

When should we expect early bursts of trait evolution in comparative data? Predictions from an evolutionary food web model

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Keywords:

body size;
Brownian motion;
early burst model;
evolutionary assembly model;
omnivory;
Ornstein-Uhlenbeck model;
trophic position.

Abstract

Conceptual models of adaptive radiation predict that competitive interactions among species will result in an early burst of speciation and trait evolution followed by a slowdown in diversification rates. Empirical studies often show early accumulation of lineages in phylogenetic trees, but usually fail to detect early bursts of phenotypic evolution. We use an evolutionary simulation model to assemble food webs through adaptive radiation, and examine patterns in the resulting phylogenetic trees and species' traits (body size and trophic position). We find that when foraging trade-offs result in food webs where all species occupy integer trophic levels, lineage diversity and trait disparity are concentrated early in the tree, consistent with the early burst model. In contrast, in food webs in which many omnivorous species feed at multiple trophic levels, high levels of turnover of species' identities and traits tend to eliminate the early burst signal. These results suggest testable predictions about how the niche structure of ecological communities may be reflected by macroevolutionary patterns.

Introduction

Comparative methods increasingly allow us to use molecular phylogenies to test hypotheses about evolutionary radiations, including adaptive radiations in which a common ancestor diversifies into an ecologically and phenotypically diverse clade (Schluter, 2000). In a classic vision of adaptive radiation, a clade experiencing ecological opportunity undergoes an 'early burst' of rapid speciation and trait evolution, followed by a reduction in diversification rates as ecological space becomes full (Simpson, 1953). This conceptual model makes two key predictions about extant members of a clade: most branching events in a reconstructed phylogenetic tree will occur early in the clade's evolutionary history, and earlier branching events will account for most of the disparity (phenotypic diversity) among species. The first of these predictions is often supported

by data, as models in which speciation rates are initially high and decline over time can explain the branching structure of many empirical phylogenetic trees (McPeck, 2008; Phillimore & Price, 2008; Rabosky & Lovette, 2008). In contrast, models in which the rate of morphological evolution slows over time fail to explain the phylogenetic distribution of body size and shape in most clades, including many recognized as classic adaptive radiations (Harmon *et al.*, 2010). When early bursts of morphological evolution are detected, it is often at the scale of very large and old clades such as birds (Harmon *et al.*, 2010) or mammals (Cooper & Purvis, 2010). Although these analyses have not typically been applied to the same sets of clades (but see Harmon *et al.*, 2003), when considered together they suggest that speciation rates may indeed decline as diversity accumulates, but that the same trend may not apply to trait evolution (Yoder *et al.*, 2010). To address this apparent paradox, it will be useful to develop theoretical predictions for the ecological conditions under which we should expect both lineage diversity and trait disparity to conform to the early burst pattern.

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The early burst model of adaptive radiation usually involves ecological opportunity for the radiating species resulting from invasion of a depauperate habitat, extinction of competitors, or the evolution of a 'key innovation' (Yoder *et al.*, 2010). Whatever its cause, the early burst is expected to be followed by reduced diversification rates, as increased species richness results in stronger constraints due to interspecific competition. More generally, biotic interactions among lineages are important elements of many conceptual models of macroevolution (Simpson, 1953; Jablonski, 2008), as well as key drivers of contemporary evolution (Reznick *et al.*, 1997; Grant & Grant, 2006). Unfortunately, it is challenging to incorporate such biotic interactions directly into analytically tractable comparative methods. Many such methods make simplifying assumptions such as homogeneity of evolutionary processes and rates, or shifts in rates that occur uniformly across the tree (Felsenstein, 1985; Blomberg *et al.*, 2003; Harmon *et al.*, 2010). Although more flexible methods are being developed that can allow for heterogeneity in evolutionary rates and selective regimes across the tree (Butler & King, 2004; O'Meara *et al.*, 2006; Eastman *et al.*, 2011), they typically cannot incorporate interactions between lineages. A recent methodological advance in this direction models the rate of evolution declining in proportion to the (inferred) number of competing species (Mahler *et al.*, 2010). This method indicates that species interactions result in early burst-like patterns in the body size and limb lengths of Caribbean *Anolis* lizards, a result that is not clearly supported by an early burst model that assumes a uniform rate decline across the tree (Harmon *et al.*, 2010). This approach is promising, but substantial work remains before comparative methods will allow the explicit inclusion of multiple types of species interactions.

