

The Ecological Dynamics of Clade Diversification and Community Assembly

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ABSTRACT: Clades diversify in an ecological context, but most macroevolutionary models do not directly encapsulate ecological mechanisms that influence speciation and extinction. A data set of 245 chordate, arthropod, mollusk, and magnoliophyte phylogenies had a majority of clades that showed rapid lineage accumulation early with a slowing more recently, whereas a small but significant minority showed accelerated lineage accumulation in their recent histories. Previous analyses have demonstrated that macroevolutionary birth-death models can replicate the pattern of slowing lineage accumulation only by a strong decrease in speciation rate with increasing species richness and extinction rate held extremely low or absent. In contrast, the metacommunity model presented here could generate the full range of patterns seen in the real phylogenies by simply manipulating the degree of ecological differentiation of new species at the time of speciation. Specifically, the metacommunity model predicts that clades showing decelerating lineage accumulation rates are those that have diversified by ecological modes of speciation, whereas clades showing accelerating lineage accumulation rates are those that have diversified primarily by modes of speciation that generate little or no ecological diversification. A number of testable predictions that integrate data from molecular systematics, community ecology, and biogeography are also discussed.

Keywords: clade diversification, extinction, macroevolution, metacommunity, phylogenetic rates, speciation.

Communities of species on both local and regional scales were assembled over evolutionary time to result in the systems that we study today. During this assembly process, lineages diversified to produce new species and new clades

by myriad speciation processes (Dobzhansky 1937; Mayr 1942; Howard and Berlocher 1998; Coyne and Orr 2004; Gavrillets 2004). However, not all new lineages persisted to the present: many lineages have become extinct because of temporal changes in abiotic conditions (e.g., climate change) or interactions with other lineages in the ecological systems in which they are embedded (Raup 1991; Lawton and May 1995). Thus, the ecological dynamics of community assembly define the macroevolutionary processes that shaped patterns of clade diversification (e.g., Ricklefs 1987, 1989; Ricklefs and Schluter 1993; McPeck and Brown 2000; Stoks and McPeck 2006).

When considered in this ecological context, speciation and extinction dynamics of component clades are not expected to be constant. For example, a lineage may initially diversify in a relatively empty ecological milieu (e.g., when a species evolves a new key innovation, enters a new “adaptive zone,” or colonizes a relatively empty environment with few ecological competitors [Simpson 1944, 1953; MacArthur 1965; Walker and Valentine 1984; Schluter 2000; Gavrillets and Vose 2005]). Speciation rate may thus initially be high as the clade ecologically diversifies to fill the available niche space, but speciation rate should slow and eventually cease as more niches become occupied (MacArthur 1965; Rosenzweig 1978; Pimm 1979; Walker and Valentine 1984; Brown 1995; Schluter 2000; Gavrillets and Vose 2005). Speciation rate may also be a declining function of either the density or the frequency of a particular lineage under other speciation modes as well (e.g., Hubbell 2001). After all niches are filled, new species can enter only if previously filled niches became vacant, if the new species can displace an existing species (MacArthur 1965; Jablonski and Sepkoski 1996), or if new ecological niche opportunities are created by diversification in other clades (Odling-Smee et al. 2003). In parallel, extinction rate may increase as niche space fills and thus forces interactions with a more diverse species assemblage. Whether a particular species will ultimately persist in the assemblage will be defined by whether they are able to coexist (in the strict mathematical sense) with the other species comprising the local community (Chesson 2000).

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Even species that cannot persist indefinitely in the community may nonetheless have important effects on community structure that shape macroevolutionary processes and thus the resulting patterns of clade diversification. Many modes of speciation may produce new species that are ecologically very similar to their progenitors (e.g., sexual selection, as in the Hawaiian *Drosophila* or African lake cichlids [Kaneshiro 1988; McKaye 1991; Boake et al. 1997; Seehausen et al. 1997; Turner et al. 2001; Ready et al. 2006]; autotetraploidy [Ramsey and Schemske 1998, 2002]; chromosomal rearrangements [King 1993]), while others may make phenotypes that are ecologically divergent from their progenitors but without regard to the available niches in the system (e.g., allotetraploidy and hybridization [Barrett 1989; Rieseberg 1997]). In lineages where these speciation modes predominate, transient species that are being driven to extinction or randomly walking to extinction may be common at any given time (Hubbell 2001; Chave 2004; Leibold and McPeck 2006; McPeck 2007). In addition, extinction dynamics will be influenced by the rate at which such species are introduced into the community and by the degree of their ecological differentiation from those that are best adapted to the available ecological opportunities (McPeck 2007).

These dynamics should be apparent in taxa that have a detailed fossil record, but extremely few taxa have such records. Species-level molecular phylogenies offer an alternative data source for the dynamics of clade diversification, but like the fossil record, molecular phylogenies also have some shortcomings as records of clade diversification. Molecular phylogenies can reconstruct the phylogenetic relationships only among extant species; the phylogenetic positions and durations of extinct species are invisible to these analyses. However, molecular phylogenies are not blind to extinction dynamics; the interplay of speciation and extinction shapes the tempo of diversification that is recorded in molecular phylogenies (Harvey et al. 1994; Nee et al. 1994a). A number of phylogenetic studies of specific taxa now suggest that lineage accumulation rates in many clades are more rapid early in their histories and slow appreciably as they approach the recent, which would be consistent with scenarios of either slowing speciation rates or accelerating extinction with increases in clade age or diversity (Harmon et al. 2003; Shaw et al. 2003; Kadereit et al. 2004; Machordom and Macpherson 2004; Morrison et al. 2004; Williams and Reid 2004; Xiang et al. 2005; Kozak et al. 2006; Weir 2006; Phillimore and Price 2008). In contrast, other studies have reported accelerating lineage accumulation rates as clades have approached the recent (Barraclough and Vogler 2002; Linder et al. 2003; Turgeon et al. 2005). However, taxon sampling for phylogenetic studies and the methods used to estimate phylogenies can introduce biases and artifacts into these pat-

terns (Nee et al. 1992, 1994a; Pybus and Harvey 2000; Revell et al. 2005). Thus, molecular phylogenies could potentially be a primary data source to test the importance of various macroevolutionary processes in shaping our extant biota, but such data must be examined cautiously.

In this article, I examine the patterns of diversification illustrated by the species-level molecular phylogenies of a broad survey of 245 clades of animals and plants. I then attempt to re-create the diversification patterns seen in these real phylogenies using a metacommunity model of species interactions with clade diversification. The results of the metacommunity model show that simply varying the degree of ecological diversification generated at the time of speciation can account for the full range of patterns seen in the diversification of real clades. The analysis of this metacommunity model also suggests testable hypotheses about the phenotypic variability, community structure, and biogeography of these real clades.

Patterns in Real Phylogenies

To examine the natural patterns of diversification recorded in the phylogenies of extant clades, I analyzed the species-level molecular phylogenies in a recently constructed data set (all trees included in this analysis and relevant data about them are available as an Excel file or a tab-delimited ASCII file; see also McPeck and Brown 2007). I searched journals that routinely publish molecular phylogenies for articles that presented species-level phylogenies. To be included in this study, the article had to meet certain criteria. For this analysis, the relevant criteria were as follows: (1) ~50% or more of the species thought to be members of the clade had to be included in the analysis and (2) a phylogeny showing branch lengths calibrated to time or proportional to molecular (nucleotide or amino acid) substitution rate and a scale translating branch lengths into time or substitution rate must have been presented. These criteria were enforced because I was interested in developing an accurate picture of the rate of lineage accumulation through the history of a clade (Nee et al. 1992, 1994a; Harvey et al. 1994; Pybus and Harvey 2000). Incomplete taxon sampling will disproportionately leave internal nodes nearer the root of the phylogeny than near the tips, which will result in a false account of lineage accumulation over the history of a clade. Moreover, biased taxon sampling that explicitly tries to maximize the breadth of species sampled across the phylogeny will also strongly distort lineage accumulation rates (Nee et al. 1994a); studies in which the authors alluded to such biased sampling were also rejected from this analysis, even if they met the 50% sampling criterion. Chronograms (i.e., phylogenies with branch lengths calibrated to time) were preferentially chosen if presented in articles. For articles that

did not present chronograms, only trees produced by neighbor joining, maximum likelihood, or Bayesian analyses that produce branch length estimates proportional to the rate of nucleotide or amino acid substitutions were selected. Final trees in the data set included one branch for each putative species. Subspecies were combined into a single species. The resulting data set contained a total of 245 phylogenies meeting these two criteria—of which 182 could be calibrated to time using molecular clock estimates—and included 55 arthropod phylogenies (42 calibrated to time), 140 chordate phylogenies (111 calibrated), 11 mollusk phylogenies (9 calibrated), and 39 magnoliophyte phylogenies (20 calibrated). Please see the Excel file or the tab-delimited ASCII file for a full listing of the articles and the resulting data, and see McPeck and Brown (2007) for a full description of how data were extracted from the phylogenies.

