ORIGINAL ARTICLE

ECOLOGICAL OPPORTUNITY AND THE RATE OF MORPHOLOGICAL EVOLUTION IN THE DIVERSIFICATION OF GREATER ANTILLEAN ANOLES

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The pace of phenotypic diversification during adaptive radiation should decrease as ecological opportunity declines. We test this prediction using phylogenetic comparative analyses of a wide range of morphological traits in Greater Antillean *Anolis* lizards. We find that the rate of diversification along two important axes of *Anolis* radiation—body size and limb dimensions—decreased as opportunity declined, with opportunity quantified either as time elapsed in the radiation or as the diversity of competing anole lineages inferred to have been present on an island at different times in the past. Most previous studies of the ecological opportunity hypothesis have focused on the rate of species diversification; our results provide a complementary perspective, indicating that the rate of phenotypic diversification declines with decreasing opportunity in an adaptive radiation.

KEY WORDS: Adaptive radiation, *Anolis*, density-dependent, diversification, diversity-dependent, macroevolution, niche-filling, ecological saturation.

According to the ecological theory of adaptive radiation, ecological opportunity is a primary factor regulating the tempo of diversification (Lack 1947; Rensch 1959; Carlquist 1974; Schluter 2000; Gillespie et al. 2001; Gavrilets and Vose 2005; Ito and Dieckmann 2007; Harmon et al. 2008; Gavrilets and Losos 2009). As lineages proliferate and the diversity of competing species increases, ecological opportunity is expected to decline and the pace of diversification is expected to slow (Sepkoski 1978; Walker and Valentine 1984; Schluter 2000; Freckleton and Harvey 2006; Gavrilets and Losos 2009). Most often, empirical studies of the tempo of evolution during adaptive radiation have focused on patterns of lineage diversification—measuring rates of speciation and extinction over time in a diversifying lineage. These studies test a specific prediction of the ecological theory of adaptive radiation: that greater ecological opportunity will increase the likelihood of lineage divergence.

Traditionally, such investigations have been conducted by paleontologists charting patterns of radiation in fossil lineages over geological timescales (Simpson 1953; Stanley 1979; Raup 1985; Peters 2005; Alroy et al. 2008; Alroy 2009; Benton 2009). For many taxa, lineage diversity increased rapidly in the early Phanerozoic, subsequently slowing in a manner consistent with ecological saturation (Sepkoski 1978, 1982, 2002; Gould 1989). In addition, rates of cladogenesis are often observed to have increased following mass extinctions, suggesting the occurrence of 'diversification recoveries' driven by ecological opportunity (Sepkoski 1982, 2002; Erwin et al. 1987; Erwin 2001).

Recently, neontologists have begun to test for the signature of ecological opportunity in the form of diversity-dependent[1] patterns of diversification using time-calibrated phylogenies of extant taxa (Nee et al. 1992; Harvey et al. 1994; Mooers and Heard 1997; Phillimore and Price 2009). Several studies have provided support for the ecological opportunity hypothesis by documenting a temporal slowdown in species diversification rate (e.g., Lovette and Bermingham 1999; Weir 2006; Phillimore and Price 2008; McPeek 2008), and at least one study has documented a decrease in the rate of cladogenesis associated with an increase in the inferred number of lineages in a clade (Rabosky and Lovette 2008).

These studies, both paleontological and molecular phylogenetic, assume that observed decreases in the rate of species diversification are primarily due to increasing saturation of niche space and a decline of ecological opportunity as a clade acquires more species during the course of its radiation. However, rates of species diversification may vary for reasons unrelated to ecological opportunity, a possibility that must be considered when interpreting lineage diversification patterns. For example, in so-called non-adaptive radiations, species richness does not strongly correlate with ecological diversity, and some such radiations exhibit apparent diversity-dependent diversification patterns even though they are largely composed of ecologically similar "allospecies" (Kozak et al. 2006; Rundell and Price 2009), which suggests that some process unrelated to ecological interactions within communities is regulating species proliferation. One potential solution to this problem is to test for the signature of ecological opportunity in patterns of morphological evolution, which may be more directly affected by niche-filling and the erosion of ecological opportunity than species diversification rate (Ricklefs and Travis 1980; Roy and Foote 1997; Yoder et al. 2010).

Indeed, studies of paleontological data have found evidence for a relationship between ecological opportunity and the rate of morphological evolution. As with lineage diversification, in many taxa, the rate of increase in morphological disparity was greatest early during the Cambrian explosion and declined through time; disparity also increased dramatically following mass extinction events in many clades (Ward 1980; Saunders and Swan 1984; Gould 1989; Foote 1992, 1994, 1996, 1997; Wagner 1995; Friedman 2010; reviewed in Erwin 2007).

[1]We prefer the term "diversity-dependent" to "density-dependent" when describing models in which diversification is influenced by the number of species present. Although the latter term has been used widely to describe such models (but see McPeek 2008; Rabosky 2009), it may be unintentionally confused with "density-dependent" phenomena in population ecology (in which the density of individuals, not species, is of interest). "Diversity" more accurately describes the density of species, and indeed, early ecological diversification models were described by their authors as "diversity-dependent" (dating at least to Sepkoski 1978).

Such paleontological investigations, however, have been necessarily restricted to organisms with exceptional fossil records, and rely on methods that are inapplicable to a wealth of recent radiations—including many extant groups for which we have a rich understanding of ecology and microevolution. To date, few studies have employed phylogenetic methods to test the effect of ecological opportunity on phenotypic diversification using neontological data (e.g., Harmon et al. 2003; Burbrink and Pyron 2010). In this study, we investigate whether the rate of ecological diversification slows during the course of adaptive radiation by estimating rates of morphological evolution in five ecological trait axes in the well-studied adaptive radiation of Greater Antillean anoles.

A critical aspect of any test involving historical ecological opportunity is the manner in which such opportunity is estimated over the course of an evolutionary radiation. We take two approaches. First, we examine whether the rate of phenotypic evolution slows with time (we refer to this as the time model). This model assumes that all clade members co-occur in the same area, and that the greater species diversity that accrues through time translates into reduced ecological opportunity, with such opportunity declining linearly with time.

