CHAPTER THIRTEEN

Ecological influences on the temporal pattern of speciation

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Introduction

Nearly all speciation events in animals seem to involve spatial separation of populations, at least in the initial stages of divergence, and we have few compelling examples of sympatric speciation (Mayr 1947; Coyne & Orr 2004). Given the requirement of geographical isolation, following Mayr (1947), we consider three steps that limit the rate at which new species form. First, gene flow between populations must be restricted. Second, populations diverge in various traits that generate reproductive isolation. Third, populations must expand ranges. This third stage is essential, for without range expansions, newly produced species would remain geographical replacements of one another, severely limiting the total number of species that can be produced from a common ancestor.

Stage 2, that is the generation of reproductive isolation, is usually taken to be synonymous with speciation (Coyne & Orr 2004). Ecological conditions experienced by different taxa can drive and accelerate the rate of attainment of reproductive isolation ('ecological speciation', Schluter 2001; Rundle & Nosil 2005), thereby accelerating speciation. This has been the focus of much recent study and is one of the main topics considered in this volume. However, ecological influences on any of the three stages – not just the acquisition of reproductive isolation – can limit the rate at which new species form (Mayr 1947).

In this chapter, we first summarize various ecological and nonecological factors that may limit each of the three stages of speciation. Then we ask if speciation events are temporally distributed in some way, which is predicted from many ecological models of speciation. In particular, ecological factors may promote speciation more rapidly early in adaptive radiation rather than later, because range expansion is easier at this time due to fewer competitors (Mayr 1942, 1947), or because reproductive isolation evolves more quickly (Rice & Hostert 1993; Schluter 2000, 2001). Gavrilets and Vose (2005, this volume) also find a burst of speciation early in adaptive radiation in their simulations, partly because as species evolve to become specialists in one particular niche, they can

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less easily evolve to occupy alternative niches when they become available. If any of these factors apply in adaptive radiation, speciation should slow through time. In the second part of the chapter we test this prediction, by investigating patterns of speciation through time, based on an analysis of a collection of molecular phylogenies of birds.

Stages of speciation

In this section we briefly review ecological and nonecological influences on the three stages of speciation, as envisaged by Mayr (1942, 1947), drawing on some examples from birds by way of illustration.

Stage 1. *Populations become geographically isolated*. A geographical barrier, such as a water gap for land birds, is one common nonecological way that populations may be separated, but intervening ecologically unsuitable habitat in which it is difficult to survive and reproduce is another (Mayr 1947). Alterations in the distribution of preferred habitats in response to climate change can lead to range fragmentation, setting the stage for population divergence and speciation (Wiens 2004). For example, Keast (1961) and Cracraft (1986) showed how distributions of related bird species fit postulated climatic refugia in Australia. The ongoing debate about causes of speciation in the Amazon is focused on when and where both nonecological and ecological barriers appeared (reviewed by Moritz *et al.* 2000; Newton 2003, his chapters 10 and 11; Aleixo 2004). Nonecological factors include wide rivers and islands created by a rise in sea level, and ecological factors include both pre-Pleistocene and Pleistocene climatic refugia.

Sometimes the barriers, whether ecological or nonecological, may be absolute. Other times they may be leaky, with migrants occasionally dispersing across the barrier. In this case, ecological factors in both the recipient and the source population can cause gene flow to be reduced to zero. For example, immigrants from one population may have low fitness in the alternative environment, especially in competition with residents (Mayr 1947; Nosil *et al.* 2005). Alternatively, selection in the source population may favour reduced dispersal propensity, as in the evolution of flightlessness on islands (see below).

Stage 2. *Geographically separated populations diverge*. In the hypothesis of ecological speciation, populations occupying different environments experience divergent selection pressures, causing evolution of traits that affect reproductive isolation (Schluter 2001; Rundle & Nosil 2005; Funk *et al.* 2006). Traits may diverge in response to both natural and sexual selection pressures. For example, body size and habitat choice may evolve in response to natural selection pressures, whereas traits used in communication and mate attraction may diverge in response to shifting targets of sexual selection, for example, some environments favour transmission of songs at different frequencies than others (Slabbekoorn & Smith 2002). Such differences often affect premating isolation when populations spread into sympatry. Habitat differences automatically result in many members of one incipient species not encountering members of another, and in many taxa songs are used to recognize conspecifics. Differences may also lead to postmating isolation, because hybrids are often different from either parent in ecologically relevant traits (e.g. body size) and thus may be at a disadvantage, at least in competition with the parental species. Finally, hybrids may also suffer intrinsic loss of fitness (i.e. developmental problems leading to infertility or inviability), and this may sometimes arise as a side effect of adaptation of the parental taxa to ecological conditions (Funk *et al.* 2006). Muller (1942) noted that adaptation to different temperature regimes could lead to developmental problems for hybrids, irrespective of the temperature they experience.