For those phylogenies that could be calibrated to time, I used the time-calibrated distance from the root to the tips of the phylogeny as the estimate for clade age, and I estimated diversification rate for each phylogeny by calculating λ according to equation (7) of Nee (2001). The parameter λ is a standard measure of diversification rate for molecular phylogenies that assumes speciation but no extinctions (Baldwin and Sanderson 1998; Nee 2001) and has units of $(10^6 \text{ years})^{-1}$. Molecular phylogenies record the rate of accumulation of lineages that survive into the present. Therefore, I also calculated γ , a metric of whether the rate of lineage accumulation changes over the history of a clade (Cox and Lewis 1966; Pybus and Harvey 2000). The parameter γ is insensitive to the units of branch lengths and so was calculated for all phylogenies. If a clade accumulated lineages at a constant rate throughout its history, $\gamma = 0$ (i.e., linearity for the relationship of $\log(\text{number of lineages})$ against time, i.e., a lineage through time [LTT] plot). If the lineage accumulation rate slowed appreciably over the clade's history, $\gamma < 0$ (i.e., this relationship has a steeper slope for the early history of the clade than in the recent past). Finally, if the rate of lineage accumulation accelerated in the recent past, $\gamma > 0$ (i.e., the relationship turns up in the very recent).

Previous analyses have shown that γ can be biased toward more negative values if simple nucleotide substitution models are used when more complicated models that correct for multiple unseen mutations, differences in base frequencies, variation rates of different substitution types (e.g., transitions vs. transversions), the proportion of invariant sites, and rate heterogeneity among sites are more appropriate (Revell et al. 2005). This is because more complicated substitution models disproportionately lengthen branches earlier in the phylogeny (Gojobori et al. 1982; Kuhner and Felsenstein 1994; Revell et al. 2005). To test for this, I compared the distribution of γ among the var-

ious models used to estimate phylogenies in this data set. Because incomplete taxon sampling can also bias the estimates of γ (Nee et al. 1994a; Pybus and Harvey 2000), I examined the correlation of γ with the percent of species thought to be members of the clade that were included in the study.

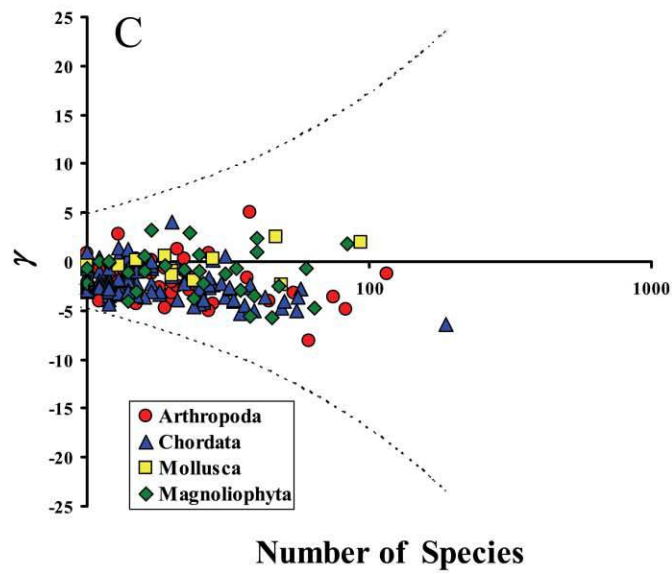
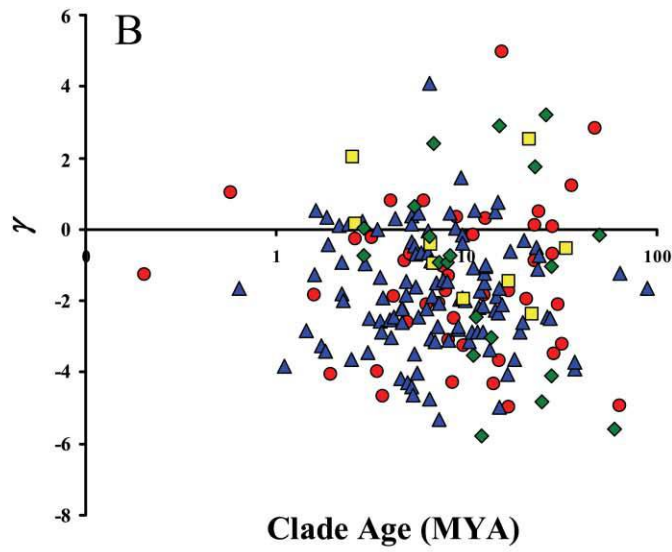
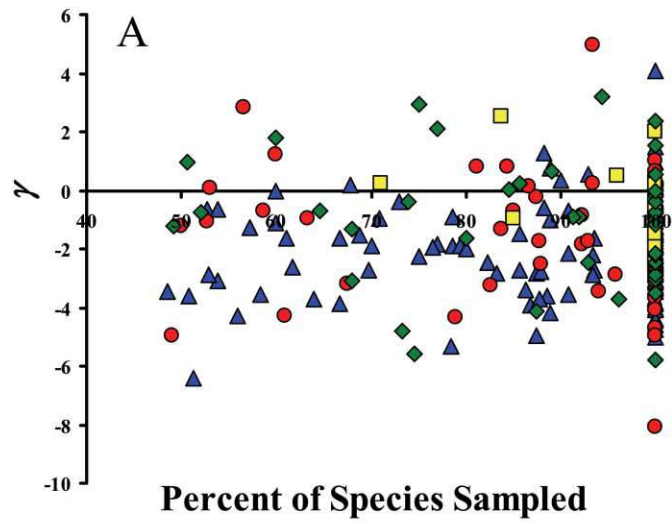
The resulting data set showed little to no evidence of these biases. The parameter γ did not differ among the various substitution models used to reconstruct the underlying phylogenies ($F = 1.27$, $df = 20, 224$, $P > .20$), indicating that the potential biases identified by Revell et al. (2005) are not important in this data set. In addition, 56% of the clades in the data set included all known species, and 78% of the clades included $>80\%$ of the known species. Results of analyses of only the phylogenies with 100% species coverage were also quantitatively nearly identical to the results of analyses of the full data set. Moreover, γ was uncorrelated with the percent of sampled species in a clade (fig. 1A; $r = 0.01$, $df = 243$, $P > .85$) and with clade age (fig. 1B; $r = -0.01$, $df = 179$, $P > .98$; see also Phillimore and Price 2008).

However, γ was correlated with the number of species included in the phylogeny (fig. 1C; $r = -0.22$, $df = 243$, $P < .001$). Phillimore and Price (2008) also found a negative correlation between γ and clade size in their survey of 45 bird clades, and they attributed this partly to the random distribution of speciation events; they argued that clades that quickly reach a large size will be those that have already experienced above-average diversification rates early in their histories. However, another bias is inherent here. The maximum magnitude of γ is constrained by the number of species in the phylogeny. The parameter γ is maximized for a star phylogeny and minimized for a phylogeny with one basal split and all branches except the basal two having length 0, and so γ is constrained to the interval

$$\left[-\frac{1/2}{\sqrt{1/[12(n-2)]}}, \frac{1/2}{\sqrt{1/[12(n-2)]}} \right],$$

where n is the number of species in the phylogeny (see fig. 1C). This limit on magnitude is symmetrical about 0 and so does not bias γ values to be positive or negative. Thus, because negative γ values predominate across the entire range of clade richness (fig. 1C), this inherent constraint does not obviate the general picture that the majority of clades have $\gamma < 0$, as previous studies and this one indicate.

Clades showed great heterogeneity in γ across all phylogenies, ranging from -8.09 to 4.96 . Figure 2 shows LTT plots for representative clades with extreme values of γ . Across the entire data set, the average γ was well below 0



(-1.56 ± 1.85 [mean \pm 1 SD], $t = -13.27$, $df = 244$, $P < .001$ for difference from 0.0), with 80% of the clades having $\gamma < 0$ and 42% having $\gamma < -1.96$. The parameter γ was also weakly positively correlated with λ ($r = 0.19$, $df = 179$, $P < .02$).

Although the four major taxonomic groups all had representatives with values at both extremes (fig. 3A) and all averaged $\gamma < 0$, chordates had the most negative average γ , while mollusks had the least negative average γ (tests for heterogeneity among the four groups: $F = 3.76$, $df = 3, 241$, $P < .02$). However, these differences may be a function of sampling across the four taxa because the taxa represented by more clades in the data set had more negative γ 's.

A Metacommunity Model of Diversification

The above analysis provides a very striking picture of diversification for animals and plants. Each taxon shows a broad range of diversification histories among clades, but in general, the majority of clades showed a pattern of slowing diversification over time ($\gamma < 0$). This general pattern across major groups of animals and plants confirms the results of a number of taxonomically more limited analyses (see the first section of this article).