However, these assumptions may not always hold true, particularly for clades that have diversified at an uneven pace, or in multiple geographically disjunct areas. For these reasons, we introduce a second method to test for the role of ecological opportunity, which we call the lineage diversity model. This model more explicitly measures ecological opportunity by estimating the number of competing lineages from within a radiation that are present in the same geographic area (see Nee et al. 1992 and Rabosky and Lovette 2008 for application of similar models to patterns of lineage diversification rather than phenotypic evolution).

In the radiation of Greater Antillean *Anolis*, the lineage diversity and time models predict different patterns of evolutionary diversification because anoles have colonized and radiated on four large islands for the most part independently, with in situ diversification occurring at different times on different islands (Losos et al. 2006; Losos 2009). For example, when the first lineage to reach Jamaica arrived and began to radiate, diversification was already well underway in Cuba and Hispaniola. Therefore, time since the beginning of the radiation does not capture the difference in the timing of decline of ecological opportunity among the islands of the Greater Antilles.

In the present study, we use new quantitative, likelihood-based phylogenetic methods to test the ecological opportunity hypothesis for the pace of evolutionary diversification in Greater Antillean anoles. We ask if the rate of phenotypic diversification for ecologically relevant traits was constant over time, or whether it varied as a function of the diversity of competing lineages or time since the origin of the radiation.

ANOLES AS A MODEL SYSTEM FOR THE STUDY OF DIVERSIFICATION

Anolis lizards found on Greater Antillean islands—Cuba, Hispaniola, Jamaica, and Puerto Rico—are a model system for investigating adaptive radiation (Williams 1983; Schluter 2000; Losos 2009). Anoles are primarily arboreal lizards distinguished by their adhesive toepads, extensible throat flap (the dewlap), and remarkable range of diversity in both size and shape. Much of the diversity of anoles results from adaptation to different microhabitat and dietary resources. Some of the strongest evidence for adaptation and specialization comes from the observation that similar suites of microhabitat specialists, termed ecomorphs, have evolved independently on each island of the Greater Antilles (Williams 1983; Losos et al. 1998), suggesting that deterministic ecological processes have been largely responsible for moderating the outcome of diversification in anoles on these islands. Each ecomorph class is morphologically and ecologically distinct, and the species in them are similar in a wide variety of morphological characteristics, including relative limb lengths and toepad shape, as well as preferred habitat and behavior (reviewed in Losos 2009).

Greater Antillean anoles are the result of a single overwater colonization event from a mainland source population (Nicholson et al. 2005). Although portions of the extant Greater Antillean islands have been interconnected at various points in their histories, most anole diversification appears to have occurred subsequent to island fragmentation (Hedges 2006; Losos 2009). In general terms, diversification began first on the islands of Hispaniola and Cuba, followed fairly rapidly by the occupation of Puerto Rico by two lineages which did not diversify (Fig. 1). Later, diversification proceeded greatly on Puerto Rico after the arrival of a third lineage and on Jamaica, which probably was underwater until some point during the Oligocene (Buskirk 1985). Thus, the pattern of diversification was heterogeneous, as lineage diversity was low at different times on different islands.

Methods

SAMPLING

We conducted near-comprehensive sampling of Greater Antillean anole species to create phylogenetic and morphometric datasets. We first sampled molecular sequence data from 187 anole species occurring throughout the New World tropics to generate a time-calibrated phylogenetic estimate for *Anolis*. For the comparative analyses, we pruned the 87 (primarily non-Greater Antillean) species not included in our morphological dataset to obtain a tree with 100 species. Nineteen Greater Antillean species were not included in our analysis either because molecular sequence data were unavailable (17 species) or because specimens of sufficient quality were not available for measurement (2 species). Because the majority of these species are closely related to and
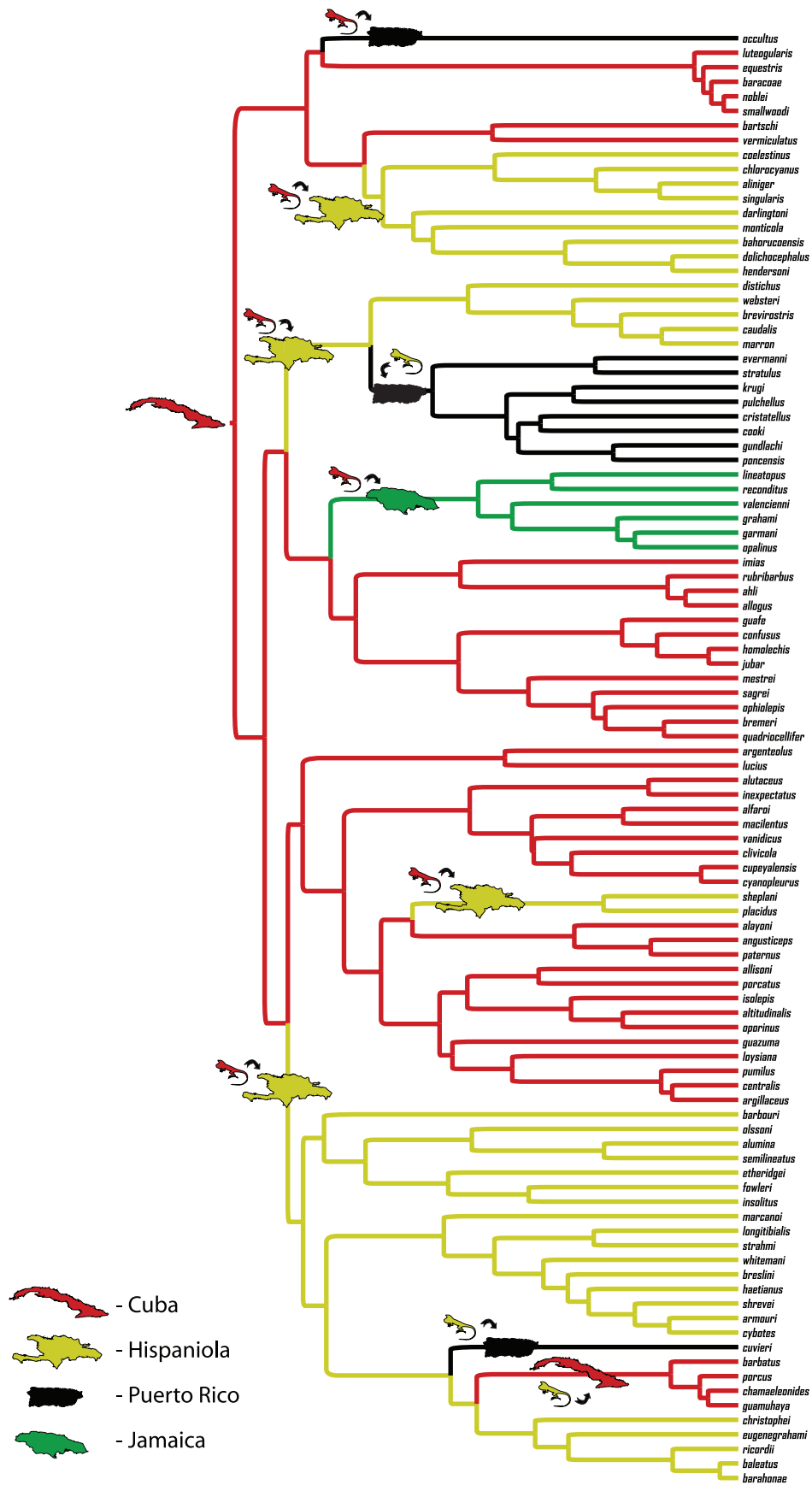
morphologically similar to species included in our analysis, their exclusion is unlikely to artifactually produce an apparent pattern of decreased rate of diversification through time; rather, if anything, it may have made such a pattern more difficult to detect.