While we await the development of methods that account for species interactions directly, we demonstrate in this paper an alternative approach to infer how these interactions shape the outcome of evolutionary radiations. We simulate data using a mechanistic model that includes a range of species interactions, including resource and interference competition as well as predation. Using the resulting trait data and phylogenetic trees, we then fit simple macroevolutionary models that describe the tempo of trait evolution, focusing on the contrast between early bursts and later accumulation of trait disparity. The simulation model focuses on food web interactions, allowing complex trophic structures to emerge through speciation, extinction and trait evolution, subject to constraints imposed by size-structured consumer–resource interactions. Several such evolutionary assembly models have been shown to produce broadly realistic food web structures using a few simple ecological rules (McKane, 2004; Loeuille & Loreau, 2005; Rossberg *et al.*, 2005; Guill & Drossel, 2008). We previously used one of these models to predict a positive relationship between an aspect of food web structure

(the mean value of a quantitative measure of omnivory) and rates of species turnover, which resulted from variation in model foraging parameters (Ingram *et al.*, 2009). Here, we extend these results to explore whether macroevolutionary patterns of trait evolution – in particular the early burst pattern – can also be predicted by the structure of the food web and the rules governing its assembly.

We examine the evolution of two ecologically important traits: body size and trophic position. Body size is the best-studied trait in comparative analyses (Cooper & Purvis, 2010; Harmon *et al.*, 2010), because it is both easily measured and important for nearly all aspects of organismal ecology and physiology (Peters, 1983). Trophic position, a continuous measure of trophic level quantified as the average number of trophic steps separating a species from the base of its food web, is a more direct measure of a species' functional role. The distribution of species' trophic positions captures crucial aspects of trophic structure and can be quantified using food web link data (Levine, 1980; Williams & Martinez, 2004) or nitrogen isotope ratios (Post, 2002). While some adaptive radiations involve little diversification in trophic position (e.g. many clades of phytophagous insects; Mitter *et al.*, 1988), many clades evolve considerable trophic position diversity. For example, herbivory has repeatedly evolved in liolaemid lizards (Espinoza *et al.*, 2004), as has piscivory in centrarchid fish (Collar *et al.*, 2009), and a wide range of feeding strategies in African cichlid radiations (Rüber *et al.*, 1999; Wagner *et al.*, 2009). Trophic position has only rarely been studied in a macroevolutionary context. Some signal of phylogeny has been detected in trophic position based on food web link data for a taxonomically diverse assemblage of Caribbean fishes (Rezende *et al.*, 2009) and based on nitrogen stable isotopes in Lake Tanganyika cichlids (Wagner *et al.*, 2009), Pacific rockfish (Ingram, 2011) and Antarctic notothenioid fishes (Rutschmann *et al.*, 2011). One of the goals of the present study is to generate biological hypotheses about macroevolutionary patterns of trophic position and to motivate additional empirical studies.

We focus on three simple macroevolutionary models that differ in how trait disparity accumulates over time. Under Brownian motion (BM), traits evolve following a random walk with a constant rate of diffusion over time, which may result from genetic drift or adaptive evolution towards a randomly moving optimum trait value (Felsenstein, 1985). Under BM, the variance among independently evolving lineages increases linearly with time. This contrasts with some empirical results suggesting that variance plateaus over sufficiently long time periods (Ackerly, 2009; Harmon *et al.*, 2010), and with a similar evolutionary food web assembly model (related to the model described here), in which body size disparity stops increasing after the early stages of assembly (Stegen & Swenson, 2009). There are two distinct reasons that