A number of theoretical analyses have explored whether macroevolutionary models of lineage diversification can generate these differences in lineage accumulation rate heterogeneity over the history of a clade. Very specific conditions are needed to generate clades with decelerating lineage accumulation rates (Nee et al. 1992, 1994a; Rabosky 2006; Weir 2006; Phillimore and Price 2008; Rabosky and Lovette 2008). If speciation and extinction rates are constant over most of a clade's history, it accumulates lineages at a rate proportional to speciation minus extinction rate, but the lineage accumulation rate accelerates near the recent—becoming proportional to just the speciation rate—because extinction has been unimportant for extant species (Nee et al. 1994a; Phillimore and Price 2008; Rabosky and Lovette 2008). Thus, clades experiencing significant extinction rates typically have $\gamma > 0$, whereas clades produced with no extinction are generally centered on $\gamma = 0$ (Nee et al. 1994a; Rabosky and Lovette 2008). However, $\gamma < 0$ implies a decreasing lineage accumulation rate over a clade's history, which intuitively would seem to be caused by either a declining speciation rate or in-

creasing extinction rate with time or increasing species richness in the clade. Simulation studies have shown that if the speciation rate declines substantially over a clade's history and the extinction rate is held at 0 or very small values, clades with $\gamma < 0$ will be consistently produced (Weir 2006; Rabosky and Lovette 2008). However, increasing the extinction rate over a clade's history produces $\gamma > 0$ with either constant or declining speciation rates (Rabosky and Lovette 2008). Thus, these models of diversifying lineages with lineage-specific speciation and extinction rates find that extinction erases the signature of earlier diversification as lineages are pruned from the tree so that more recent events dominate the phylogenetic signal.

On the basis of these kinds of model results, declining speciation rates over the histories of clades have been favored as the cause of the preponderance of clades with $\gamma < 0$ and has been taken as evidence for adaptive radiations (e.g., Harmon et al. 2003; Weir 2006; Phillimore and Price 2008; Rabosky and Lovette 2008). However, these model results imply that extinction rates were exceedingly low over the history of these clades as well (Rabosky and Lovette 2008), a conclusion that is difficult to square with the fossil record (e.g., Raup 1991; Gilinsky 1994; Alroy 1996; Stanley 1998, 2007; Foote 2000). Thus, these models may produce a false picture of the mechanisms that generated these real clades. The missing elements of these birth-death models of lineage diversification are the ecological contexts of speciation and extinction.

To investigate what ecological conditions could potentially generate the diversity of lineage accumulation patterns represented in real phylogenies, I studied the macroevolutionary dynamics of a model of species interacting and diversifying in a metacommunity of patches along an environmental gradient (McPeck 2007; see also Tilman 2004). Each patch in the metacommunity occupied a random position along an environmental gradient. The dynamics of species i in patch j was governed by a form of the discrete logistic equation

$$N_{ij}(t+1) = N_{ij}(t) \exp\left(1 - \frac{\sum_j N_{ij}(t)}{K_{ij}}\right)$$

(Case 2000; Turchin 2003). In this model, all species were symmetrical competitors, and intraspecific competition

Figure 1: Relationships between γ and the percent of species thought to be members of the clade that were sampled to construct the phylogeny (A), the clade age (given in millions of years; B), and the number of species included in the phylogeny (C). The symbols in the key in C identify clades in the four major taxonomic groups represented in the data set. The dashed lines in C identify the minimum and maximum γ values possible for a given number of species. Also, note that B has fewer data points than do A and C because clade age was available for only a subset of the clades in the data set. For ease of presentation, the abscissas for B and C are on logarithmic scales.

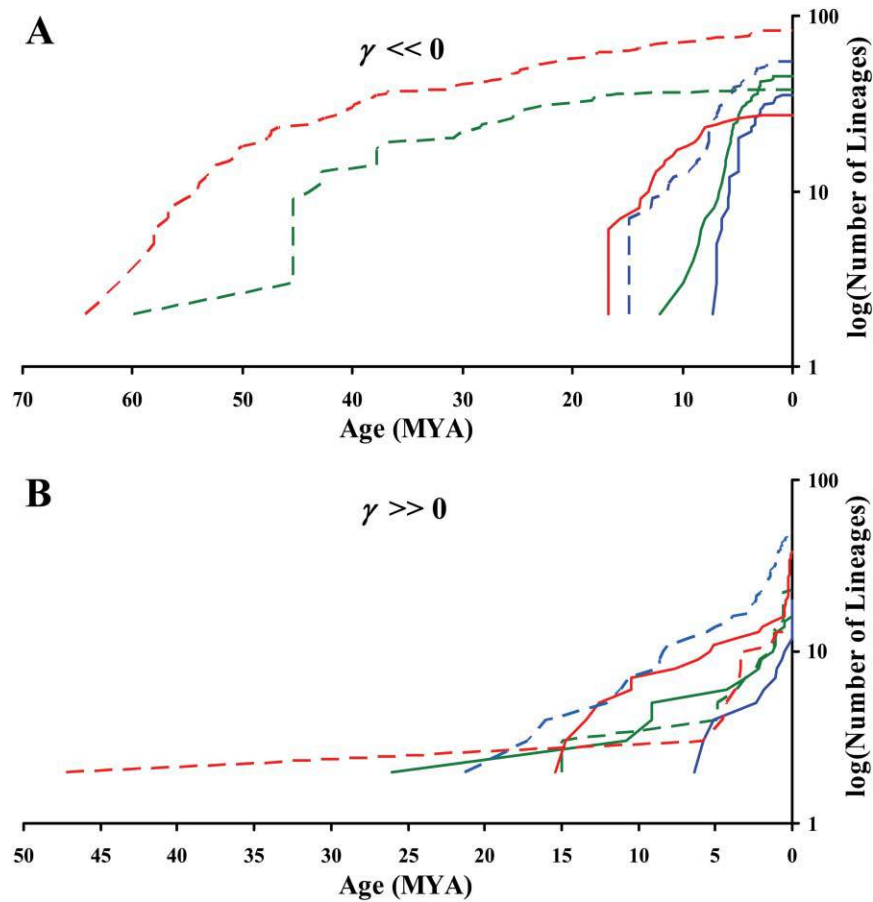


Figure 2: Representative lineage through time plots for real clades in the data set. *A*, Lineage through time plots for the six clades with the most negative γ values. *Green solid line*, Lledo et al. (2005); *green dashed line*, Kay et al. (2005); *blue solid line*, Gill et al. (2005); *blue dashed line*, Parr-Olea et al. (2004); *red solid line*, Morrison et al. (2004); *red dashed line*, McKenna and Farrell (2005). *B*, Lineage through time plots for the six clades with the most positive γ values. *Green solid line*, Simpson et al. (2004); *green dashed line*, Comes and Abbott (2001); *blue solid line*, Sorenson et al. (2004); *blue dashed line*, Cunha et al. (2005); *red solid line*, Turgeon et al. (2005); *red dashed line*, Johnson et al. (2005).

and interspecific competition were equivalent (i.e., the standard competition coefficients are all 1.0). The carrying capacity of a species varied along the environmental gradient according to

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

where E_j is the gradient position of patch j , E_i^* is the gradient position where species i has its highest carrying capacity, K_{opt} is the carrying capacity at E_i^* , and ω is the parameter determining the steepness with which the carrying capacity decreases away from the optimum; $\omega = 0.1$ and $K_{\text{opt}} = 5,000$ for all species in all simulations presented here. Species differed only in their optimal positions

along the gradient (E_i^* 's). The species with the largest K_{ij} for patch j was the superior competitor in patch j and would drive all other species locally to extinction in patch j if all immigration was prevented (Charlesworth 1994). Throughout, I also assumed that 5% of each species disperses randomly among patches each iteration; dispersal rate had little effect on the results presented in this article (but see Mooers et al. 2007 for other model results where dispersal is important to diversification). Each iteration of the model consisted of regulating abundances in each patch and then dispersing a constant fraction of individuals of all species among the patches.

Each species had a constant probability of spawning a new species each iteration; in all results presented here, I have assumed a constant per-lineage speciation probability of 0.0001 each iteration. (In a previous analysis of this