PHYLOGENY

The phylogenies used in this study were generated from a continuous ~1500 bp fragment of mitochondrial DNA data extending across six complete genes (*ND2*, *tRNATrp*, *tRNAAla*, *tRNAAsn*, *tRNACys*, and *tRNATyr*) and the origin of light-strand replication, before ending shortly after the start of COI (Rabosky and Glor, unpubl. ms.). Time-calibrated trees were inferred using partitioned Bayesian analyses and the uncorrelated relaxed clock algorithms implemented by the program BEAST (Drummond and Rambaut 2007) with a root age arbitrarily set to a uniform distribution between 95 and 105. For these analyses, we used the majority rule consensus of two independent 40 million generation partitioned analyses implemented in MrBayes with one cold and three incrementally heated chains as a starting tree. This consensus tree was highly concordant with trees generated from Bayesian analyses of a more sparsely taxon-sampled dataset comprised of five nuclear loci. To ensure that our results were robust to phylogenetic uncertainty, we conducted comparative analyses on a set of 898 trees from the stationary distribution of the Bayesian phylogenetic analysis on mtDNA data generated using the program BEAST.

MORPHOLOGICAL MEASUREMENTS

We measured 22 morphological traits from preserved specimens (specimens per species: mean = 7.9; range = 1–19), focusing on traits of established ecological significance (Losos 2009). A single investigator (DLM) obtained all measurements from adult males, employing strict controls for measurement drift and other sources of bias (the first 1/3 of the measurements taken were discarded and retaken as a precaution against measurement "burnin"). We natural log transformed raw measurements and averaged individual values to obtain species mean values for each trait. We controlled for the effect of lizard size (represented by snout-to-vent length, SVL) by performing a phylogenetic linear regression of each trait on ln(SVL) (Grafen 1989; Rohlf 2001) to obtain residual values for each species (following Revell 2009; note that we separately regressed tail length on SVL using a dataset including only individuals with intact tails). We then performed a phylogenetic principal component analysis (PCA) on the residuals, extracted the eigenstructure of the PC axes from a correlation matrix, and obtained PC scores for the original species (Revell 2009). We used body size and PC scores for the first four PC axes (eigenvalues greater than one) for our analyses of evolutionary rate.

ESTIMATING ECOLOGICAL OPPORTUNITY AND RATE

To test the hypothesis that the rate of phenotypic evolution in Caribbean *Anolis* has varied as a function of ecological opportunity, we (1) estimated opportunity as the richness of sympatric lineages at each node in the tree (for the lineage diversity model) or as the relative age of each node (for the time model), (2) calculated independent contrasts for body size and values on the four PC axes obtained from our morphometric dataset, and (3) used a model-fitting analysis to ask if the rate of morphological evolution is predicted by estimates of lineage diversity or time.

To measure lineage diversity at internal nodes, we estimated the number of anole lineages present on an island at the time that a focal lineage on that island was undergoing speciation. Uncertainty exists in the reconstruction of both the geography of the node at which lineage divergence is occurring, as well as the geographic location of all other lineages present at that time, many of which might occur on the same island as the diverging lineage. To incorporate uncertainty in ancestral reconstruction of island occupancy, we developed a new three-step method to estimate island lineage diversity at each internal node in the tree while accounting for the maximum likelihood probabilities that each node occurred at a variety of possible geographic locations. This procedure is illustrated in Figure 2 and described in detail here.

In Step 1, we estimated the geographic location of each node in the tree using a maximum likelihood reconstruction of ancestral island status in which the model of character evolution was discrete and all transition rates were equal (implemented by the ace function of ape in R; Pagel 1994; Paradis 2006; R Core Development Team). This reconstruction provides a set of probabilities that the ancestral species at a particular internal node was found on each of the four Greater Antillean isles (termed marginal probabilities).

In Step 2, for each node in the tree, we used these reconstructed localities to estimate the number of lineages present on each island at the time of occurrence of that particular node. To do this, we summed the marginal probabilities estimated for each island at all earlier nodes (including those that were not direct ancestors), obtaining lineage richness estimates for each island at the time of the node of interest. This method investigates every node from the root of the tree to the time of interest, adding to a cumulative tally of geographic location each time a node is investigated (e.g., if an early node is reconstructed as having occurred on Cuba, one species is added to the lineage score for Cuba, and

zero species are added to the scores of the other candidate islands). This exercise produces an estimate of the number of species that occurred on each island at the time of occurrence of the focal node. In practice, the geography of many nodes is ambiguously reconstructed, which is why marginal probabilities are used for this tally—adding marginal probabilities records the accumulation of lineages at a particular location in direct proportion to the maximum likelihood probability that those lineages accumulated there.