Ecological speciation can be compared to alternative nonecological factors that might drive reproductive isolation. Although the role of genetic drift and founder effects has been emphasized in the literature on nonecological speciation (Gavrilets 2004; see Coyne & Orr 2004 for a critique), an alternative and potentially important mode of nonecological divergence is through the occasional production of a mutation that is favoured on the genetic background on which it arises. This includes mutations that may be favoured under sexual selection (Gulick 1890), sexual conflict (Rice 1998) and intragenomic conflict (Hurst *et al.* 1996; Burt & Trivers 2006). For example, consider a new mutation that increases the frequency at which it is itself transmitted from parent to offspring, for example, by killing sperm carrying the other nonmutated form (meiotic drive). Such a mutation may rapidly increase in a population, and different mutations may spread in different populations. Interference between such mutations could cause postmating reproductive isolation. Whilst such mechanisms may be important in speciation, empirical evidence is only just accumulating (Orr *et al.* 2004; Coyne & Orr 2004).

A major difference between the nonecological model described here and ecological speciation is that gene flow is much more homogenizing in the nonecological model. Under the nonecological model, a new mutation may be favoured everywhere in the species range, and even a trickle of gene flow between two populations greatly slows the rate at which they diverge. The favoured mutation rapidly increases in the population in which it arises and once it is fixed in that population it will be introduced into the other population with every immigrant, giving the mutation a high chance of spreading through the whole species (Barton 1979). In order for populations to become substantially divergent in this model, either a long period of complete separation is needed so that many different mutations can accumulate in each population which then interfere with each other, or else the mutation rate has to be so high that different mutations arise more or less simultaneously in different parts of the species range (Kondrashov 2003). Alternatively, in the ecological model, populations occupy different environments and alleles that are favoured in one place may be disfavoured in another place. In this scenario populations will diverge if selection is strong enough to overcome any retarding effect of gene flow.

Stage 3. *Species expand ranges enabling renewed rounds of geographical isolation.* In the absence of range expansions any successive speciation events take place within smaller and smaller areas. When area is small, the likelihood that a new barrier will arise within the area is low, and if a barrier does appear, small population sizes may lead to extinction (Rosenzweig 1995). Thus, without range expansions, opportunities for speciation decay through time.

Range expansions may result from nonecological factors, specifically the disappearance of barriers. In addition, many ecological factors affect the chances of a population getting to, and becoming established in, a new location. Range expansions are likely to be easiest when individuals colonize an environment that is generally similar to that of the ancestral environment, but has few competitors, predators, etc. (Mayr 1947). Many examples (Schluter 2000) make a clear case for the absence of competitors in enabling a population to persist in an unusual niche, eventually leading to substantial divergence from its ancestor. Striking examples come from oceanic islands. Darwin (1859, p. 391) noted that 'islands are sometimes deficient in certain classes and their places are apparently occupied by other inhabitants; in the Galápagos reptiles and in New Zealand giant wingless birds, take the place of mammals'. This implies that speciation is limited by ecological opportunity, and in particular the ability to persist in a new location that is already occupied by a superior competitor (Mayr 1947).

If filling up the environment with species represents an important impediment to range expansion, it should eventually be reflected by the failure of sister species to diverge sufficiently ecologically to enable them to spread into each other's range. Indeed, in many groups, closely related species are often geographically separated or show limited overlap (Jordan 1905; Allen 1907; Phillimore *et al.* 2008); together they form a superspecies composed of ecologically and morphologically similar species (Amadon 1966; Mayr & Diamond 2001), which may often be quite old (Weir & Schluter 2007). The best explanation for the failure of ecologically similar sister species to penetrate into each other's range seems to be competitive exclusion, coupled with adaptation to environmental factors that give the competitive edge to each species in its own range. Goldberg and Lande (2006) show that hybridization may limit expansion of sister species, because individuals at the leading edge of the range mate with members of the other species, producing low fitness offspring. However, this as well as some other nonecological explanations reviewed in Price (2008) seem less generally applicable than ecological competition.