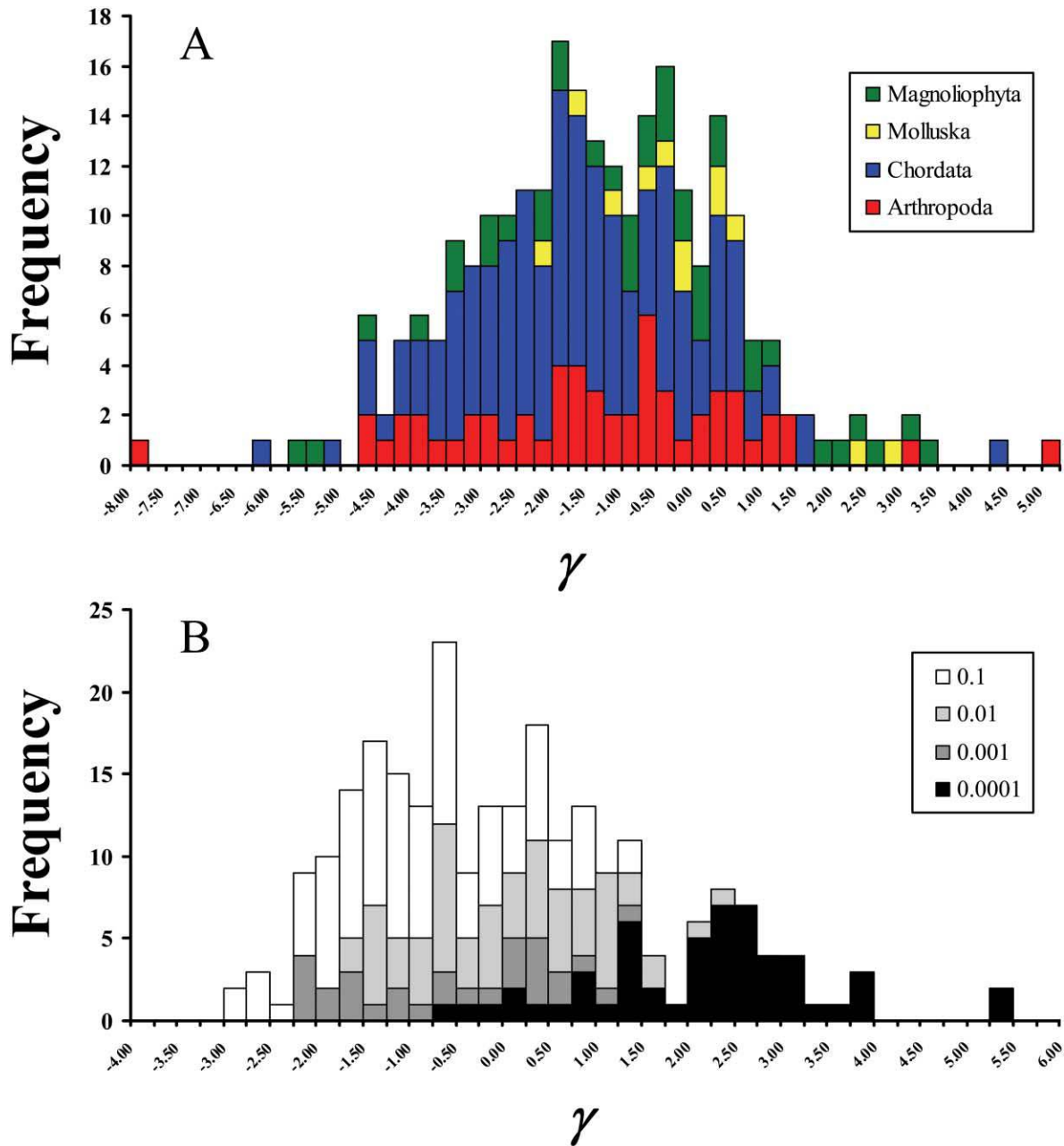


Figure 3: Frequency histograms of γ for real clades (A) and simulated clades (B) under the metacommunity model of clade diversification. In A, the colors identify the four major taxonomic groups in the data set, as given in the key. In B, the colors identify replicates of the metacommunity clade diversification model with different values of (σ_E^*) , as given in the key.

model [McPeck 2007], I used a speciation rate that was not a constant per-lineage probability but rather a constant probability of a speciation event happening per iteration.) The optimum for a new species i , E_i^* , was determined by drawing a random deviate from a normal distribution with zero mean and a specified standard deviation (σ_E^*) and

adding this random deviate to the E_i^* of its progenitor. Varying σ_E^* thus altered the degree to which new species could be ecologically differentiated from their progenitors, with larger values permitting greater ecological differentiation. New species were established in a randomly chosen patch at $K_{ij}/100$. Extinctions occurred only because inter-

actions with other species depressed a species' abundance to <1 in every patch. Each run of the simulation started with one species at its carrying capacities in all patches and a second species at $K_{ij}/100$ in one randomly chosen patch. I performed 500,000 iterations for each replicate simulation and 100 replicates for each parameter combination. I maintained a phylogenetic record of species throughout each replicate to produce a phylogeny of the extant species at the end, and from these phylogenies I calculated the same set of metrics as above. Obviously, many other scenarios of speciation (e.g., each lineage may speciate with a probability proportional to its relative abundance in the metacommunity [e.g., Hubbell 2001], vicariant events within the metacommunity may divide species into allopatric subunits within the overall system, or new species may be produced as they colonize underutilized patches [Gavrilets and Vose 2005]) and extinction (e.g., extinction due to demographic stochasticity [Lande et al. 2003; Primack 2006], mass extinctions [Erwin 2001; Jablonski 2001], or simple bad luck [Raup 1991]) can be imagined and explored in the context of this model, but in this article, I chose to focus on this simple scenario. Future articles will consider these alternative situations.

Varying σ_E^* leaves a clear signature in phylogenies. I have evaluated the speciation, extinction, and species richness dynamics of this model previously (McPeck 2007), and so I summarize only these dynamics here and focus on their effects on γ . When σ_E^* was large (e.g., $\sigma_E^* = 0.1$ in the results presented here), replicates initially accumulated species until they reached a plateau in which the ecological gradient was relatively full. Successful species were those that had E_i^* values nearer the gradient position of ≥ 1 patches in the metacommunity. After reaching this plateau, only new species with E_i^* closer to some patch environmental value could invade and, in so doing, quickly drive some other species to extinction. Those new species that did not have E_i^* closer to some patch environmental value than others were themselves quickly driven to extinction. At the end of replicates, assemblages contained ecologically well-differentiated and coexisting species that completely filled the gradient (McPeck 2007).

Thus, the macroevolutionary dynamics of these assemblages ($\sigma_E^* = 0.1$) generally had an initial period of diversification in which most new species found a place in the metacommunity (i.e., niche-filling phase), followed by a slowing of diversification rate where most subsequent new species were unsuccessful and quickly driven to extinction, and those successful few generally displaced existing species (i.e., species replacement phase; for results from an explicitly genetic model of speciation with similar diversification dynamics, see also Gavrilets and Vose 2005). Consequently, γ calculated from the resulting phylogenies averaged -1.28 ± 0.10 (mean ± 1 SE; test for difference

from 0.0, $t = -11.26$, $df = 98$, $P < .001$), which quantifies this pattern (fig. 3B). Visual examination of replicate LTT plots confirmed this conclusion. Because extinction times were rapid, almost all species in the system were coexisting in the strict ecological and mathematical sense (sensu Chesson 2000) at any given time (McPeck 2007).

As σ_E^* was decreased, the macroevolutionary dynamics of clades and their resulting ecological structures of the metacommunity changed. As σ_E^* was initially decreased (e.g., to values of 0.01 and 0.001 presented here), clades became less able to explore and fill the available gradient because new species were constrained to be more similar to their progenitors. In addition, times to extinction increased greatly because of species' ecological similarity, and so the frequency of transient species that were being slowly driven to extinction (what I will refer to as co-occurring species) increased and the frequency of coexisting species (i.e., those that could persist indefinitely in the system, given the current collection of species) decreased with decreasing σ_E^* (McPeck 2007). At these intermediate σ_E^* levels, the distribution of γ shifted toward 0 but remained <0 on average (fig. 3B).

However, as σ_E^* was decreased further toward 0, these patterns reversed. With σ_E^* very close to 0 (e.g., $\sigma_E^* = 0.0001$), all new species were ecologically very similar to their progenitors, and so clades could not differentiate to any substantial degree along the environmental gradient. Moreover, times to extinction were quite long, and as a result, final assemblages contained phenotypically very similar species (based on E_i^*) that were mostly co-occurring and not coexisting (i.e., most species present in the system at any given time were being very slowly driven to extinction by one or two others [McPeck 2007]). The parameter γ also shifted to average 1.91 ± 0.17 (mean ± 1 SE), which was significantly >0 ($t = 11.08$, $df = 54$, $P < .001$; fig. 3B).

Taken together, these results predict that clades in which ecological speciation is the primary mode creating new species (i.e., σ_E^* large) should generally show decelerating diversification rates over the histories of clades (i.e., $\gamma < 0$). Alternatively, taxa in which speciation is accomplished primarily by modes that generate little ecological differentiation (i.e., σ_E^* very small) should have phylogenetic histories that show accelerating diversification rates over their clade histories (i.e., $\gamma > 0$).

Discussion

Alternative modeling frameworks of macroevolutionary dynamics offer contrasting explanations for the patterns of γ seen in real phylogenies. One is the venerable approach of modeling speciation and extinction as lineage-specific probabilities and incorporating ecology into these

rates by making them functions of either time or clade species richness (Raup et al. 1973; Gould et al. 1977; Sepkoski 1978, 1979, 1998; Raup 1985; Maurer 1989; Przeworski and Wall 1998; Nee 2006; Weir 2006; Phillimore and Price 2008; Rabosky and Lovette 2008). This modeling approach is particularly appealing because methods now exist to estimate more complicated functional forms of these rates from phylogenies (Nee et al. 1994*b*; Nee 2006; Rabosky 2006). Previous considerations of these models have shown that constant speciation and extinction rates across lineages are inconsistent with the branching structure and tree balance seen in real phylogenies (Heard 1992, 1996; Mooers and Heard 1997). The implication derived from these models in the present context is that speciation rates declined substantially over their histories and that extinction rates were exceedingly low throughout their histories for the majority of real clades (i.e., those with $\gamma < 0$; fig. 3A); any significant amount of extinction erases the early signature of more rapid speciation (Weir 2006; Phillimore and Price 2008; Rabosky and Lovette 2008). Alternatively, these models would account for those clades with $\gamma > 0$ as having experienced much higher extinction rates, regardless of the relationship of speciation rates over clade histories (Nee et al. 1994*a*; Rabosky and Lovette 2008).