In Step 3, for each node in the tree, we combined information about the number of contemporaneous lineages present on each island with our estimate of the geographic location of that particular node to estimate the node's "lineage diversity" value. We calculated the element-by-element product of the vector of island-specific lineage diversity values (from Step 2) and the vector of marginal probabilities from the node of interest (from Step 1) to obtain lineage diversity at the focal node. This final sum is the weighted mean of the estimated lineage diversities on each island at the time of our focal node, where the weights are derived from the marginal probability that the node species resides on each of the four Greater Antillean islands.

Next, to estimate rate, we calculated standardized independent contrasts from the size and PCA data using the pic function of the R package ape (Felsenstein 1985; Paradis 2006). Using values for independent contrasts and estimates of lineage diversity, we then fit a model in which the expected variance of the contrasts varies as a function of lineage diversity. The variance of standardized independent contrasts is an estimate of the evolutionary rate because the mean square of the contrasts in a clade has an expectation that is equivalent to the Brownian motion rate parameter for this clade (Revell et al. 2007; Revell 2008). To fit the lineage diversity model, we used the principle of maximum likelihood and maximized the following equation for the log likelihood:

$$
\log\left[L\left(\sigma_0^2, \psi\right)\right] = \sum_{i=1}^{n-1}\left[-\frac{1}{2}c_i^2 \big/ \left(\psi \cdot l_i + \sigma_0^2\right) \right.
$$
$$
\left. - \frac{1}{2}\log\left(\psi \cdot l_i + \sigma_0^2\right) - \frac{1}{2}\log(2\pi)\right]. \quad (1)
$$

In this equation, which is based on the normal probability density function, σ_0^2 is the rate of phenotypic evolution when the number of co-occurring lineages is 0, and ψ is the slope of the relationship between rate and the number of lineages. The slope,

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Figure 1. The Bayesian maximum clade credibility phylogeny for the Greater Antillean radiation of *Anolis* lizards, in which branch lengths are calibrated to represent relative time. The maximum likelihood estimate of geographic history based on current species distributions is mapped onto the tree. Character states at internal nodes have been resolved unambiguously by assigning them their most probable states. Branches, lizards, and islands are colored by geography. Arrows and lizards indicate inferred colonization events, in which the colonizing lizard is colored to match its source.
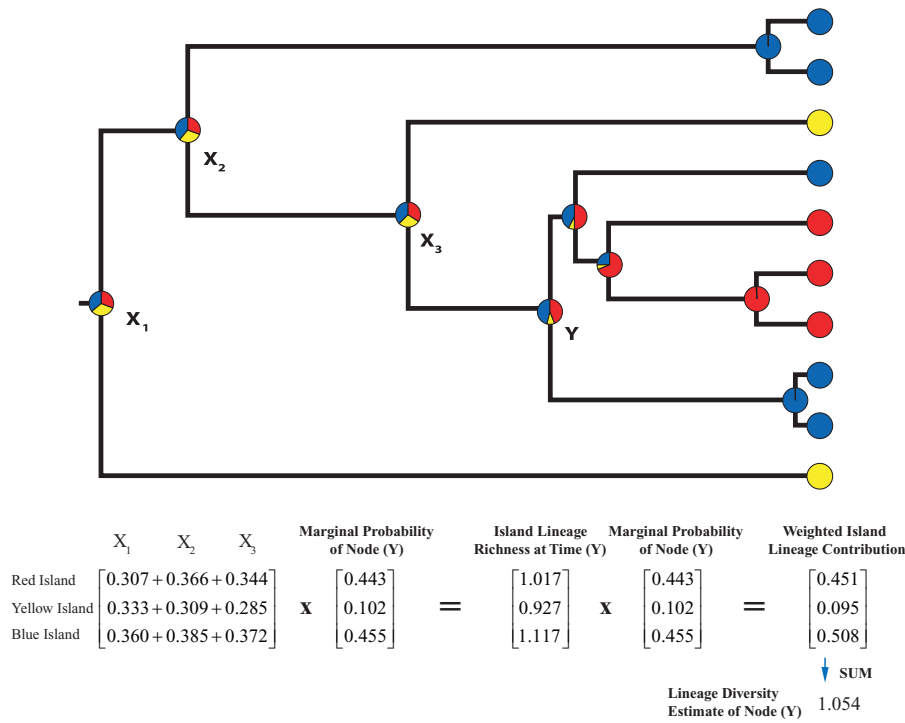
Figure 2. Method for estimating lineage diversity at Node Y using maximum likelihood ancestral reconstruction of historical values for island geography (three islands are represented by different colors). In general terms, for Node Y, the diversity of sympatric competing lineages is estimated by multiplying the probability that Node Y occurred on a particular island by the maximum likelihood estimate of the number of competing lineages also present on that same island. See text for further explanation.

ψ, is simply the slope of the best-fitting linear model for the change in rate per unit change in lineage diversity on an island. Thus, negative values of ψ indicate the decrease in evolutionary rate expected on average due to the addition of a new lineage to an island. The terms c_i and l_i are the phylogenetic contrast score and the estimated lineage diversity at node i, respectively, and the summation is performed over all $n-1$ internal nodes in the tree.

To maximize this equation, we used numerical optimization on a grid with predefined bounds. We defined the bounds based on some simple constraints on possible values for σ_0^2 and ψ; for example $\sigma_0^2 > 0$ and $\psi \cdot l_{max} + \sigma_0^2 > 0$ (i.e., the evolutionary rate cannot be negative).

To fit the time model, we scaled the tree to unit length to make the results from trees in the posterior distribution more directly comparable, and measured relative time as the ages of nodes on each tree. We then fit a model in which the expected variance of contrasts changed as a linear function of relative time using maximum likelihood. We again maximized equation (1) to obtain the log likelihood, but this time replaced the lineage diversity term l_i with the term t_i for time from the root of the tree. Our time model is similar to the node height test of Freckleton and Harvey (2006), although the model-fitting procedure is different—their method calculates the correlation between the absolute value of phylogenetic contrasts and time from the root of the tree, whereas

our method models the variance of contrasts as a function of time from the root of the tree.

