in the system, because more of the gradient is exposed for species to utilize (Text-fig. 4). However, the number of patches has a much smaller effect on the frequency of transient species in the system. This difference is evident by comparing the changes in species richness with number of patches when  $\sigma_E^* = 0.1$  against  $\sigma_E^* = 0.001$  (Text-fig. 4). The frequency of transients is much higher and changes much less with patch number in the latter than in the former (see Text-fig. 6).

What do we know about species' carrying capacity gradients (i.e.  $\omega$ ) in real systems? Results of many of the classic experimental studies of competitive segregation along an ecological gradient would suggest that carrying capacity gradients are quite steep, because these experiments show that superior competitors at different points along the gradient effectively can exclude poorer competitors (e.g. Connell 1961; Hairston 1980). However, the pattern of sharp segregation that these experimental studies would imply is usually not evident in broader surveys of entire assemblages (e.g. Whittaker 1975; Roff *et al.* 1981; Hubbell 2001). Also, if local species interactions limit the number of locally coexisting species, an asymptote is expected in the relationship between local and regional species richness ('saturated' communities of MacArthur 1965; Cornell 1985a, b; Cornell and Lawton 1992). However, almost all compilations of data across a wide taxonomic range produce relationships having local species richness increasing as a constant proportion of the regional species pool (e.g. corals: Cornell and Karlson 1996; Witman *et al.* 2004; zooplankton: Shurin *et al.* 2000; terrestrial insects: Cornell 1985a, b; Stevens 1986; Hawkins and Compton 1992; fish: Hugueny and Paugy 1995; birds: Ricklefs 1987; Wiens 1989; cross-taxa comparisons: Caley and Schluter 1997; but see Aho and Bush 1993 for an example of a saturating relationship in parasites of fishes). Ricklefs (1987) and Cornell and Lawton (1992) have reviewed how dispersal and ecological mechanisms causing spatiotemporal heterogeneity can generate

these 'unsaturated' community patterns. A similar, non-asymptotic relationship between local and regional species richness is also expected if the frequency of transients in each system is high. In fact, in this case it would be conceptually more appropriate to argue that local assemblages are 'super-saturated' with species because more species are present than can coexist locally.

The parameter  $\sigma_E^*$  also influences the ecological similarity of species in the system, but by influencing the optimal positions of new species on the gradient relative to their ancestors. Species with more similar optimal positions along the gradient (i.e.  $E_i^*$ ) will have carrying capacities that are more similar to one another in all patches along the gradient. If  $\sigma_E^*$  is relatively large, new species will typically be ecologically differentiated from their progenitors when they enter the system, and species richness increases with  $\sigma_E^*$  because species can differentiate along the available gradient. In effect, a large  $\sigma_E^*$  value is comparable with ecological speciation (Schluter 2000). When speciation occurs as a by-product of a daughter lineage filling an unoccupied area of the environmental gradient [e.g. lizards diversifying to utilize different areas in trees (Losos 1990, 1992; Losos *et al.* 1998), damselflies invading ponds and lakes with different types of predators (McPeck and Brown 2000; Stoks and McPeck in press), fish diversifying to fill different feeding niches in lakes (Bernatchez and Dodson 1991; Nagel and Schluter 1998; Lu and Bernatchez 1999; Turgeon *et al.* 1999), true fruit-flies adapting to living on different host plants (Feder *et al.* 1995; Filchak *et al.* 2000)], species will automatically be capable of coexisting in all local communities in the biogeographical region in which this niche is available.

However, most speciation events are probably not accomplished by filling new or unoccupied niches. Speciation is the process that generates reproductive isolation, and reproductive isolation can be generated by myriad processes, many of which involve no necessary adaptive ecological differentiation at all (Dobzhansky 1937; Mayr 1942; Carson 1985). These speciation mechanisms may generate the full spectrum of degrees of ecological divergence, from almost none (e.g. changes in genital morphology; Eberhard 1988) to large differences (e.g. hybridization; Rieseberg 1997), but without regard to whether these differences promote coexistence among taxa. Consequently, different modes of speciation may have characteristic  $\sigma_E^*$  values. The greater species richness of clades in which sexual selection is common (Barracough *et al.* 1995; Møller and Cuervo 1998; Arnqvist *et al.* 1999; Stuart-Fox and Owens 2003) and the prevalence of cryptic sympatric species in many taxa certainly suggest that other speciation modes in addition to ecological speciation are important for the creation of biodiversity. In addition, a similarly wide spectrum of ecological diversification is possible when local adaptation in allopatry is the

cause of speciation (Rice and Hostern 1993; McPeck 1996), which will play a crucial role in the dynamics of range boundaries and secondary contact between lineages (Pease *et al.* 1989; Brown *et al.* 1996; Kirkpatrick and Barton 1997; García-Ramos *et al.* 2000; Case *et al.* 2005). Consequently, the continual introduction and persistence of transient species in ecological systems may be the norm and not the exception.