A declining speciation rate with increasing clade species richness is expected under many speciation mechanisms (see review in the first section of this article), and so this mechanism is typically invoked to explain declining diversification rates over the histories of clades (e.g., Nee et al. 1992; Harmon et al. 2003; McKenna and Farrell 2005; Weir 2006; Phillimore and Price 2008; Price 2008; Rabosky and Lovette 2008). Declining origination rates with taxon richness are also apparent at higher taxonomic levels in the fossil record (e.g., Sepkoski 1998; Foote 2000; Kirchner and Weil 2000*a*, 2000*b*). However, the prediction of low extinction rates for the majority of clades is more problematic. Of course, what is “low” is an empirical question that can be answered only by more focused examination using empirically parameterized models. However, the fossil records of most groups certainly provide a clear picture that extinctions at higher taxonomic levels (e.g., genera and families) are common and that background extinction rates (excluding mass extinction events) at these levels are nontrivial (e.g., Raup 1991; Gilinsky 1994; Alroy 1996; Stanley 1998, 2007; Foote 2000). If extinction rates could be measured at the species level in the fossil record, they could only be higher than at these higher taxonomic levels. Thus, the molecular phylogenetic results that diversification rates decline over the histories of a majority of clades (fig. 3A) would seem to be quite inconsistent with interpretations based on these models.

In contrast, the metacommunity model of species in-

teractions presented here offers an alternative interpretation for the patterns of lineage accumulation seen in real clades. Specifically, these model results suggest that the degree of ecological differentiation generated at the time of speciation can account for much of the pattern of diversification recorded in the molecular phylogenies of animal and plant clades. This model also provides an alternative framework for understanding the dynamics of speciation and extinction that are recorded in fossils and molecular phylogenies (see also McPeck 2007). The majority of real clades in the data set had phylogenetic patterns indicative of diversification via ecological speciation mechanisms (i.e., σ_E^* large), namely, those having $\gamma < 0$ (see also Harmon et al. 2003; Linder et al. 2003; Shaw et al. 2003; Kadereit et al. 2004; Machordom and Macpherson 2004; Williams and Reid 2004; Rüber and Zardoya 2005; Kozak et al. 2006; Weir 2006; Phillimore and Price 2008). Most phylogenies in the data set are of entire subgenera, genera, or families, suggesting that these patterns may result from lineages colonizing new adaptive zones to establish higher taxonomic groups (Simpson 1944). Once in the new adaptive zone, lineages may have diversified to fill the available niche space according to diversity-dependent speciation and extinction modes (MacArthur 1965; Walker and Valentine 1984; Schluter 2000; Gavrillets and Vose 2005). Broad-scale analyses of origination and extinction rates in fossil animal genera are also consistent with these expectations: peaks in origination and extinction do not coincide (e.g., Kirchner and Weil 2000*b*), and over the post-Paleozoic, both origination and extinction rates are “diversity dependent” (Foote 2000).

The results of the metacommunity model also illustrate that the ecological dynamics of species richness are not exactly recorded in the phylogeny of a clade. During most replicates in which new species could be well differentiated from their progenitors (e.g., $\sigma_E^* = 0.1$), species richness initially increased rapidly up to a plateau that marked the end of the niche-filling phase; this corresponded to the initial period of rapid lineage accumulation. Thereafter in the species replacement phase, overall species richness remained relatively constant at a steady state equilibrium, with most new species being rapidly driven to extinction and only a few replacing existing species (McPeck 2007). Thus, the more shallow increase in LTT plots during the species replacement phase reflects not the dynamics of species richness but rather the accumulation of lineages leading to extant species.

In addition, these model results show that the macroevolutionary dynamics recorded in a phylogeny do not necessarily reflect the true pattern of speciation and extinction. Again, rapid diversification at the base of a clade followed by deceleration is typically taken as evidence for the kind of rapid speciation during an initial adaptive

radiation phase followed by a slowing of speciation rate as niches fill (Harmon et al. 2003; Weir 2006; Phillimore and Price 2008; Price 2008). In contrast, the metacommunity model generated this same pattern not with elevated speciation probabilities in response to ecological opportunities but rather from a constant lineage-specific speciation probability and ecological modulation of extinction through species interactions. The genetically explicit model of ecological speciation studied by Gavrilets and Vose (2005) showed these same lineage accumulation dynamics. They too attribute the concentration of speciation events in the early history of a clade to the greater ecological opportunities available to be exploited by newly formed species. However, declining diversification in their model was caused directly by a decreasing speciation rate as the environment filled with species. In real clades, ecological modulation of both speciation and extinction rates probably contributed to the changes in diversification seen over their histories. The absence of diversity-dependent speciation from the present metacommunity model may be one reason why the γ values generated by the model were not as negative as those seen in real trees. Disentangling speciation and extinction rates from phylogenetic patterns is largely a futile empirical exercise (Paradis 2004), and so it may be impossible to partition the relative contributions of diversity-dependent speciation from the ecological modulation of extinction.

Moreover, close considerations of the real and apparent speciation and extinction rates in the metacommunity model highlight even more fundamental problems with these interpretations. The phylogenetic dynamics of the metacommunity model recorded the decrease in the “apparent” speciation rate because only lineages that persist to the end of the simulation (i.e., the present) are recorded in the phylogeny. The persistence of these lineages is recorded as the slowing of the apparent diversification rate (i.e., $\gamma < 0$), which requires the persistence of old lineages and old species into the present. Thus, the functional form of speciation rate inferred from the phylogenetic dynamics provided a substantially false impression of the true form and rate of speciation that generated assemblages in the metacommunity model. This is probably also true for the real phylogenies.

Likewise, the true extinction rate was very different from the “apparent” extinction rate recorded in the phylogenies under these conditions in the metacommunity model. During the niche-filling phase, the real extinction rate was relatively low because most new species were usually ecologically well differentiated from their progenitors and would find unexploited areas of the gradient. Once the gradient was relatively full, most new species were quickly driven to extinction. Hence, the true extinction rate actually increased greatly during the species replacement

phase. However, species replacements were the only extinction events that would influence the phylogenetic signal, and this apparent extinction rate due to species replacements was low enough to retain the signal of slowing realized speciation rates in the historical record written into the phylogeny. It is interesting to note that the fossil histories of many real clades have large numbers of “singleton” taxa—those represented in the fossil record by only one or a few occurrences (e.g., Alroy 1996; Foote and Raup 1996; Stanley 2008). These singletons are usually taken as evidence of the imperfection of the fossil record, and such taxa are usually excluded from analyses of fossil patterns (justifiably so in most cases; e.g., Foote et al. 2007). However, the metacommunity model results suggest that fossil singletons should be common and represent the many species that originate but are then quickly driven to extinction during the species replacement phase of a clade’s diversification (see also Stanley 2008).

These differences in real and apparent speciation and extinction rates in the metacommunity model underscore the false impression one obtains from taking the dynamics revealed in molecular phylogenies at face value. As an anonymous reviewer of this article astutely observed, “This raises significant questions about what we even mean by an extinction rate or a speciation rate in the context of the birth-death model. Is the extinction of incipient species in the author’s patch dynamic simulations really an extinction event? Or is it the failure of a speciation event?” Moreover, these differences argue that we cannot understand the true macroevolutionary dynamics of systems by ignoring the ecological interactions in which those taxa are engaged. These considerations also highlight the fact that fossils and molecular phylogenies record different types of information about clade diversification, and reconciling the information in these two data sources may be a very productive avenue for understanding the processes governing diversification (e.g., McPeck 2007; McPeck and Brown 2007).

A substantially smaller but significant fraction of real clades in the data set showed phylogenetic patterns of $\gamma > 0$ (fig. 3A). All four major taxonomic groups were represented among the real phylogenies in this area of parameter space. Models of lineage-specific speciation and extinction rates would suggest that these clades have had high speciation and extinction rates. High coupled speciation and extinction rates would exaggerate the difference in slope between the major portion of the LTT plot, where the slope is expected to be speciation rate minus extinction rate for most of the clade’s history, and the most recent part of the LTT plot, where the slope is expected to be equal to just the speciation rate (Nee et al. 1994a). However, patterns apparent in the LTT plots for many of the real clades argue against these clades having

high extinction rates as a result of species turnover. Specifically, visual inspections of the LTT plots for these clades show that many have clear signatures of rapid lineage accumulation rates at their inception, followed by a slowing and then a very rapid reacceleration in the very recent (fig. 3B). For example, the three clades with the most positive γ all showed this pattern: *Enallagma* damselflies ($\gamma = 4.96$; Turgeon et al. 2005), *Vidua* finches ($\gamma = 4.10$; Sorenson et al. 2004), and the *Krameria* herbs and shrub species ($\gamma = 3.19$; Simpson et al. 2004; fig. 3B). The upturn of lineage accumulation in the very recent dominates the calculation of γ in these cases, but the fact that the initially rapid diversification signal is still clearly evident in their LTT plots suggests low overall extinction rates over the histories of these clades (Weir 2006; Rabosky and Lovette 2008), which in turn suggests that the metacommunity model may be a better explanation for their recent upturn in lineage accumulation rate.