We also calculated the likelihood of a model in which there is a single rate of phenotypic evolution for the entire phylogeny (the "single rate model"). The single evolutionary rate, σ_0^2, was here found by maximizing the following equation for the likelihood:

$$\log\left[L\left(\sigma_0^2\right)\right] = \sum_{i=1}^{n-1}\left[-\frac{1}{2}c_i^2/\sigma_0^2 - \frac{1}{2}\log\left(\sigma_0^2\right) - \frac{1}{2}\log(2\pi)\right], \quad (2)$$

which is maximized for

$$\sigma_0^2 = \frac{1}{n-1}\sum_{i=1}^{n-1}c_i^2, \quad (3)$$

where n is the number of species (not contrasts). Note that the single rate model is a special case of both the lineage diversity and the time models, in which the rate of phenotypic evolution does not change with changes in lineage diversity or the passage of time, respectively (hence, in eq. 1, when l_i [or t_i] is fixed at zero, σ_0^2 is an estimate of the rate of phenotypic evolution across the whole tree).

We compared our three alternative models (single rate, lineage diversity, and time) using the small sample corrected Akaike

information criterion (AIC$_c$), computed as follows:

$$AIC_c = 2k - 2\log(L) + \frac{2k(k+1)}{n-k-2}. \tag{4}$$

The number of parameters, k, in our models is $k = 2$ for the lineage diversity and time models and $k = 1$ for the constant rate model. The model with the lowest AIC$_c$ is the best-fitting model (Akaike 1974). Our approach differs from the typical size correction of Hurvich and Tsai (1989) by subtracting 2 instead of 1 in the denominator of the final term because n is the number of species, not contrasts, as before. Model comparison results are presented as ΔAIC$_c$ scores (in which the best-fit model has the score 0), and as AIC$_c$ weights (Table 2). We follow the criteria of Burnham and Anderson (2002) for evaluating levels of empirical support for individual models compared using AIC$_c$.

We performed all analyses, including phylogenetic size correction and PCA, estimation of ecological opportunity and evolutionary rates, and model comparison on each of 898 trees sampled randomly from the posterior distribution of the Bayesian analysis conducted in BEAST. To summarize our results, we averaged our results over all 898 trees and accounted for both phylogenetic uncertainty as well as error variance in our MLEs to estimate the standard error associated with our parameter estimates (details are provided in Appendix S1). For ease of presentation, we provide results from the Bayesian maximum clade credibility (MCC) topology (Drummond and Rambaut 2007) for the PCA and in the graphical illustrations of the evolutionary rate (results were qualitatively similar among trees).

We conducted a simulation analysis to quantify error and bias for our parameter estimation and model-selection procedures, as well as to test the sensitivity of these methods to historical extinction. In brief, we found our methods to be highly effective at identifying the correct model of evolution, even when data were evolved on phylogenies that underwent considerable extinction. High levels of extinction decreased the power of our methods to identify patterns of decreasing rates of evolution with declining ecological opportunity and biased our estimates of the rates of decline, but did not substantially increase the likelihood of falsely favoring an opportunity model. A detailed description of this analysis can be found in Appendix S2.

We performed all size correction, PCA, and opportunity and rate estimation using scripts written in R, whereas we maximized likelihood equations for our models using MATLAB scripts. All programs and computer scripts are available from the authors upon request.

Results

The first four axes produced by the PCA of shape residuals on the MCC tree represent 80.1% of the total standardized shape

Table 1. Loadings, eigenvalues, and variance explained for a phylogenetic principal component analysis on phylogenetically size-corrected shape variables for the Bayesian maximum clade credibility phylogeny for Greater Antillean *Anolis*. Values are highly concordant with principal component analyses performed on 898 phylogenies from the Bayesian stationary distribution.

Trait	PC I	PC II	PC III	PC IV
Head length	0.18	−0.92	−0.14	0.04
Head width	−0.61	−0.58	0.18	−0.34
Head height	−0.25	−0.62	0.15	−0.49
Lower jaw length	0.10	−0.91	−0.26	0.14
Jaw opening in-lever	0.17	−0.92	−0.24	0.15
Jaw closing in-lever	0.22	−0.83	−0.30	0.25
Femur length	−0.84	0.09	−0.35	0.05
Tibia length	−0.85	0.12	−0.39	0.13
Metatarsal IV length	−0.85	0.10	−0.45	0.13
Toe IV length	−0.83	0.02	−0.38	0.19
Lamella width, toe IV	−0.53	−0.13	0.64	0.17
Lamella number, toe IV	−0.25	−0.06	0.20	0.84
Humerus length	−0.82	0.07	0.19	−0.19
Radius length	−0.87	0.03	0.17	−0.15
Metacarpal IV length	−0.78	0.07	0.02	−0.01
Finger IV length	−0.89	−0.01	−0.05	0.02
Lamella width, foretoe IV	−0.53	−0.26	0.68	0.11
Lamella number, foretoe IV	−0.28	−0.18	0.51	0.67
Pelvis height	−0.53	−0.30	−0.23	−0.37
Pelvis width	−0.61	−0.28	0.40	−0.23
Tail length	−0.42	0.20	−0.64	0.18
Eigenvalue	**7.74**	**4.31**	**2.76**	**2.00**
Variance explained	**0.37**	**0.21**	**0.13**	**0.10**

variation among species (Table 1). The first PC axis correlates strongly with the lengths of the limb bones; the second correlates primarily with head size and shape; the third axis reveals a contrast between lamella width and tail length; and the fourth axis correlates most strongly with lamella number. These loadings and eigenvalues are highly similar to those from all 898 trees sampled from the posterior distribution of the Bayesian phylogenetic analysis (average subspace alignment of the first four eigenvectors = 3.82; Krzanowski [1979]; see Appendix S3 for details).

Anolis lineage diversity generally increases with time on each island in the Greater Antilles (Fig. 3). However, species diversification on Puerto Rico and Jamaica begins later than on the other islands such that lineage diversity estimates for the early nodes in these radiations are near-zero even as values are much higher on Cuba and Hispaniola (Fig. 3).