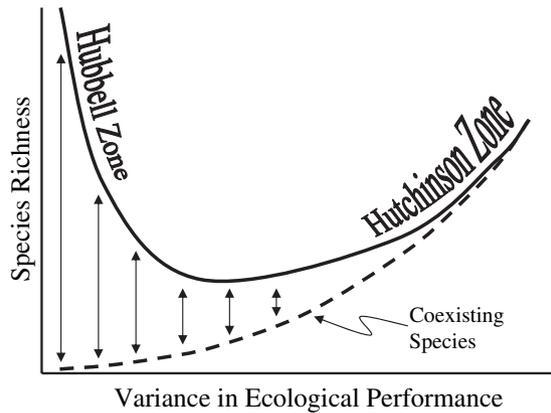
Systems with different  $\omega$  and  $\sigma_E^*$  values also had different signatures in fossil records and molecular phylogenies (Text-figs 7–8). Comparisons of these simulation results with real data on species durations from the fossil record and external branch lengths from molecular phylogenies suggest that transient species are prevalent in real ecological systems as well. The distributions of external branch lengths from molecular phylogenies showed high frequencies of young species with a smooth decreasing frequency with increasing age (Text-fig. 11). In fact, for the three phyla considered, 22 per cent of all extant species are estimated to be <1 million years old, and 37 per cent to be <2 million years old, based on this method of characterizing species ages. The coarseness of the taxonomic and temporal resolution in the Sepkoski fossil data set may make the resulting distributions of taxon durations appear to have a substantially greater frequency of very short durations than is true (Foote and Raup 1996). The frequency distributions derived from the Neptune fossil data were much more smoothly and gradually decreasing functions of duration (Text-fig. 10). The smooth declines of both the fossil and the molecular distributions are similar to those derived from model parameter combinations that gave communities with high frequencies of transient species. It is interesting to note that Hubbel's (2001) model of exact ecological equivalence predicts distributions in ecological data (e.g. rank-abundance distributions) that are quite similar to real data as well.

The consistency of real fossil and phylogenetic data with the results from areas of parameter space where transient species are prevalent suggests that understanding diversity patterns in today's biota cannot be based solely on mechanisms of coexistence. These results suggest an ecological world in which species diversity patterns are temporally dynamic, with continual species input, turnover and flux. From a theoretical perspective, this implies that ecological communities are not at stable equilibrium in which the dynamics of each system promotes the long-term persistence of all species present (cf. MacArthur 1972; Chesson 2000). If the conclusions drawn from this analysis are true, they do not, however, justify the wholesale abandonment of the theoretical edifice of coexistence in favour of the 'neutral' perspective. Rather, what these conclusions do suggest is that we need to expand our theoretical framework to one that incorporates both types of mechanisms (see also McPeck and Gomulkiewicz 2005;

Leibold and McPeck 2006). Some species are most certainly maintained in the system by coexistence mechanisms, some have only recently been introduced to the system (evolutionarily speaking) and still others are being driven extinct by species interactions.

In fact, because modes of speciation may play a critical role in defining the relative importance of transient species, various taxa may systematically differ in the likelihood that species are transients or coexisting within the same community. At one extreme, taxa in which ecological speciation is predominant should have few transient taxa because speciation is a by-product of ecological differentiation. Large ecological differences are generated between species at the time of speciation, and coexistence mechanisms should thus be clearly operating in these taxa because in most cases the mechanisms promoting coexistence are those that also acted as selection pressures to generate the ecological differentiation. Thus, their ecological performances should co-vary with ecological gradients, and species should display negative correlations in performance along these gradients when compared with one another (i.e. they should display trade-offs between species) (Chesson 2000). In contrast, taxa in which new species are generated via speciation modes that accomplish reproductive isolation with little or no associated ecological differentiation (e.g. sexual selection) should have a high frequency of transient species in communities. The ecological performances of species in these taxa will also co-vary with ecological gradients, but positive correlations should be apparent in their performances along these gradients (Chesson 2000). For other speciation modes that may generate intermediate levels of ecological differentiation, fewer species are expected because fewer are produced that can coexist with existing species from the start, and the time to extinction for these species is also expected to be shorter. This difference is, in fact, equivalent to varying  $\sigma_E^*$  in the simulation models, which predicts a U-shaped relationship of overall species diversity across these types of speciation mechanisms (Text-fig. 12).