In the metacommunity model results, phylogenies with $\gamma > 0$ were generated when the degree of ecological differentiation at the time of speciation was very small (i.e., $\sigma_E^* = 0.0001$). Speciation modes that generate reproductive isolation without significant ecological differentiation (e.g., speciation via sexual selection, changes in genital morphology, autotetraploidy, chromosomal rearrangements) should be most prevalent in these clades. In this area of parameter space, the true extinction rates were greatly slowed by the ecological similarity between new species and their progenitors (McPeck 2007). In addition, because the time to extinction is exceedingly long for competing species that are ecologically very similar to one another, even species that were ultimately being driven to extinction would remain in the system for very long times. In other words, the shift to a high frequency of young species and lineages was due mainly to the increased time to remove ecologically inferior species from the system (McPeck 2007). Also, these model assemblages consisted of many ecologically very similar species that occupied only a very narrow portion of the available ecological gradient and thus displayed a structure that would permit "neutral ecological drift" to dominate community structure (although stochastic dynamics were not incorporated into the model presented here; Hubbell 2001). Most species at any given time were transients that were slowly being driven to extinction by species interactions, and only a very few species were actually coexisting in the theoretical sense (McPeck 2007).

We know little about the ecological contexts or the reasons for diversification in many of the real clades with large positive values of γ . However, our work on the diversification of *Enallagma* damselflies, the clade with the most positive γ , does support the interpretations based on the metacommunity model results. *Enallagma* radiated

across the Holarctic to more than double in lineage richness over the past 250,000 years (Turgeon et al. 2005). Terminating the *Enallagma* LTT plot at 250,000 years ago gives $\gamma = -1.37$ (this value is, however, not quite statistically significant on its own for a one-tailed test; $P < .09$). Although some of the recent speciation events were also clearly the result of ecological diversification, most involved morphological alterations of mating structures involved in species recognition and little else (McPeck and Brown 2000; Turgeon et al. 2005; Stoks and McPeck 2006; McPeck et al. 2008). Moreover, if the deep period of rapid diversification was caused by exploiting new ecological opportunities, and if rapid recent diversification was driven primarily by reproductive differentiation without ecological differentiation, major subclades within the genus should be substantially ecologically differentiated from one another, but little to no ecological differentiation should exist within subclades for species that are sympatric. We are currently testing these predictions in field experiments evaluating coexistence and the strengths of species interactions. Like *Enallagma*, most clades probably diversify by more than one mode, and so the signal that is apparent in their phylogenies will represent an integration of the ways, times, and rates that various lineages within the clade have come into being and have become extinct.

The relative frequencies of real clades along the gradient of γ (fig. 3A) also may not represent the real distributions because of biases in what clades are subjected to the types of molecular systematics analyses that met our criteria for inclusion. For example, highly diverse clades that radiated very rapidly and very recently (e.g., African lake cichlids) will show almost no phylogenetic resolution at the species level using DNA sequence data (e.g., Albertson et al. 1999). Also, molecular systematic studies of highly diverse clades frequently include only a small percentage of the total species in the clade and bias their taxon sampling so that representatives of all major lineages are present for the phylogenetic analysis (which will also provide incorrect estimates of lineage accumulation over the histories of clades; Nee et al. 1994a; Pybus and Harvey 2000). Both of these factors would bias against clades with patterns of rapid and recent radiations being represented in the data set and so may account for the apparent overrepresentation of clades with $\gamma < 0$. The other obvious potential bias is the paucity of very old clades in the data set. Although the oldest of the time-calibrated clades had a last common ancestor dated to 89 million years ago, 50% had root nodes that date to ≤ 8 million years ago, and 90% had root nodes dating to ≤ 26 million years ago. Here again, the inclusion of more species is the greatest impediment to extending the age of the root node for any systematic study.

Although patterns that can be gleaned from phylogenies and fossils are instructive, we must also match these de-

scriptive patterns with (1) field experimental results identifying the ecological processes regulating the population dynamics and community membership in these clades and (2) the phenotypic diversity of ecologically important characters that make them successful or unsuccessful in the face of these regulating processes to validate the predictions of the metacommunity model. The metacommunity model makes clear predictions about the types of community structures that should be apparent in clades with different γ 's. Clades with $\gamma < 0$ should have species that are well differentiated ecologically from one another and from other members of the communities in which they are embedded; that is, coexistence mechanisms should predominate in regulating their abundances and places in ecological communities (Chesson 2000). Coexistence requires species to possess different phenotypes that make them differentially successful in the various ecological processes that contribute to regulating their abundances (Chesson 2000). Thus, these clades should also display large disparities among species in ecologically important phenotypes, specifically those phenotypes that foster coexistence and not just any character that influences survival and reproduction (Leibold and McPeck 2006). Such ecological disparities may also be expressed at the level of species ranges: species in these clades may show a relatively high degree of allopatry from one another.

In contrast, clades with $\gamma > 0$ should have species that are poorly differentiated ecologically from one another and from other members of the communities in which they are embedded; that is, these are the taxa that should show characteristics of ecological drift in assemblage structure (*sensu* Hubbell 2001). This should result from species being very similar to one another in ecologically important phenotypic characters; many species in these clades may be distinguishable only by characters associated with breeding (e.g., *Enallagma* damselflies [McPeck et al. 2008], African rift lake cichlids [Seehausen et al. 1997; Ready et al. 2006]) and may potentially contain a high proportion of cryptic species (Henry et al. 1999; Witt and Hebert 2000; Gomez et al. 2002; Pfenniger and Schwenk 2007). They should also have greater range overlap because of their similarity in ecological requirements. Such features are certainly true for the *Enallagma* damselfly clade, which has the most positive γ (McPeck and Brown 2000; Donnelly 2004; Stoks and McPeck 2006; McPeck et al. 2008), and experimental analyses of other clades with these phylogenetic parameters would provide strong tests of these predictions.

Patterns of biodiversity were generated by past macroevolutionary processes that shaped the dynamics of speciation and extinction and are currently maintained by ecological processes that define the distributions and abundances of species today. Just as the ecological processes in

the past strongly contributed to defining the past macroevolutionary processes, today's ecological processes structure macroevolutionary dynamics going forward. The analyses presented in this article strongly suggest that macroevolutionary diversification cannot be understood in an ecological vacuum that ignores the communities and landscapes in which clade members are embedded. Likewise, the assembly and resulting structure of biological communities cannot be understood in a macroevolutionary vacuum that ignores the processes generating the species being assembled (McPeck and Brown 2000; Webb et al. 2002; Cavender-Bares et al. 2004, 2006; Stoks and McPeck 2006). More directly integrating the mechanisms of community ecology and macroevolution will allow us to better understand patterns in the distributions and abundances of species over long timescales.

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Literature Cited

- Albertson, R. C., J. A. Markert, P. D. Danley, and T. D. Kocher. 1999. Phylogeny of a rapidly evolving clade: the cichlid fishes of Lake Malawi, East Africa. *Proceedings of the National Academy of Sciences of the USA* 96:5107–5110.
- Alroy, J. 1996. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeography Palaeoclimatology Palaeoecology* 127:285–311.
- Baldwin, B. G., and M. J. Sanderson. 1998. Age and rate of diversification of the Hawaiian silversword alliance (Compositae). *Proceedings of the National Academy of Sciences of the USA* 95:9402–9406.
- Barraclough, T. G., and A. P. Vogler. 2002. Recent diversification rates in North American tiger beetles estimated from a dated mtDNA phylogenetic tree. *Molecular Biology and Evolution* 19:1706–1716.
- Barrett, S. C. H. 1989. Mating system evolution and speciation in heterostylous plants. Pages 257–283 *in* D. Otte and J. A. Endler, eds. *Speciation and its consequences*. Sinauer, Sunderland, MA.
- Boake, C. R. B., M. P. DeAngelis, and D. K. Andreadis. 1997. Is sexual