Although dispersal may often be limited by ecological conditions in foreign locations, the rate of establishment in new locations can also vary among taxa (summarized in Price 2008, chapter 7). Phillimore *et al.* (2006) find that across families of birds a crude measure of dispersal propensity exhibits a strong positive correlation with diversification (speciation–extinction) rate. Families with many species, such as parrots and finches, include species that on average tend to be dispersive. In species-poor or monotypic families, such as the ostrich, the constituent species tend to have low dispersal capabilities. In so far as ecological conditions drive the evolution of dispersal, they have a strong influence on the probability of speciation.

Easy dispersal (stage 3) and the restriction of gene flow (stage 1) are flip sides of one another and the most favourable situation for ongoing speciation must be when dispersal and range expansion are followed by the prevention of further interchange between locations. Sometimes ecological factors may produce this combination, resulting in the generation of many species. This is seen in the evolution of flightless rails (Olson 1973; Trewick 1997; Livezey 2003). First, a flying ancestor is able to disperse into and throughout the archipelago (stage 3 in our outline), but subsequent loss of flight eliminates dispersal between the islands of the archipelago and evolution of flightlessness likely gives residents an advantage in competition with immigrants (stage 1). The result is that each island population then evolves independently (stage 2). It is possible that every reasonable-sized island in the Pacific has or had its own endemic species of flightless rail and at least five flightless species appear to have been present on Mangaia (Steadman 2006).

Finally, we note that nonecological and ecological factors may operate at different stages. For example, nonecological factors, such as some processes of sexual selection that lead to reproductive isolation (stage 2) may result in the production of ecologically similar species competitively excluded from each other's range (stage 3; West-Eberhard 1983).

Temporal patterns of speciation

Although multiple factors clearly affect the rate at which new species are formed, in the theory of adaptive radiation, speciation rates are high early on and slow down later. This is implied in common definitions of adaptive radiation (Simpson 1953; Schluter 2000). For example, according to Schluter (2000, p. 10) adaptive radiation is 'the evolution of ecological and morphological diversity within a rapidly multiplying lineage'. Because lineages cannot multiply rapidly for long, the implication is that speciation must slow through time. On entry into a new location or after a mass extinction, rapid divergence from a single lineage to exploit a diversity of resources may accelerate ecological speciation, as well as present the opportunity for frequent successful range expansions. As the environment fills up, ecological speciation slows, and range expansions become less easy.

Studies of young adaptive radiations, such as fish in postglacial lakes and Darwin's finches, provide supporting evidence for an association of rapid speciation with ecological divergence (Schluter 2000, 2001). We ask here if the predicted slowdown develops in older species radiations.

Tests of slowdown in molecular phylogenies

Patterns of species diversification through time can be assessed using time-calibrated molecular phylogenies. The basic idea is to tally the total number of lineages in the tree as a function of time, starting at the root (where there are two lineages) up to the present day (where the number of lineages equals the number of species). Under a null model of constant probability of branching through time, and no extinction (the 'pure-birth' model), the expected increase in the logarithm of the number of lineages against time follows a straight line (Nee *et al.* 1994a; see also Ricklefs, this volume). In the null model, variation in the so-called γ-statistic (Pybus & Harvey 2000) follows a known distribution (a normal distribution with a $\text{mean} = 0$ and a $\text{standard deviation} = 1$). A large negative value of γ allows one to reject the pure birth null hypothesis, and is taken to imply that speciation rate has slowed towards the present. It has been suggested that the presence of a slowdown towards the present could result from accelerated extinction (Zink *et al.* 2004). However, this is only expected if extinction is highly nonrandom (e.g. if one member of a sister pair consistently goes extinct); simulations show that a slowdown is highly unlikely under a model of random (accelerating) extinction (Weir 2006, Rabosky & Lovette 2008). Thus, the γ statistic provides a reasonably strong test for a slowdown in speciation rate, provided branch-lengths in the phylogeny adequately represent time (Phillimore & Price 2008).

A large positive value of γ (i.e. an increasing rate of lineage accumulation towards the present in the reconstructed phylogeny) rejects a model of constant probability of speciation without extinction, but the pattern can arise in two ways. First, the speciation rate may have increased over time. Second, whenever extinction is present, reconstructed phylogenies (i.e. those that do not include fossil data) should show accelerated cladogenesis towards the present. This is because more recent extinctions remove few potential descendants in the reconstructed phylogeny, whereas older extinctions remove many more (Nee *et al.* 1994b; Ricklefs, this volume).