total trait disparity may plateau over time. The first is that the rate of trait evolution slows, as in the early burst model. We focus on an implementation of the early burst model in which evolution occurs by BM, but with a rate of diffusion that declines exponentially over time (Blomberg *et al.*, 2003; Harmon *et al.*, 2010). This simple model can serve as an approximation for models where rapid early trait evolution leads to different lineages occupying distinct and stable adaptive peaks. Under the early burst model, the earliest divergences in the phylogenetic tree account for a substantial fraction of the total trait disparity in a clade. The other reason trait disparity may plateau is that although evolution continues at a relatively high rate, there are constraints on the extent of trait space that can be explored. The Ornstein-Uhlenbeck (OU) model combines a random walk with a deterministic tendency for trait values to return to an 'optimum' intermediate value. This model can describe stabilizing selection with a single optimum trait value, and may also provide a reasonable description of a random walk with bounds on trait space, or adaptation to a fluctuating optimum that is itself constrained (Hansen & Martins, 1996; Hansen, 1997; Estes & Arnold, 2007). Because the same trait space is explored repeatedly, earlier divergence is 'overwritten' and recent evolution accounts for most of the total trait disparity in a clade evolving under the OU model.

We simulate the evolution of body size and trophic position under a range of ecological conditions, and examine the distributions of these traits on the resulting phylogenetic trees. We find that the early burst model of trait evolution performs best in simulations where food webs have distinct trophic levels, whereas when omnivory is prevalent the trait data are more likely to fit the BM or OU models. This result is consistent with our earlier finding that species turnover is also higher in more omnivorous food webs (Ingram *et al.*, 2009). We interpret these results as reflecting variation in the degree to which trophic niches are stable throughout the evolutionary history of clades and suggest testable hypotheses about the links between ecology and macroevolutionary patterns.

Model presentation

Here we briefly describe the key features of the evolutionary assembly model. Ingram *et al.* (2009) provide a detailed description of the model, which was modified from a model by Loeuille & Loreau (2005).

The model simulates the radiation of a single ancestor into a food web containing a diversity of feeding morphs (for clarity we refer to these as species, although the model does not treat reproductive isolation directly). Each species i is defined by two traits: its body size x_i (on a \log_{10} scale), and its niche width s_i . Predation is size-structured such that each consumer most efficiently feeds on prey $x_i - d$ smaller than itself, where $d = 2$ for all

species (Barnes *et al.*, 2010), while its niche width determines the shape of its Gaussian resource utilization function. This imposes a trade-off where higher s_i increases the range of prey sizes a consumer can eat, at the expense of a reduced attack rate on its preferred prey size. The strength of this trade-off is modified by two model parameters: an 'optimum' niche width s_0 , and a cost parameter c , higher values of which result in greater penalization of attack rates as species deviate from s_0 . Different values of these parameters can confer fitness advantages to trophic generalists (high s_0 , high c), specialists (low s_0 , high c) or neither (low c), and may reflect ecological factors such as the degree of environmental heterogeneity experienced by foragers (Ingram *et al.*, 2009).

The food web is supported by a single basal resource, which has open population dynamics but does not evolve. For each species in the food web, growth in population biomass is based on its total consumption of smaller species, which in turn depends on its utilization function and the body sizes and biomasses of each prey species. Metabolic conversion efficiency follows basic allometric scaling that declines with body size (Barnes *et al.*, 2010), and consumers have weakly saturating type II functional responses. Population losses come from predation by larger species, weak Gaussian interference competition between similar-sized species and intrinsic mortality that also declines allometrically with body size (Loeuille & Loreau, 2005).

The model begins with a single consumer species feeding on the basal resource. With low probability at each timestep, one extant species is selected to give rise to a daughter species with trait values x and s drawn from normal distributions around the parent trait values (with s.d. σ_x and σ_s). This may be followed by one of several outcomes, depending on the fitness (population growth rate when rare) of the new species. If its growth rate is negative, it will fail to establish in the community, whereas if its growth rate is positive, it will establish in the community and increase in density. Subsequently, the new species may drive its parent species to extinction, or if the two are sufficiently different from one another to prevent exclusion, both species may coexist. Although trait change occurs in discrete steps at speciation, trait evolution in the model can approximate both directional evolution within lineages (when daughter species replace parents) and evolutionary branching (when the two coexist). Thus, discrete mutations can result in the appearance of continuous trait evolution, as occurs in a related model that employs adaptive dynamics (Brännström *et al.*, 2011). This makes it reasonable to fit continuous macroevolutionary models (EB, BM and OU) to the simulated trait data.