- selection and species recognition a continuum? mating behavior of the stalk-eyed fly *Drosophila heteroneura*. *Proceedings of the National Academy of Sciences of the USA* 94:12442–12445.
- Brown, J. H. 1995. *Macroecology*. University of Chicago Press, Chicago.
- Case, T. J. 2000. *An illustrated guide to theoretical ecology*. Oxford University Press, New York.
- Cavender-Bares, J., D. D. Ackerly, D. A. Baum, and F. A. Bazzaz. 2004. Phylogenetic overdispersion in Floridian oak communities. *American Naturalist* 163:823–843.
- Cavender-Bares, J., A. Keen, and B. Miles. 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. *Ecology* 87:S109–S122.
- Charlesworth, B. 1994. *Evolution in age-structured populations*. 2nd ed. Cambridge University Press, Cambridge.
- Chave, J. 2004. Neutral theory and community ecology. *Ecology Letters* 7:241–253.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31:343–366.
- Comes, H. P., and R. J. Abbott. 2001. Molecular phylogeography, reticulation, and lineage sorting in Mediterranean *Senecio* sect. *Senecio* (Asteraceae). *Evolution* 55:1943–1962.
- Cox, D. R., and P. A. W. Lewis. 1966. *The statistical analysis of series of events*. Methuen, London.
- Coyne, J. A., and H. A. Orr. 2004. *Speciation*. Sinauer, Sunderland, MA.
- Cunha, R. L., R. Castilho, L. Ruber, and R. Zardoya. 2005. Patterns of cladogenesis in the venomous marine gastropod genus *Conus* from the Cape Verde Islands. *Systematic Biology* 54:634–650.
- Dobzhansky, T. 1937. *Genetics and the origin of species*. Columbia University Press, New York.
- Donnelly, T. W. 2004. Distribution of North American Odonata. III. Calopterygidae, Lestidae, Coenagrionidae, Protoneuridae, Platystictidae. *Bulletin of American Odonatology* 8:33–99.
- Erwin, D. H. 2001. Lessons from the past: biotic recoveries from mass extinctions. *Proceedings of the National Academy of Sciences of the USA* 98:5399–5403.
- Foote, M. 2000. Origination and extinction components of taxonomic diversity: Paleozoic and post-Paleozoic dynamics. *Paleobiology* 26:578–605.
- Foote, M., and D. M. Raup. 1996. Fossil preservation and the stratigraphic ranges of taxa. *Paleobiology* 22:121–140.
- Foote, M., J. S. Crampton, A. G. Beu, B. A. Marshall, R. A. Cooper, P. A. Maxwell, and I. Matcham. 2007. Rise and fall of species occupancy in Cenozoic fossil mollusks. *Science* 318:1131–1134.
- Gavrilets, S. 2004. *Fitness landscapes and the origin of species*. Princeton University Press, Princeton, NJ.
- Gavrilets, S., and A. Vose. 2005. Dynamic patterns of adaptive radiation. *Proceedings of the National Academy of Sciences of the USA* 102:18040–18045.
- Gilinsky, N. L. 1994. Volatility and the Phanerozoic decline of background extinction intensity. *Paleobiology* 20:445–458.
- Gill, F. B., B. Slikas, and F. H. Sheldon. 2005. Phylogeny of titmice (Paridae). II. Species relationships based on sequences of the mitochondrial cytochrome-*b* gene. *Auk* 122:121–143.
- Gojobori, T., K. Ishii, and M. Nei. 1982. Estimation of average number of nucleotide substitutions when the rate of substitution varies with nucleotide. *Journal of Molecular Evolution* 18:414–423.
- Gomez, A., M. Serra, G. R. Carvalho, and D. H. Lunt. 2002. Speciation in ancient cryptic species complexes: evidence from the molecular phylogeny of *Brachionus plicatilis* (Rotifera). *Evolution* 56:1431–1444.
- Gould, S. J., D. M. Raup, J. J. Sepkoski Jr., T. J. M. Schopf, and D. S. Simberloff. 1977. The shape of evolution: a comparison of real and random clades. *Paleobiology* 3:23–40.
- Harmon, L. J., J. A. Schulte, A. Larson, and J. B. Losos. 2003. Tempo and model of evolutionary radiation in iguanian lizards. *Science* 301:961–964.
- Harvey, P. H., R. M. May, and S. Nee. 1994. Phylogenies without fossils. *Evolution* 48:523–529.
- Heard, S. B. 1992. Patterns in tree balance among cladistic, phenetic, and randomly generated phylogenetic trees. *Evolution* 46:1818–1826.
- . 1996. Patterns in phylogenetic tree balance with variable and evolving speciation rates. *Evolution* 50:2141–2148.
- Henry, C. S., M. L. M. Wells, and C. M. Simon. 1999. Convergent evolution of courtship songs among cryptic species of the Carnea group of green lacewings (Neuroptera: Chrysopidae: *Chrysoperla*). *Evolution* 53:1165–1179.
- Howard, D. J., and S. H. Berlocher. 1998. *Endless forms: species and speciation*. Oxford University Press, Oxford.
- Hubbell, S. P. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ.
- Jablonski, D. 2001. Lessons from the past: evolutionary impacts of mass extinctions. *Proceedings of the National Academy of Sciences of the USA* 98:5393–5398.
- Jablonski, D., and J. J. Sepkoski. 1996. Paleobiology, community ecology, and scales of ecological pattern. *Ecology* 77:1367–1378.
- Johnson, D. G., B. C. Carstens, W. S. Sheppard, and R. S. Zach. 2005. Phylogeny of leafhopper subgenus *Errhomus* (*Erronus*) (Hemiptera: Cicadellidae) based on mitochondrial DNA sequences. *Annals of the Entomological Society of America* 98:165–172.
- Kadereit, J. W., E. M. Greibler, and H. P. Comes. 2004. Quaternary diversification in European alpine plants: pattern and process. *Philosophical Transactions of the Royal Society B: Biological Sciences* 359:265–274.
- Kaneshiro, K. Y. 1988. Speciation in the Hawaiian *Drosophila*: sexual selection appears to play an important role. *BioScience* 38:258–263.
- Kay, K. M., P. A. Reeves, R. G. Olmstead, and D. W. Schemske. 2005. Rapid speciation and the evolution of hummingbird pollination in Neotropical *Costus* subgenus *Costus* (Costaceae): evidence from nrDNA ITS and ETS sequences. *American Journal of Botany* 92:1899–1910.
- King, M. 1993. *Species evolution: the role of chromosome change*. Cambridge University Press, Cambridge.
- Kirchner, J. W., and A. Weil. 2000a. Correlations in fossil extinction and origination rates through geological time. *Proceedings of the Royal Society B: Biological Sciences* 267:1301–1309.
- . 2000b. Delayed biological recovery from extinction throughout the fossil record. *Nature* 404:177–180.
- Kozak, K. H., D. W. Weisrock, and A. Larson. 2006. Rapid lineage accumulation in a non-adaptive radiation: phylogenetic analysis of diversification rates in eastern North American woodland salamanders (Plethodontidae: *Plethodon*). *Proceedings of the Royal Society B: Biological Sciences* 273:539–546.
- Kuhner, M. K., and J. Felsenstein. 1994. A simulation comparison of phylogeny algorithms under equal and unequal evolutionary rates. *Molecular Biology and Evolution* 11:459–468.
- Lande, R., S. Engen, and B.-E. Sæther. 2003. Stochastic population