As described in more detail in Phillimore and Price (2008), we selected 45 bird clades at the genus to family level, for which more than 65% of all species have been sequenced for mitochondrial protein coding genes. We reconstructed each phylogenetic tree using a relaxed clock Bayesian method implemented in *Beast* (Drummond *et al.* 2006). We set the mean rate of molecular evolution to be 1% per lineage per million years and a $\text{GTR} + \text{I} + \Gamma$ model of nucleotide substitution (Weir & Schluter 2007). An advantage of using a relaxed clock approach is that the tree can be rooted without requiring an outgroup. We sampled trees from the posterior distribution, and for all sampled trees calculated γ based on

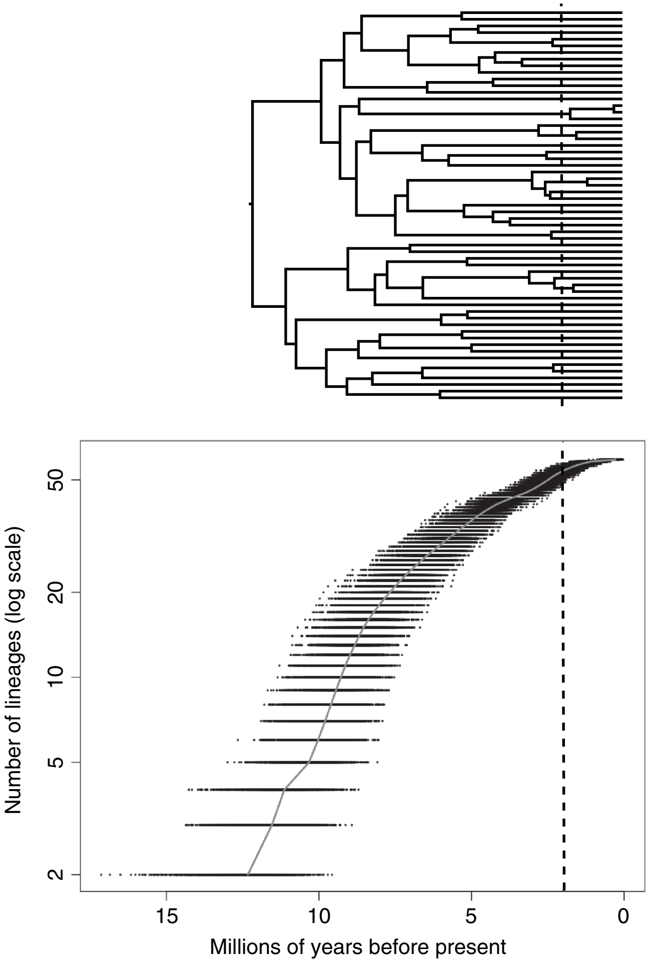

Figure 13.1 Estimated phylogeny and a lineage-through-time plot (on a semi-log scale) for warblers in the *Phylloscopus* and *Seicercus* genera, based on mitochondrial sequences in Johansson *et al.* (2007). The phylogeny was obtained using the Bayesian relaxed clock method in the program *Beast* (Drummond *et al.* 2006; described further in Phillimore & Price 2008). The lineage-through-time plot is based on a sample of 2000 trees from the posterior distribution; the line connects the median values at each value on the y axis. The γ statistic is calculated for each of the posterior topologies from the root up until 2 million years before the present and has a median value of -3.33, indicating a highly significant slowdown ($P < 0.01$). Eleven of the 70 species in this clade are missing and, after correcting for this, $\gamma = -2.96$.

internode distances between the root of the tree and the last node that lies earlier than 2 million years. We set a cut-off of 2 million years because lineage splitting more recently may be under-recorded (especially under the biological species concept; Avise & Walker 1998), or over-recorded (as a result of excessive splitting of distinctive populations; Isaac *et al.* 2004). An example of a phylogeny and the corresponding lineage through time plot for the *Phylloscopus* and *Seicercus* clade is shown in Fig. 13.1. We obtained a value of γ for each tree sampled from the posterior distribution using the *LASER* R library (Rabosky 2006) and used the median value as an estimate of slowdown for the phylogeny. We corrected all γ values for the number of present-day species absent from the phylogeny using methods outlined by Pybus and Harvey (2000) and Harmon *et al.* (2003), because incomplete taxon sampling can generate apparent slowdowns (Pybus & Harvey 2000).