Standardized independent contrasts of body size and PC I are plotted against estimated lineage diversity and time in Figure 4,
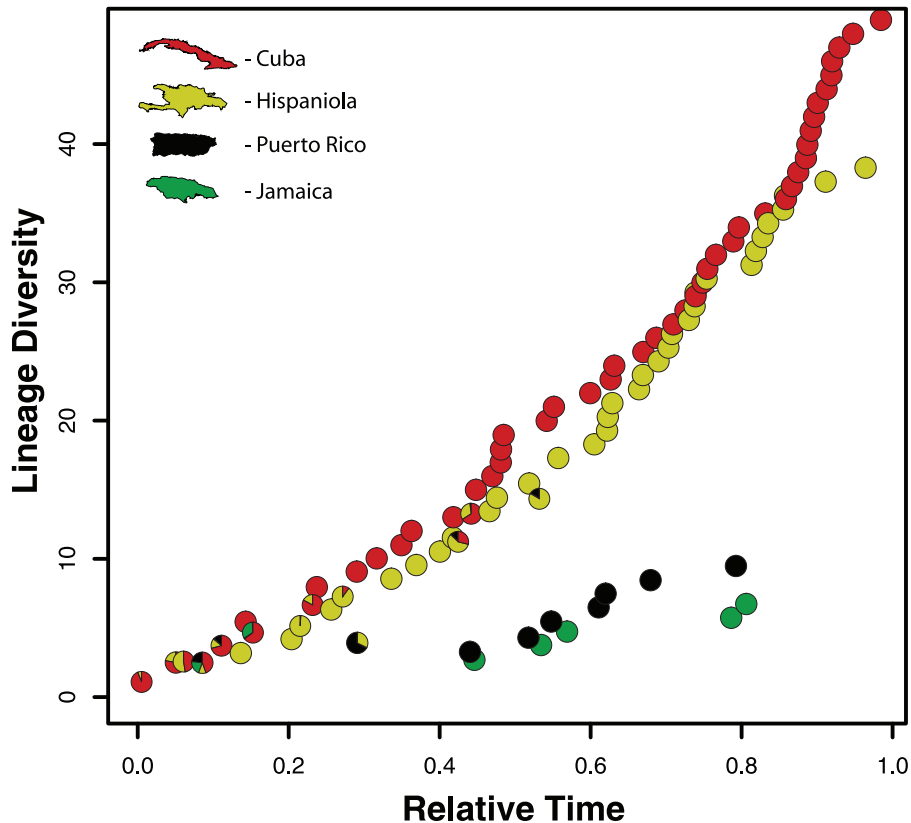
Figure 3. Comparison of historical lineage diversity estimates and relative branching time estimates for each node in the Bayesian MCC phylogenetic topology, colored by island likelihood. Lineage diversity generally increases with increasing time from the root, but the specific pattern of increase depends on geography.

and exhibit decreasing rates of phenotypic diversification with increasing values on these axes. For body size, the lineage diversity model fits the data better than either the time model or the single rate model (Fig. 5A,B; Table 2). For PC I, both the time and lineage diversity models are favored over the single rate model (Fig. 5C,D; Table 2). For the remaining PC axes, the rate of evolution is relatively uniform with increasing lineage diversity and time, and all three models of rate variation exhibit similar levels of support (Table 2; Fig. S7 in Appendix S4).

Discussion

The ecological theory of adaptive radiation predicts that the tempo of diversification should decline as ecological opportunity diminishes during a radiation. Studies of diversification patterns in extant taxa have primarily investigated the rate of lineage diversification, perhaps because of the wide availability of time-calibrated phylogenetic trees that constitute the primary source of data for such analyses. Many studies have reported patterns consistent with the ecological opportunity hypothesis, primarily in the form of decreasing diversification rates over time (Lovette and Bermingham 1999; Weir 2006; McPeek 2008; Phillimore

and Price 2008; Rabosky and Lovette 2008), which implies that the process of speciation is influenced by ecological opportunity. This approach, however, offers little insight on how opportunity influences the evolution of the ecological features of these species.

Our study provides a new perspective by (1) estimating rates of evolution in ecomorphological traits rather than the number of lineages, and (2) testing whether such rates are related to ecological opportunity estimated using a new metric, the diversity of existing lineages, in addition to the more conventional metric of time since the evolutionary origin of a clade. We find that phenotypic diversification on two important adaptive axes—body size and relative limb length—decreased with time and increasing lineage diversity in the adaptive diversification of Caribbean anoles, which suggests that opportunity affects rates of ecological diversification, and not just rates of lineage diversification.