We analysed the set of simulations presented by Ingram *et al.* (2009): 20 simulated food webs under each of 12 parameter combinations (Table 1). Simulations

Table 1 Parameter values used in simulations, and macroevolutionary model fits.*

c	s ₀	σ _x	σ _s	N	O	TP			Size		
						W _{EB}	W _{BM}	W _{OU}	W _{EB}	W _{BM}	W _{OU}
4.0	0.5	0.2	0.1	20	0.00	0.91	0.06	0.02	0.55	0.24	0.22
		0.5	0.2	20	0.00	0.94	0.04	0.02	0.64	0.21	0.15
	1.0	0.2	0.1	20	0.09	0.76	0.11	0.13	0.77	0.06	0.17
		0.5	0.2	20	0.09	0.59	0.27	0.14	0.60	0.25	0.15
0.5	0.5	0.2	0.1	20	0.03	0.94	0.05	0.02	0.77	0.13	0.10
		0.5	0.2	20	0.04	0.73	0.14	0.13	0.68	0.23	0.10
	1.0	0.2	0.1	20	0.11	0.71	0.15	0.14	0.67	0.10	0.23
		0.5	0.2	20	0.11	0.22	0.41	0.37	0.18	0.47	0.35
0	0.5	0.2	0.1	13	0.40	0.30	0.57	0.13	0.22	0.61	0.17
		0.5	0.2	20	0.42	0.14	0.30	0.56	0.11	0.36	0.53
	1.0	0.2	0.1	15	0.30	0.23	0.49	0.28	0.13	0.52	0.35
		0.5	0.2	20	0.43	0.10	0.29	0.62	0.12	0.42	0.46

EB, early burst; BM, Brownian motion; OU, Ornstein-Uhlenbeck.

N is the number of successful simulations used in the analysis, and O is Mean Omnivory. O and Akaike weights are averaged across all replicates for each parameter combination.

*See text for definitions of parameters.

were conducted with absent, moderate and strong costs ($c = 0, 0.5$, and 4), small or large optimum niche widths ($s_0 = 0.5$ and 1) and low or high mutational variances ($\sigma_x = 0.25$ and 0.5 , $\sigma_s = 0.1$ and 0.2). Each simulation lasted 10^6 generations, at which time the model had generally reached a 'quasi-equilibrium' state where the properties of the system were stable despite some turnover in species identity. We excluded 12 simulations in which a diverse food web failed to evolve or collapsed (maximum trophic position < 1.1), which occasionally occurred with $c = 0$ and low σ_x and σ_s . This left 228 simulations with between 7 and 69 taxa each for analyses of trophic structure and trait evolution.

We retained the phylogenetic tree relating all extant species, pruned to exclude extinct lineages. This mimics a typical data set where a phylogenetic tree and trait data are available for extant species, but the number and characteristics of extinct species are unknown. We scaled each tree to a total depth of 1.0 time units. For trait data, we used body sizes x of each extant species, as well as trophic position estimated from biomass flow in the food web. Trophic position is calculated as the mean number of trophic steps separating a species from the basal resource (Levine, 1980). As a measure of trophic structure that incorporates the quantitative flow of energy, we calculated the mean value across all species of a measure of omnivory. Omnivory, broadly defined as feeding at multiple trophic levels, can be quantified on a continuous scale as the variance in trophic positions of a consumer's prey items, weighted by their importance in its diet (Levine, 1980; Williams & Martinez, 2004). Calculations at different points during simulations showed that in most cases trophic structure established early and remained relatively consistent, so mean omnivory reflects the trophic structure throughout a simulation.