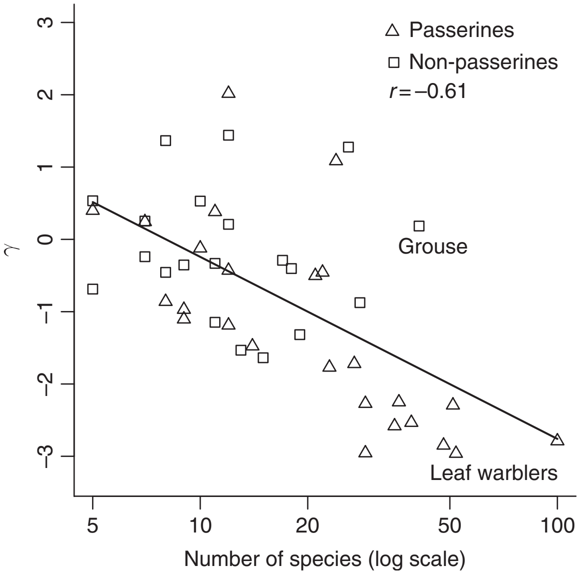

Figure 13.2 Plot of γ estimated from the root of the clade to the last bifurcation event prior to 2 million years versus clade size, where clade size is the total number of lineages estimated to be present 2 million years ago (and ignoring all species not sequenced) for 45 bird clades (from Phillimore & Price 2008). The least squares regression line is $b = -1.09 \pm 0.22$, $P < 0.001$. The Old World leaf warblers (*Phylloscopus* and *Seicercus*), whose phylogenetic relationships are illustrated in Figure 13.1, are indicated.

Many of the larger phylogenies have significantly negative γ values, implying a slowdown (Fig. 13.2). The Old World leaf warbler clade in Fig. 13.1 is the most extreme example. Conversely, many of the smaller clades have γ values that are close to zero, or even positive. In fact, if one considers that (1) many clades that have not been analysed tend to be small and (2) small clades tend to have positive γ values, then we surmise that the average avian clade may actually show a γ value that is close to zero or positive. Thus, across clades as a whole we find no evidence that slowdowns are the norm; very young clades show a speedup, which compensates for the slowdown in old clades.

These patterns might be expected in an adaptive radiation model; as clades get larger their available niche space becomes filled making it increasingly difficult for further speciation events. However, the same pattern is also expected from a model of uniform probability of diversification through time (Raup *et al.* 1973; Phillimore & Price 2008). Because of the exponential growth inherent in diversification, a large clade is produced when, by chance, many speciation events happen early in the clade's history, and a small clade is produced when, by chance, few speciation events happen early. Subsequently, both large and small clades regress towards a universal average rate, resulting in a slowdown in large clades and a speedup in small ones. This is a regression effect (Kelly & Price 2005) that operates over timescales of many millions of years. The patterns can be easily demonstrated by simulation (Phillimore & Price 2008).

A way to see why a correlation of slowdown with clade size should arise under the uniform probability model is through analogy with coin tossing. Here 'Heads' results in a lineage-splitting event in a given time interval and 'Tails' indicates a failure to speciate. For simplicity, extinction is not allowed. Imagine that five coin tosses result in five heads, hence five lineage-splitting events early in diversification. This lucky clade has already produced six lineages and the probability is high that the clade will quickly grow to be large. On the other hand, suppose that those five coin tosses all gave tails, hence no speciation, and the clade is on a trajectory to be small. In the next time interval, the large clade will on average produce three splitting events, whereas the small clade will on average split half the time: the rate of splitting has decreased in the large clade and increased in the small one. Regression towards the mean is particularly powerful in phylogenies that grow under a constant rate process, because as time goes on the increase in the number of lineages results in a more precise estimate of the universal diversification rate.