Our results corroborate paleontological investigations of morphological disparity over time in fossil lineages radiating under conditions of both high and low ecological opportunity (reviewed in Valentine 2004; Erwin 2007). In general, these studies show initial rapid increases in disparity in lineages presented with new ecological opportunities, followed by a slowdown in morphospace occupation (e.g., Foote 1992, 1994, 1996; Wagner
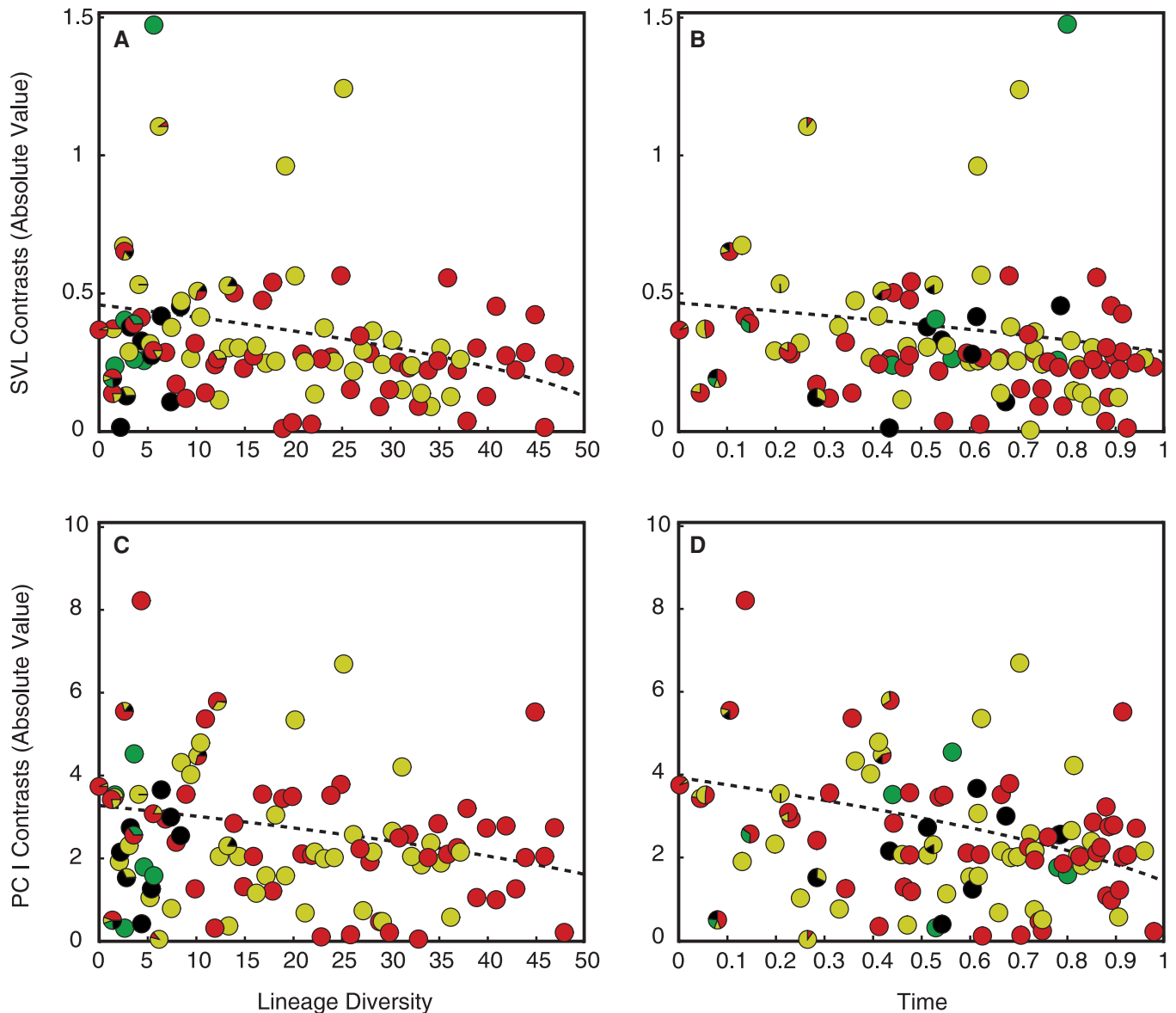
Figure 4. Absolute values of standardized phylogenetically independent contrasts of morphological traits for the Bayesian MCC phylogeny of Greater Antillean *Anolis*. (A) and (B) show body size contrasts with increasing lineage diversity and relative time, respectively. (C) and (D) show PC I contrasts with increasing lineage diversity and relative time, respectively. Dashed lines show the expected standard deviation of the contrasts under the best-fit model in which the evolutionary rate varies as a function of the number of lineages (left panels) or time (right panels). Colors represent the islands on which nodes occurred, estimated using maximum likelihood, as in Figure 3.

1995). Such patterns match those observed in *Anolis,* in which rates of morphological evolution are high early in the radiation and when the diversity of competing lineages is low. Unlike most of these paleontological studies, however, previous work on the ecology and behavior of anoles allowed us to investigate traits that have been demonstrated to be adaptively important. Consequently, our observation of decreasing rates of evolution in these traits with declining ecological opportunity can be directly interpreted as a decrease in the rate of adaptive differentiation.

OPPORTUNITY, RATE, AND ECOMORPHOLOGY IN *ANOLIS*

Greater Antillean anoles are well known as an example of replicated adaptive radiation, in which diversification on different islands has produced similar outcomes despite largely independent histories. We estimated rates of evolution for a set of ecomorphologically significant traits that vary substantially among species specialized to use different parts of the environment (Williams 1983; Losos 2009). We found support for the ecological

Table 2. Comparison of models of rate variation. All values represent results averaged from 898 topologies sampled randomly from a Bayesian posterior distribution. For traits in which no $\Delta AIC_c=0.00$, this indicates that different models were preferred on different phylogenies in the posterior sample. For parameter estimates, standard errors (incorporating both estimation error and phylogenetic uncertainty) are provided in parentheses.