Evolutionary model fitting

We fit the EB, BM and OU models to simulated trait data (trophic position and body size) using maximum likelihood. The BM model has two parameters: the Brownian rate parameter σ^2 , which describes the rate of diffusion, and the ancestral state at the root of the tree (\bar{z}_0), calculated as the phylogenetically weighted mean trait value (Felsenstein, 1985; O'Meara *et al.*, 2006). The early burst model has three parameters: the initial rate σ_0^2 , the exponent a that describes how fast the rate declines, and \bar{z}_0 (Blomberg *et al.*, 2003; Harmon *et al.*, 2010). The OU model has four parameters: σ^2 , the strength of the constraining force α , the optimum trait value θ , and \bar{z}_0 (Hansen, 1997). However, for an ultrametric tree the OU model reduces to three parameters because the maximum likelihood estimate of θ is equal to \bar{z}_0 . The BM model is a special case of the early burst model (when $a = 0$) and the OU model (when $\alpha = 0$).

Each of the three models results in multivariate normal expected trait values, with covariance matrix \mathbf{V} and the expected value for each species equal to \bar{z}_0 . We can obtain \mathbf{V} from the model parameters by transforming the elements of a matrix representing the structure of the tree: the early burst model increases the influence of early branches, whereas the OU model increases the influence of more recent events (Blomberg *et al.*, 2003; O'Meara *et al.*, 2006; Harmon *et al.*, 2010). For a given model, the likelihood is calculated as the multivariate normal distribution, and the parameter values can be identified that maximize the likelihood. For each simulated data set, we used optimization routines implemented in the *geiger* package (Harmon *et al.*, 2008) in the R environment (R Development Core Team, 2011) to calculate the maximum likelihood values of the parameters of each of the three models. We used these

likelihoods to calculate the small sample size-corrected Akaike Information Criterion (AIC_c), which balances model fit and complexity (Burnham & Anderson, 2002). Comparative methods using AIC_c will not always have sufficient power to support a more complex model when it is correct (Boettiger *et al.*, 2012). Simulations under the EB, BM and OU models with biologically realistic parameter values have shown that AIC_c can usually identify the correct model even for 10-taxon trees, although larger trees may be required to recover the early burst model (Harmon *et al.*, 2010). We converted AIC_c values to Akaike weights (w_A), which range from 0–1 and can be interpreted as the relative support for a model out of the set of models under consideration (Burnham & Anderson, 2002).

We compared the w_A for each of the three models to our measure of trophic structure, mean omnivory. We used Spearman's rank correlation (ρ), which provides a robust, nonparametric measure of a monotonic association between variables that does not require transformation to achieve linearity or bivariate normality. We focus on the direction and magnitude of relationships rather than significance values, which are an arbitrary result of the number of simulations conducted.

We also examined links between patterns of trait evolution and lineage accumulation. We quantified the temporal distribution of nodes in the phylogenetic tree using the γ statistic (Pybus & Harvey, 2000), which takes on more negative values when most extant lineages accumulated early in the tree and more positive values when lineage accumulation is biased towards the present. As a simple index of the temporal dynamics of trait diversification, we used the maximum likelihood value of Pagel's δ (Pagel, 1999). The δ parameter scales path lengths in the tree so that trait disparity is more influenced by branches towards the root ($\delta < 1$) or tips of the tree ($\delta > 1$). δ does not explicitly model an evolutionary process, but it provides a single parameter that can mimic the behaviour of the early burst ($\delta < 1$), BM ($\delta \approx 1$) or OU ($\delta > 1$) models. We log-transformed delta values, so negative values of γ or $\log \delta$ indicate early burst patterns of lineage accumulation or trait diversification, respectively. We used Spearman's rank correlation to examine whether γ was correlated with δ for either trophic position or body size, and thus whether lineage and trait diversity showed similar temporal patterns (Harmon *et al.*, 2003).