Different clades may well have different rates of diversification. This seems likely, if only because the number of species in a particular clade is correlated across different regions of the world (i.e. some clades consistently have more species in a region than other clades, Ricklefs, this volume). However, simulation studies show that even if net diversification rates differ between clades, a uniform probability of speciation within clades will generate a negative correlation between γ and clade size, provided extinction rates are relatively low (Phillimore & Price 2008). Simulations also show that when the extinction rate is high the correlation between clade size and slowdown is lessened. In the extreme when extinction is set equal to speciation there is no correlation (Phillimore & Price 2008). This appears to be because, when extinction rates are high, most of the rapid early cladogenesis is eroded in the reconstructed phylogeny, and all early lineages but one or two go extinct (see Fig. 14.2 in Ricklefs, this volume). In addition to the reduction in the correlation between γ and clade size, as extinction becomes more important, the values of γ themselves become generally positive; i.e. there is an upturn in cladogenesis rate on the reconstructed phylogeny. Thus if extinction is high, the presence of negative γ values in real datasets are likely to imply real slowdowns in speciation.

The pattern of slowdown in large clades is expected under constant speciation–extinction models, whenever the extinction rate is not high. Constant rate models form a simple hypothesis, so the question is, can we distinguish the observed pattern from that of constant rate? Here we suggest three approaches, based on (1) correlations with clade age, (2) correlations with geographic range attributes and (3) a comparison of the strength of slowdowns observed in large clades versus those expected by chance. All tests used the data for the bird clades shown in Fig. 13.2.

Clade age

Among the clades analysed in Fig. 13.2, age to the root varies from an estimated 4.52 million years to 24.88 million years (mean = 11.33 ± 4.63 SD). γ is not

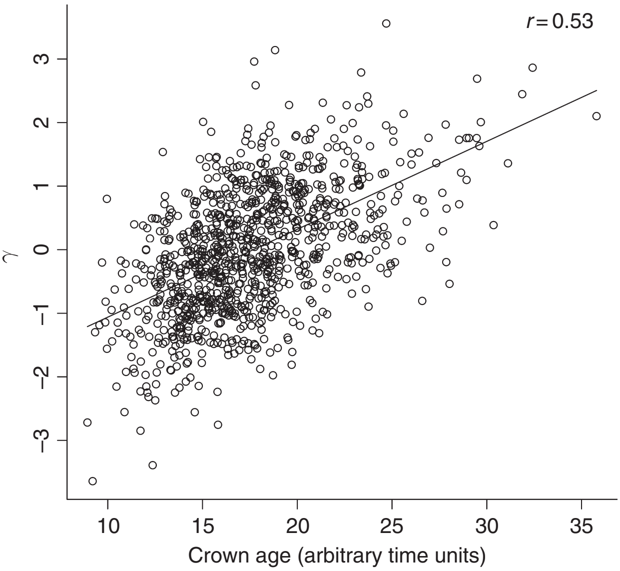

Figure 13.3 Plot of γ versus crown age obtained from 1000 pure birth simulations of phylogenies containing 50 species in *Phyl-o-gen* (http://evolve.zoo.ox.ac.uk/software.html?id=phylogen; provided by A. Rambaut). The parameters used were $b = 0.2$, $d = 0$ and clade size = 50 species.

correlated with clade age ($r = 0.02$, $P = 0.91$). However, when clade size is held constant, the partial correlation of clade age with γ is positive ($r' = 0.29$, $P < 0.05$) (the correlation and partial correlation (holding age fixed) of clade size and γ are − 0.64 and − 0.67, respectively). In a model of constant probability of birth or birth–death, a positive association of γ with clade age is expected, i.e. relatively young clades should show a slowdown (see Fig. 13.3). This is because clades that reach a certain size quickly are likely to have experienced above average initial speciation rates, and hence will later show slowdowns, whereas clades that reach a certain size slowly are likely to have had below average initial speciation rates, and hence will later show a speedup. In the adaptive radiation model the opposite pattern is expected. If clades experience an initially high opportunity for speciation, which declines or ceases once a certain number of species exist, then the older the clade the stronger the expected slowdown. Thus the results of this test are in accord with the predictions of the random speciation model and do not appear to support those of the adaptive radiation model.