Fossil and phylogenetic data have limitations, and thus the application of such data to these questions must be made with a clear understanding of the caveats that apply. The density of taxonomic sampling will influence inferences that can be derived from molecular phylogenetic data. Likewise, taxonomic and taphonomic constraints will limit the applicability of much fossil data. Obviously, fossil compilations from higher resolution fossil deposits (e.g. planktonic microfossils continually buried in ocean sediments) like the Neptune data will more accurately reflect species and community parameters over time. Also, species assignments are usually not possible for most fossils, and palaeontologists continue to debate whether data compiled at higher taxonomic levels (e.g.



**TEXT-FIG. 12.** Conceptual figure of the effects of the variance in ecological performance generated at the time of speciation on overall species diversity. The variance in ecological performance generated at the time of speciation is conceptually equivalent to the  $\sigma_E^*$  parameter of the simulation models of this study. Species richness has an overall U-shaped distribution along this axis. The solid line shows the total number of species and the dashed line shows the number of species coexisting. The difference between these two lines is the number of transient species. To the right (identified as the 'Hutchinson Zone') most species are coexisting, and to the left (identified as the 'Hubbell Zone') most species are transients.

the generic compilation of Sepkoski 2002) have any use in evaluating hypotheses at the species level (e.g. this study and Sigor 1990; Sepkoski 1998; Forey *et al.* 2004). Such limitations are real but no types of data are problem-free: the limitations must simply temper the conclusions drawn from their application. Moreover, no single test or data set will conclusively support any hypothesis. Our best understanding of community structure will come from the combined support of many, albeit individually imperfect, tests using observational and experimental data drawn from as many different vantages as possible.

One major environmental feature omitted from the model presented here is temporal ecological variability. Temporal variability occurs on various time-scales (e.g. single perturbation events to diurnal and seasonal cycles, to major climatic trends over millions of years) and over a range of magnitudes (e.g. from daily temperature changes and shifts in resource abundances to the consequences of asteroid impacts). Although some coexistence mechanisms are propagated by specific forms of temporal ecological variability (Chesson 2000; Amaresekare 2003), temporal variability also favours the persistence of transient species in systems by various means. For example, temporal variability may continually reshuffle competitive dominance hierarchies among species, and so transients will persist longer because they may be competitively superior during some times (Abrams and Holt 2002

reviewed a number of such mechanisms). Also, perturbations to a system may depress the abundances of all species, thus reducing the strengths of species interactions and thereby slowing or stopping the decline of transients (e.g. Connell 1978; Huston 1979). When various forms of temporal variability were introduced into the model presented here, the frequency and persistence of transients increased as expected (McPeck, unpublished). Thus, the results presented here are probably conservative with respect to the importance of transients.

Major environmental perturbations that cause mass extinctions (e.g. volcanism, asteroid strikes, rapid climate change), namely extremes of temporal ecological variability, have also been deemed to set palaeontology apart from the other disciplines examining the Earth's biodiversity [e.g. Gould's (1985) third tier]. It may be true that precisely predicting the winners and losers in such calamities is impossible. However, these perturbations act through their effects on ecosystems, and careful analyses have repeatedly identified phenotypic, demographic and ecological properties of species and clades that influence their success or failure and that shape the recovery of systems afterwards (reviewed in, e.g., Jablonski and Sepkoski 1996; Roy *et al.* 1996; Erwin 2001; Jablonski 2001). In fact, the communities we study today may be structured as much by species' properties that allowed them to weather Pleistocene climate change as by their adaptations to interact with one another today.

More generally, integrating insights about macroevolutionary processes from palaeontology and molecular systematics provides community ecology with a very different perspective for understanding the development of community structure. Previous considerations of how natural communities are 'assembled' have focused on invasion-dominated systems where all species in the community are drawn from a pre-existing species pool (e.g. Diamond 1975; Post and Pimm 1983; Drake 1990, 1991; Drake *et al.* 1993; Lockwood *et al.* 1997; Loreau and Mouquet 1999). This type of analysis may be applicable to some systems (e.g. islands with high rates of immigration from nearby continents) but not to others in which speciation directly contributes new species to local and regional species pools. Previous analyses of community assembly also beg the question of where the species in the pool came from in the first place. For many systems, speciation and extinction dynamics define the path to the community structure we see today. Moreover, competitive exclusion can be an ongoing process that may effectively never reach completion. Ecologists should embrace the possibility of 'communities in transition between equilibria' of ecological and evolutionary determination, and the fact that the 'processes responsible for the addition and removal of species from local communities may be

mostly indifferent to the number of species present' (Ricklefs 1987, p. 170). Melding of concepts of community ecology and macroevolution provides the necessary foundation for exploring the causes of the distributions and abundances of species.

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