Results

These analyses revealed intriguing links between trophic structure, trait evolution and lineage accumulation in the model. We found that the relative fit of the early burst model to trait data was related to the extent of omnivory in the food web, which in turn depended on the parameters governing foraging trade-offs (Table 1; Ingram *et al.*, 2009). When there was a strong intrinsic

fitness advantage to trophic specialists (low s_0 and high c), food webs included very little omnivory and most species occupied integer trophic levels. In these simulations, the early burst model tended to fit best for both trophic position and body size (Table 1; Fig. 1a,b), although there was substantial variation in the Akaike weights. In simulations in which food webs were characterized by extensive omnivory, the early burst model generally fit very poorly, and either the BM or OU models received the most support. These visual patterns were reflected by Spearman's rank correlations between Akaike weights and mean omnivory; relationships were generally stronger for trophic position (EB: $\rho = -0.74$; BM: $\rho = 0.62$; OU: $\rho = 0.73$) than for body size (EB: $\rho = -0.40$; BM: $\rho = 0.28$; OU: $\rho = 0.47$) but had similar shapes. The concordance of patterns for the two traits is unsurprising, as the size-structured framework of the model results in strong relationships between size and trophic position. Akaike weights for the three models were not related to the number of surviving species in the food web (all $-0.02 < \rho < 0.06$), suggesting that tree sizes were large enough to detect support for any of the three models, and that variation in model support comes from structural features of the food webs other than species richness.

Across the range of model conditions investigated, we found that the tempo of lineage diversification tended to be linked to the tempo of trait evolution (Fig. 1c,d). Simulations in which lineage accumulation occurs early in the phylogenetic tree (negative γ) also tended to feature early burst patterns for trophic position and body size (negative $\log \delta$), whereas higher values of γ tended to be accompanied by higher $\log \delta$ (although the relationship for body size may be somewhat unimodal). Our model thus produces a continuum of outcomes, the extremes of which are presented in Fig. 2. In simulations in which the food web has very little omnivory, nodes are biased towards the root of the tree, and trait diversity (e.g. trophic position) is partitioned mainly among subclades that diverged early (Fig. 2a). In contrast, in simulations in which the food web contains many omnivores, high turnover leads to nodes in the tree biased towards the tips and partitioning of trait disparity within rather than among subclades (Fig. 2b).

Discussion

According to classic ideas about adaptive radiation, both early bursts of trait evolution and early accumulation of lineages in phylogenetic trees should be widespread. Many empirical trees show the early lineage accumulation (McPeck, 2008; Phillimore & Price, 2008; Rabosky & Lovette, 2008) expected from a slowdown in speciation rates (but see Etienne & Rosindell, 2012), but a broad survey of trait data sets rarely found evidence for the early burst pattern (Harmon *et al.*, 2010). Our simulations rarely resulted in early lineage accumulation but not early bursts