Correlates with sympatry and other aspects of range size

In the adaptive radiation model an important cause of speciation slowdown is a failure of species to expand their ranges and come into sympatry, because of ecological competition from their close relatives. This model leads to three predictions. First, because it should become increasingly difficult for additional species to establish sympatric distributions, we predict a pattern of increased slowdown in association with the maximum number of co-occurring

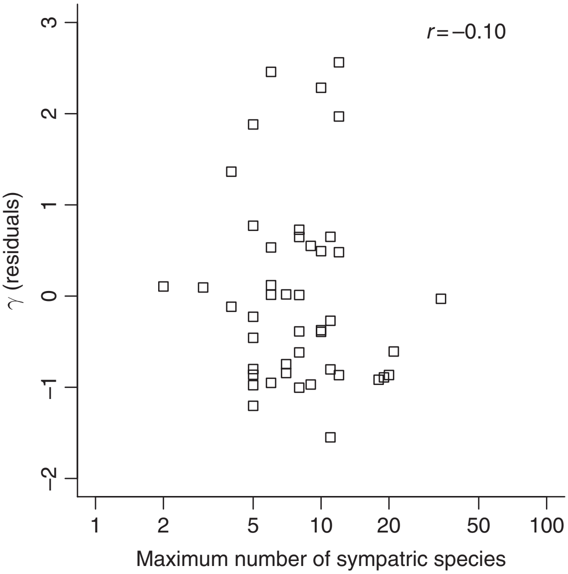

Figure 13.4 Plot of γ (residuals from the multiple regression on clade size [ln transformed] and clade age) versus number of sympatric species. Number of sympatric species is estimated as the maximum number of species that are present in a single grid cell (approximately 96 km by 96 km) across the world (from Orme *et al.* 2005, 2006; see Figure 13.5 legend for details).

(sympatric) species in a clade. Second, clades with a circumscribed geographic range should show strong slowdown if the total number of species that can coexist is limited (Ricklefs 2006; Ricklefs, this volume). Third, if range expansion is the rate-limiting step, then smaller average ranges for the species in a clade should correspond to a stronger slowdown (a more negative γ).

After controlling for clade size and age we found no correlation of γ with either the maximum number of species in sympatry (Fig. 13.4; cf. Weir's (2006) finding for a sample of Amazon clades) or total geographical range size of the clade (Fig. 13.5, left). The relationship between species mean range size and γ was significant (Fig. 13.5, right, $b = -0.09 \pm 0.041$ se, $P < 0.05$). However, the slope was of the opposite sign to that predicted under adaptive radiation reasoning; stronger slowdowns were associated with larger range sizes. We suggest that the negative relationship between average range size and γ reflects the signature of recent allopatric speciation. Unless post-speciation range expansion is very rapid, clades that have experienced high rates of recent allopatric speciation are likely to contain species with ranges that are smaller on average (Phillimore *et al.* 2006).

The power of the tests may be low and overall evidence is weak, but more generally the tests point in the direction of a slowdown being attributable to the signature of constant probability of diversification. It would be worthwhile constructing other tests that use traits that are not *a priori* expected to correlate with speciation under the constant-probability model. For example, dispersal propensity or body size could be tested for their correlation with slowdown, after controlling for clade age and clade size.

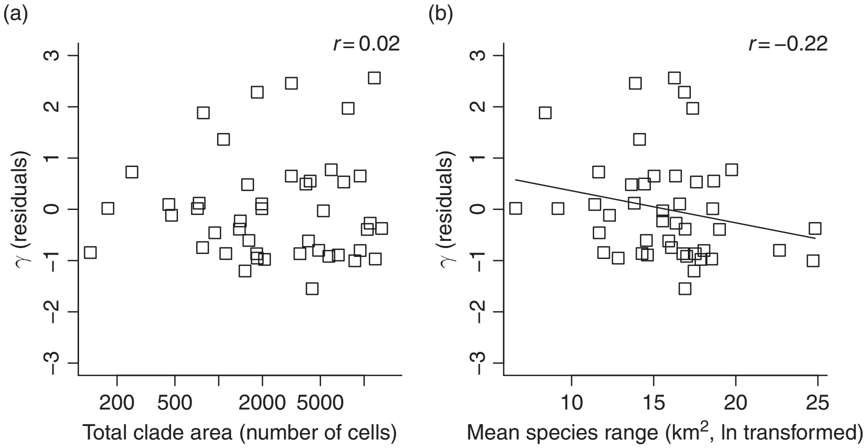

Figure 13.5 (a) Plot of γ (residuals from the multiple regression on clade size [ln transformed] and clade age) versus total clade area. Total clade area was calculated from a global dataset of bird species ranges projected on a Behrman equal area grid in which grid cells were approximately 96 km by 96 km in size (Orme *et al.* 2005, 2006). Area was estimated as the total number of cells in which a clade member was present. (b) Plot of γ (residuals from the multiple regression on clade size [ln transformed] and clade age) versus the mean range size of the species in a clade. Range sizes were obtained from a global database of species distribution shape-files (Orme *et al.* 2005). Range sizes (in km^2) were transformed by the exponent 0.2 to normalise the data prior to obtaining the arithmetic mean (Phillimore *et al.* 2007). Note that species ranges are based on the taxonomy of Sibley and Monroe (1990, 1993), whereas in some instances our phylogenetic reconstructions are based on more recent taxonomy.