- dynamics in ecology and conservation. Oxford University Press, Oxford.
- Lawton, J. H., and R. M. May. 1995. Extinction rates. Oxford University Press, Oxford.
- Leibold, M. A., and M. A. McPeck. 2006. Coexistence of the niche and neutral perspectives in community ecology. *Ecology* 87:1399–1410.
- Linder, H. P., P. Eldenäs, and B. G. Briggs. 2003. Contrasting patterns of radiation in African and Australian Restionaceae. *Evolution* 57:2688–2702.
- Lledo, M. D., M. B. Crespo, M. F. Fay, and M. W. Chase. 2005. Molecular phylogenetics of *Limonium* and related genera (Plumbaginaceae): biogeographical and systematic implications. *American Journal of Botany* 92:1189–1198.
- MacArthur, R. H. 1965. Patterns of species diversity. *Biological Reviews of the Cambridge Philosophical Society* 40:510–533.
- Machordom, A., and E. Macpherson. 2004. Rapid radiation and cryptic speciation in squat lobsters of the genus *Munida* (Crustacea, Decapoda) and related genera in the south west Pacific: molecular and morphological evidence. *Molecular Phylogenetics and Evolution* 33:259–279.
- Maurer, B. A. 1989. Diversity-dependent species dynamics: incorporating the effects of population-level processes on species dynamics. *Paleobiology* 15:133–146.
- Mayr, E. 1942. *Systematics and the origin of species*. Columbia University Press, New York.
- McKaye, M. 1991. Sexual selection and the evolution of cichlid fishes of Lake Malawi, Africa. Pages 241–257 in M. H. A. Keenleyside, ed. *Cichlid fishes: behavior, ecology and evolution*. Chapman & Hall, New York.
- McKenna, D. D., and B. D. Farrell. 2005. Molecular phylogenetics and evolution of host plant use in the Neotropical rolled leaf “hispanic” beetle genus *Cephaloleia* (Chevrolat) (Chrysomelidae: Caddiinae). *Molecular Phylogenetics and Evolution* 37:117–131.
- McPeck, M. A. 2007. The macroevolutionary consequences of ecological differences among species. *Palaeontology* 50:111–129.
- McPeck, M. A., and J. M. Brown. 2000. Building a regional species pool: diversification of the *Enallagma* damselflies in eastern North American waters. *Ecology* 81:904–920.
- . 2007. Clade age and not diversification rate explains species richness among animal taxa. *American Naturalist* 169:E97–E106.
- McPeck, M. A., L. Shen, J. Z. Torrey, and H. Farid. 2008. The tempo and mode of three-dimensional morphological evolution in male reproductive structures. *American Naturalist* 171:E158–E178.
- Mooers, A. Ø., and S. B. Heard. 1997. Inferring evolutionary process from phylogenetic tree shape. *Quarterly Review of Biology* 72:31–54.
- Mooers, A. Ø., L. J. Harmon, M. G. B. Blum, D. H. J. Wong, and S. B. Heard. 2007. Some models of phylogenetic tree shape. Pages 149–170 in O. Gascuel and M. Steel, eds. *Reconstructing evolution: new mathematical and computational advances*. Oxford University Press, Oxford.
- Morrison, C. L., R. Rios, and J. E. Duffy. 2004. Phylogenetic evidence for an ancient rapid radiation of Caribbean sponge-dwelling snapping shrimps (*Synalpheus*). *Molecular Phylogenetics and Evolution* 30:563–581.
- Nee, S. 2001. Inferring speciation rates from phylogenies. *Evolution* 55:661–668.
- . 2006. Birth-death models in macroevolution. *Annual Review of Ecology and Systematics* 37:1–17.
- Nee, S., A. Ø. Mooers, and P. H. Harvey. 1992. Tempo and mode of evolution revealed by molecular phylogenies. *Proceedings of the National Academy of Sciences of the USA* 89:8322–8326.
- Nee, S., E. C. Holmes, R. M. May, and P. H. Harvey. 1994a. Extinction rates can be estimated from molecular phylogenies. *Philosophical Transactions of the Royal Society B: Biological Sciences* 344:77–82.
- Nee, S., R. M. May, and P. H. Harvey. 1994b. The reconstructed evolutionary process. *Philosophical Transactions of the Royal Society B: Biological Sciences* 344:305–311.
- Odling-Smee, F. J., K. N. Laland, and M. W. Feldman. 2003. *Niche construction: the neglected process in evolution*. Princeton University Press, Princeton, NJ.
- Paradis, E. 2004. Can extinction rates be estimated without fossils? *Journal of Theoretical Biology* 229:19–30.
- Parra-Olea, G., M. Garcia-Paris, and D. B. Wake. 2004. Molecular diversification of salamanders of the tropical American genus *Bolitoglossa* (Caudata: Plethodontidae) and its evolutionary and biogeographical implications. *Biological Journal of the Linnean Society* 81:325–346.
- Pfenninger, M., and K. Schwenk. 2007. Cryptic animal species are homogeneously distributed among taxa and biogeographic regions. *BMC Evolutionary Biology* 121:121–126.
- Phillimore, A. B., and T. D. Price. 2008. Density-dependent cladogenesis in birds. *PLoS Biology* 6:0483–0489.
- Pimm, S. L. 1979. Sympatric speciation: a simulation model. *Biological Journal of the Linnean Society* 11:131–139.
- Price, T. 2008. *Speciation in birds*. Roberts, Greenwood Village, CO.
- Primack, R. 2006. *Essentials of conservation biology*. 4th ed. Sinauer, Sunderland, MA.
- Przeworski, M., and J. D. Wall. 1998. An evaluation of a hierarchical branching process as a model for species diversification. *Paleobiology* 24:498–511.
- Pybus, R. G., and P. H. Harvey. 2000. Testing macro-evolutionary models using incomplete molecular phylogenies. *Proceedings of the Royal Society B: Biological Sciences* 267:2267–2272.
- Rabosky, D. L. 2006. Likelihood methods for detecting temporal shifts in diversification rates. *Evolution* 60:1152–1164.
- Rabosky, D. L., and I. J. Lovette. 2008. Explosive evolutionary radiations: decreasing speciation or increasing extinction through time? *Evolution* 62:1866–1875.
- Ramsey, J., and D. W. Schemske. 1998. Pathways, mechanisms, and rates of polyploid formation in flowering plants. *Annual Review of Ecology and Systematics* 29:467–501.
- . 2002. Neopolyploidy in flowering plants. *Annual Review of Ecology and Systematics* 33:589–639.
- Raup, D. M. 1985. Mathematical models of cladogenesis. *Paleobiology* 11:42–52.
- . 1991. *Extinction: bad genes or bad luck?* Norton, New York.
- Raup, D. M., S. J. Gould, T. J. M. Schopf, and D. S. Simberloff. 1973. Stochastic models of phylogeny and the evolution of diversity. *Journal of Geology* 81:525–542.
- Ready, J. S., I. Sampaio, H. Schneider, C. Vinson, T. dos Santos, and G. F. Turner. 2006. Colour forms of Amazonian cichlid fish represent reproductively isolated species. *Journal of Evolutionary Biology* 19:1139–1148.
- Revell, L. J., L. J. Harmon, and R. E. Glor. 2005. Underparameterized model of sequence evolution leads to bias in the estimation of diversification rates from molecular phylogenies. *Systematic Biology* 54:973–983.

- Ricklefs, R. E. 1987. Community diversity: relative roles of local and regional processes. *Science* 235:167–171.
- . 1989. Speciation and diversity: the integration of local and regional processes. Pages 599–622 in D. Otte and J. A. Endler, eds. *Speciation and its consequences*. Sinauer, Sunderland, MA.
- Ricklefs, R. E., and D. Schluter. 1993. Species diversity in ecological communities. University of Chicago Press, Chicago.
- Rieseberg, L. H. 1997. Hybrid origins of plant species. *Annual Review of Ecology and Systematics* 28:359–389.
- Rosenzweig, M. L. 1978. Competitive speciation. *Biological Journal of the Linnean Society* 10:275–289.
- Rüber, L., and R. Zardoya. 2005. Rapid cladogenesis in marine fishes revised. *Evolution* 59:1119–1127.
- Schluter, D. 2000. *The ecology of adaptive radiation*. Oxford University Press, Oxford.
- Seehausen, O., J. J. M. van Alphen, and F. Witte. 1997. Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* 277:1808–1811.
- Sepkoski, J. J., Jr. 1978. A kinetic model of Phanerozoic taxonomic diversity. I. Analysis of marine orders. *Paleobiology* 4:223–252.
- . 1979. A kinetic model of Phanerozoic taxonomic diversity. I. Early Phanerozoic families and multiple equilibria. *Paleobiology* 5:222–251.
- . 1998. Rates of speciation in the fossil record. *Philosophical Transactions of the Royal Society B: Biological Sciences* 353:315–326.
- Shaw, A. J., C. J. Cox., B. Goffinet, W. R. Buck, and S. B. Boles. 2003. Phylogenetic evidence of a rapid radiation of pleurocarpous mosses (Bryophyta). *Evolution* 57:2226–2241.
- Simpson, B. B., A. Weeks, D. M. Helfgott, and L. L. Larkin. 2004. Species relationships in *Krameria* (Krameriaceae) based on ITS sequences and morphology: implications for character utility and biogeography. *Systematic Botany* 29:97–108.
- Simpson, G. G. 1944. *Tempo and mode in evolution*. Columbia University Press, New York.
- . 1953. *The major features of evolution*. Columbia University Press, New York.
- Sorenson, M. D., C. N. Balakrishnan, and R. B. Payne. 2004. Clade-limited colonization in brood parasitic finches (*Vidua* spp.). *Systematic Biology* 53:140–153.
- Stanley, S. M. 1998. *Macroevolution: pattern and process*. Johns Hopkins University Press, Baltimore.
- . 2007. An analysis of the history of marine animal diversity. *Paleobiology* 33:1–55.
- . 2008. Predation defeats competition on the seafloor. *Paleobiology* 34:1–21.
- Stoks, R., and M. A. McPeck. 2006. A tale of two diversifications: reciprocal habitat shifts to fill ecological space along the pond permanence gradient. *American Naturalist* 168(suppl.):S50–S72.
- Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences of the USA* 101:10854–10861.
- Turchin, P. 2003. *Complex population dynamics: a theoretical/empirical synthesis*. Princeton University Press, Princeton, NJ.
- Turgeon, J., R. Stoks, R. A. Thum, J. M. Brown, and M. A. McPeck. 2005. Simultaneous Quaternary radiations of three damselfly clades across the Holarctic. *American Naturalist* 165:E78–E107.
- Turner, G. E., O. Seehausen, M. E. Knight, C. J. Allender, and R. L. Robinson. 2001. How many species of cichlid fishes are there in African lakes? *Molecular Ecology* 10:793–806.
- Walker, T. D., and J. W. Valentine. 1984. Equilibrium models of evolutionary species diversity and the number of empty niches. *American Naturalist* 124:887–899.
- Webb, C. O., D. D. Ackerly, M. A. McPeck, and M. J. Donoghue. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33:475–505.
- Weir, J. 2006. Divergent timing and patterns of species accumulation in lowland and highland Neotropical birds. *Evolution* 60:842–855.
- Williams, S. T., and D. G. Reid. 2004. Speciation and diversity on tropical rocky shores: a global phylogeny of snails of the genus *Echinolittorina*. *Evolution* 58:2227–2251.
- Witt, J. D. S., and P. D. N. Hebert. 2000. Cryptic species diversity and evolution in the amphipod genus *Hyaella* within central glaciated North America: a molecular phylogenetic approach. *Canadian Journal of Fisheries and Aquatic Sciences* 57:687–698.
- Xiang, Q.-Y., S. R. Manchester, D. T. Thoma, W. Zhang, and C. Fan. 2005. Phylogeny, biogeography, and molecular dating of cornelian cherries (*Cornus*, Cornaceae): tracking Tertiary plant migration. *Evolution* 59:1685–1700.

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