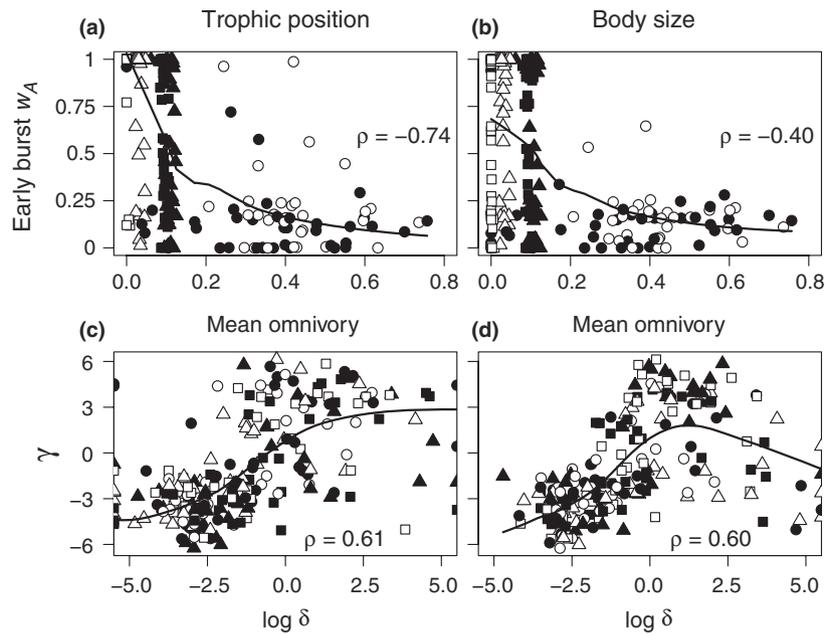


Fig. 1 Relationships between food web structure, evolutionary model fits and phylogenetic tree shape. The degree of omnivory in the model food webs is negatively related to the relative support (Akaïke Weight) for the early burst (EB) model for both trophic position (a) and body size (b). Variation in model parameters resulted in a correlation between $\log \delta$ and γ for both traits (c, d), where negative values of $\log \delta$ indicate early bursts of trait evolution, while negative γ indicates early accumulation of extant lineages. Symbols indicate values of the key model parameters: optimal niche width (open symbols: $s_0 = 0.5$; filled symbols: $s_0 = 1$) and cost of deviating from s_0 (circles: $c = 0$; triangles: $c = 0.5$; squares: $c = 4$). Lines are locally weighted polynomial regressions (lowess) with a smoothing parameter of 0.75. In (c) and (d), some $\log \delta$ values were too extreme to display clearly; their corresponding γ values are indicated by the symbols that overlap the edge of the panel.

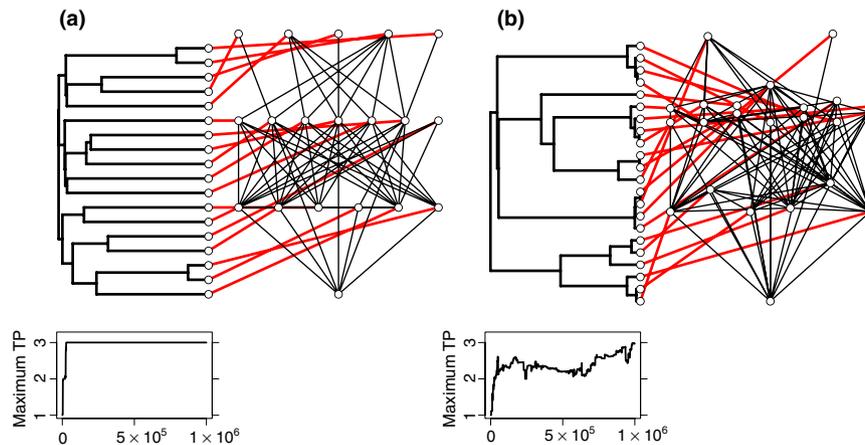


Fig. 2 Phylogenetic trees and food webs produced by model simulations that illustrate the range of outcomes described here. Trees are pruned to include only extant species, which are connected to the corresponding species in the food web to indicate the phylogenetic structure of the food web. Vertical positions in the food web indicate species' trophic positions, and links connect predators to their prey (minimum 5% of diet). (a) Stability of trophic niches results in early accumulation of both lineage diversity and trophic position disparity in a simulation in which the food web has discrete trophic levels (mean omnivory < 0.01). (b) Higher species turnover results in more recent accumulation of lineage diversity and trait disparity in a simulation in which the food web contains extensive omnivory (mean omnivory = 0.35). Panels below each phylogenetic tree show the maximum trophic position present in the food web over the course of the simulation.

of trait evolution (i.e. low γ and high δ), so they do not address the disconnect directly. However, it is important to note that the lack of an early burst pattern in comparative data does not mean that early stages of a radiation did not involve the evolution of considerable species diversity and morphological disparity. Indeed, all types of food webs in our model reached a high diversity and trait disparity early in the simulation (see also Stegen & Swenson, 2009). Instead, the persistence of an early burst pattern will depend on the extent to which there is subsequent turnover in lineages and traits through speciation, extinction and recurrent trait evolution. In our model, speciation was defined by divergence in body size; models in which speciation and ecological divergence are governed by different factors may be useful in resolving the apparent contradiction between lineage accumulation and trait disparity seen in empirical studies.