Strength of slowdowns

A final test is to ask if the pattern of slowdown in the data (Fig. 13.2) is stronger than that predicted from the constant rate models. We asked whether the frequency of strong slowdowns (defined as γ values < -1.645) in large clades (those containing ≥ 15 species) departs from the null expectation under a constant rate model (Phillimore & Price 2008). We found that across a wide parameter space (simulation duration and the ratio of speciation to extinction were both varied), strong slowdowns were significantly more frequent than expected. Indeed, when the death rate is nonzero the probability that a constant rate model produces the observed frequency of strong slowdowns in large clades is infinitesimal. Studies on fossils indicate that extinction rates in many groups are high and may approach speciation rates (Alroy, this volume), so the slowdowns in Fig. 13.3 do seem to reflect a deterministic slowing of speciation towards the present.

Discussion

A slowdown in cladogenesis has been regularly found in studies of single phylogenies and has often been interpreted in terms of adaptive radiation and niche filling (Nee *et al.* 1992; McKenna & Farrell 2006; Weir 2006; Price 2008). Although others have suggested slowdowns result from nonrandom extinction (Zink & Slowinski 1995; Zink *et al.* 2004), or episodic appearances of multiple barriers (Zink & Slowinski 1995; Lovette & Bermingham 1999; Kozak *et al.* 2005), niche filling limiting range expansions is also often implied in these examples. We show here that slowdowns appear when speciation follows a model of constant probability of speciation through time. Some tests yielded results that did not support the adaptive radiation model but were consistent with this model. However the presence of strong slowdowns in large clades are in accord with a model of density-dependent speciation. Ricklefs (this volume) notes that evidence for density-dependent regulation is also implied by a lack of correlation between clade age and clade numbers in birds, at least for clades considered at and around the family level. As Ricklefs also notes such regulation could be driven either by an increase in extinction or decrease in speciation as species accumulate. Our analysis of lineage-through-time plots suggests that a decrease in speciation rate is an important contributor.

There is quite strong evidence for a very high – and unsustainable over long periods – speciation rate in association with ecological opportunity, such as following mass extinctions (Foote 1997) or in young archipelagos such as the Galápagos islands (Schluter 2000, 2001). Some Pleistocene radiations on continents also seem to be exceptionally rapid, such as the production of 81 species of *Lupinus* in the Andes during the last 2 million years (Hughes & Eastwood 2006). These observations fit models of what is to be expected in the early stages of adaptive radiation (Gavrilets & Vose 2005, this volume), i.e. when a single founding species enters a new environment. Those models predict a slowdown. Our results suggest that such slowdowns are a real feature of large clades.

We draw two main conclusions from the analysis. First, several temporal patterns in diversification rates can be explained on the basis of a model of constant probability of speciation or diversification. Speciation is affected by very many factors including occasional extinctions that create new ecological opportunities, appearance of habitat that can be exploited by multiple lineages (rather than a single lineage that rapidly diversifies), the strength and persistence of barriers, chance dispersal events, and the occasional evolution of traits within lineages that affect speciation probability. If these factors operate more or less independently, then a random pattern of speciation through time is expected (Raup 1977). The second conclusion is that the presence of exceptionally rapid speciation in some young radiations, coupled with the evidence for strong slowdowns in large clades, support models of ecological controls on the rate at which new species form. It seems likely that both more or less continuous species turnover through time, plus a process of adaptive radiation followed by niche filling, contribute to patterns of speciation through history (Nee *et al.* 1992; Ricklefs, this volume).

Ecological controls on speciation may affect the speed at which reproductive isolation develops, but a main factor limiting speciation is likely to be changes in the ease of range expansions. Range expansions are an essential requirement for ongoing allopatric speciation. We suggest that those factors that affect the ability of new populations to become established and persist in local communities are likely to have an important influence on regional speciation rates.

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