The patterns presented here suggest that early burst patterns in trait data should indeed be expected in some situations, but that their prevalence may vary among taxa and ecosystems. We found that the prevalence of omnivory in food webs was predictive of whether the early burst pattern persisted. This variation in food web structure in turn depended on the ecological parameters that dictate the strength of the trade-off experienced by foragers; trade-offs that favoured trophic specialists were associated with early bursts followed by relatively low turnover. Our model therefore suggests that the rarity of early burst patterns in empirical data sets may be explained in part by the ubiquity of omnivory in natural food webs and predicts that variation in the degree of omnivory (Williams & Martinez, 2004; Thompson *et al.*, 2007) should predict the occurrence of EBs. As measures of omnivory are available for many organisms (Williams & Martinez, 2004), it should be possible to test whether early bursts are more common in clades containing more omnivorous taxa. However, this prediction is conditional on certain assumptions of our model. First, feeding interactions in our model are strongly size-structured: this is often true in nature (Barnes *et al.*, 2010), but the predictions related to body size do not apply in taxa that lack size-structure. Second, the model assumes that entire food webs emerge in a single adaptive radiation, which is unlikely to occur in nature. However, many evolutionary radiations involve diversification across 2–3 trophic levels (e.g. Wagner *et al.*, 2009), and these clades may be most appropriate for testing our predictions concerning trophic position.

Evolutionary simulation models that include ecological interactions may prove useful for generating hypotheses and helping to interpret empirical patterns. One example is a competition model by McPeck (2008), which suggested that clades that undergo extensive niche divergence during speciation should produce phylogenetic trees with early bursts of lineage accumulation (i.e. negative γ). In contrast, models in which speciation and extinction of ecologically equivalent species occur in a

neutral metacommunity framework (Hubbell, 2001) tend to produce trees with nodes biased towards the present (McPeck, 2008; Davies *et al.*, 2011). All versions of our model included niche structure and trait divergence during speciation, but our result has some similarities to the pattern presented by McPeck (2008). In simulations in which strong foraging trade-offs resulted in the presence of well-defined trophic levels, the niche structure was especially strong and the trophic levels corresponded to steep and stable adaptive peaks. These conditions produced early burst patterns in both lineage accumulation and trait disparity, whereas ecological conditions that favoured extensive omnivory also appeared to allow species with a wider range of trait combinations to successfully establish in the community. This resulted in both higher rates of speciation and extinction as species displaced one another (Ingram *et al.*, 2009), and the recurrent evolution of similar trait values that eliminated the signal of early diversification.

Our simulations resulted in a correlation between the tempo of accumulation of lineage diversity and trait disparity. We are aware of only one study that has tested for such a pattern by examining both tree shape and trait evolution in the same set of clades: a detailed analysis of four iguanian lizard taxa by Harmon *et al.* (2003). Consistent with our results, Harmon *et al.* (2003) found that clades with earlier lineage accumulation also tended to partition morphological disparity early in the tree. Intriguingly, the clade in this analysis with the least evidence for early burst patterns – genus *Liolaemus* – has also been shown to evolve herbivory (i.e. lower trophic position) at a higher rate than any other lizard group (Espinoza *et al.*, 2004). In contrast, the clade with the strongest early burst patterns – Australian agamids – appears to have a more phylogenetically conserved diet (Rabosky *et al.*, 2011). Clearly, many more comparisons will be required to test for a general relationship between omnivory and the tempo of adaptive radiation, but these cases suggest that this hypothesis is worth pursuing.

Our analysis of the model focuses on omnivory as a predictor of macroevolutionary patterns, but hints at more general factors that may influence when early bursts occur. The ability of early burst patterns to persist over long time periods in the model is dependent on the fact that the available niches – trophic levels – are distinct from one another and are stable over time. In other cases where the important ecological divergence involves traits other than size or trophic position, early bursts may be more likely when alternative resources, natural enemies, or habitat types are distinct, stable, and subject to strong trade-offs. Adaptive radiations often involve divergence on one or more different types of niche axis, such as diet (including trophic position), natural enemies, microhabitat and climate. If we can quantify the extent to which niche differences of a particular type are stable over the relevant timescales, we may be able to predict which clades will show early bursts of diversity and disparity.

Acknowledgments

We thank D. Schluter for the suggestion that we examine patterns of trait evolution produced by this model, and J. B. Losos and D. L. Mahler for discussion of the results. Computing facilities for simulations were provided by the Western Canada Research Grid (WestGrid) and the UBC Zoology Computing Unit. This work was funded by the National Science and Engineering Research Council of Canada (NSERC).

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Data deposited at Dryad doi: 10.5061/dryad.ms06b