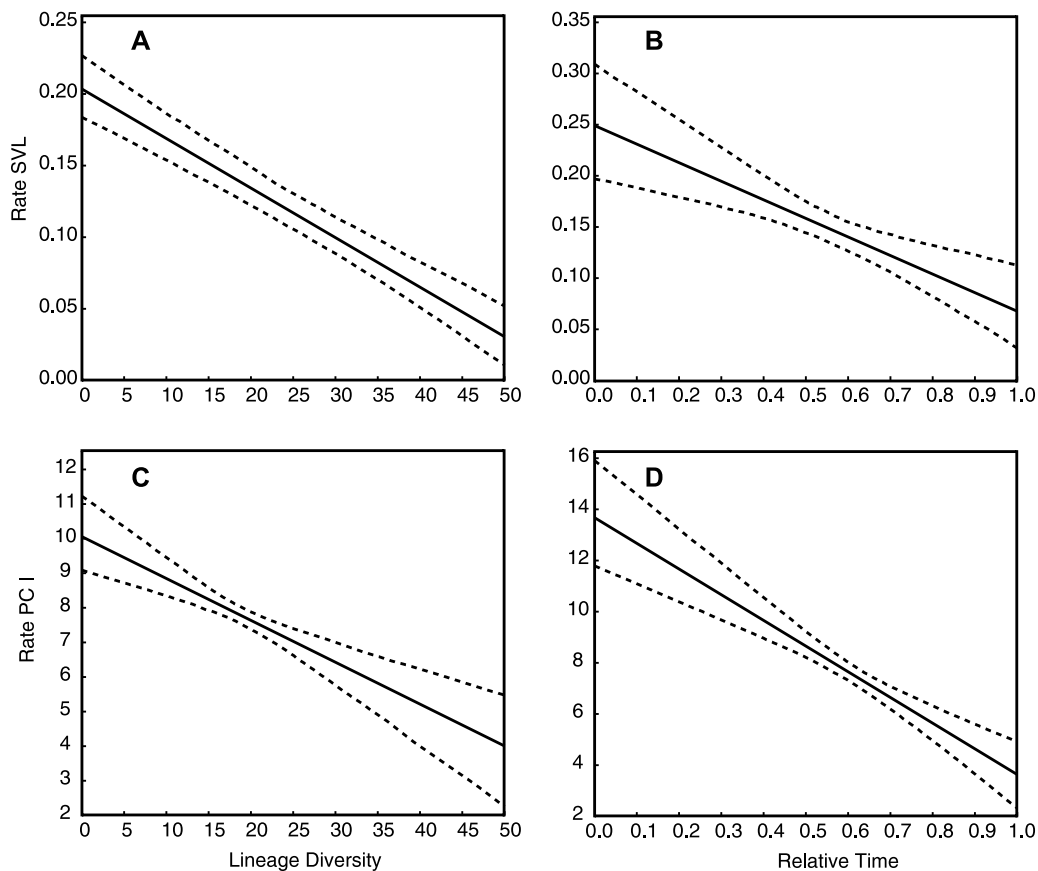| Trait	Model	σ_0^2	ψ	$\log(L)$	ΔAIC_c	AIC_c weight
Size (SVL)	Single rate	0.14 (0.02)	–	−42.67	7.21	0.04
	Time	0.25 (0.03)	−0.18 (0.05)	−40.69	5.34	0.09
	Lineage diversity	0.20 (0.02)	-3.5×10^{-3} (4.6×10^{-4})	−38.02	0.00	0.87
PC I	Single rate	7.75 (1.10)	–	−241.86	4.04	0.12
	Time	13.68 (1.28)	−10.04 (1.90)	−238.80	0.00	0.71
	Lineage diversity	10.06 (1.01)	−0.12 (0.04)	−240.19	2.80	0.18
PC II	Single rate	4.25 (0.61)	–	−212.11	0.00	0.57
	Time	4.09 (0.74)	0.27 (1.22)	−212.06	2.00	0.21
	Lineage diversity	4.11 (0.66)	0.01 (0.03)	−212.05	1.97	0.21
PC III	Single rate	2.67 (0.40)	–	−189.07	1.08	0.32
	Time	3.86 (0.53)	−2.04 (0.82)	−187.64	0.31	0.44
	Lineage diversity	3.11 (0.41)	−0.02 (0.01)	−188.22	1.47	0.24
PC IV	Single rate	2.02 (0.29)	–	−175.16	0.59	0.40
	Time	2.75 (0.30)	−1.26 (0.44)	−174.18	0.72	0.37
	Lineage diversity	2.29 (0.29)	−0.01 (0.01)	−174.68	1.32	0.23

Figure 5. Linear functions for the best-fit models in which evolutionary rate varied as a function of the number of lineages (left panels) or time (right panels) for SVL (top) and PC I (bottom). The solid line in each panel depicts the mean slope and intercept for analyses using all 898 topologies from the Bayesian posterior distribution. Broken lines outline the 95% confidence limits for the mean, in which the variation is due to uncertainty in the phylogeny.

opportunity hypothesis in both body size and relative limb lengths. For body size, we found that the lineage diversity model was most favored, which suggests that increased numbers of competing anole lineages led to a decrease in rates of body size evolution. The ecological opportunity hypothesis was also supported for relative limb lengths (PC I), but in this case, the ecological models of time and lineage diversity both exhibited statistically comparable levels of support (Burnham and Anderson 2002).

The ecological significance of body size and relative limb lengths is well established in anoles. In anole communities, interspecific body size differences are associated with differences in both diet and habitat use (Schoener 1968, 1969, 1970, 1975; Lister 1976; Pacala and Roughgarden 1982; reviewed in Losos 2009), and likely evolved in response to interspecific competition among anole species (Schoener 1970; Roughgarden and Pacala 1989; Losos 1992, 2009; Roughgarden 1995). Similarly, the functional and behavioral significance of variation in limb length is well established (e.g., Losos 1990; Irschick and Losos 1998, 1999) and sympatric species that occupy dissimilar microhabitats differ in relative limb lengths (Williams 1983; reviewed in Losos 2009).

We did not find substantial support for the role of ecological opportunity in the evolution of the remaining three trait axes, primarily representing head and toepad dimensions and tail length. Although variation in these traits is also related to ecological variation), the lack of a relationship with ecological opportunity may stem from several causes. First, some of these traits, such as head dimensions, are also the target of sexual selection (Lailvaux et al. 2004; Herrel et al. 2007); because the intensity of sexual selection need not be related to ecological opportunity, rates of evolution of such traits might not be expected to be correlated with opportunity. Also, Greater Antillean anoles exhibit a pattern of evolution in which adaptation to different structural habitats (e.g., twigs, canopy, bushes) evolved early in the radiation, but subsequent diversification along other resource axes (e.g., thermal microhabitats) continued throughout the radiation (e.g., Glor et al. 2003; Losos 2009). Some of the traits on these three axes may be involved in this secondary aspect of anole differentiation, and therefore exhibit comparatively constant rates of evolution throughout the radiation. An additional possibility is that we may not have detected a signature of ecological opportunity due to sampling error, which is expected to be more problematic for increasingly minor PC axes (the role of sampling error is explored further in Appendix S5).

THE MARK OF ECOLOGY ON DIVERSIFICATION

The result that rates of morphological evolution in anoles are correlated with historical estimates of ecological opportunity suggests that ecological processes may influence patterns of lineage diversification. However, this relationship may be generally difficult to detect, particularly because diversification often occurs over large geographical scales. Under scenarios in which lineage diversity is primarily distributed allopatrically, members of a diversifying lineage will interact little with each other. In such cases, ecological opportunity will usually be determined by a diverse suite of interacting species that are not closely related, and it may therefore be much more difficult to estimate opportunity using phylogenetic methods.

We suggest that the present methods for estimating past ecological opportunity and testing its relationship to patterns of phenotypic evolution will be most powerful when ecological interactions are primarily among members of a single clade, as is often the case in adaptive radiations on islands and in lakes (e.g., Fryer 1996; Baldwin and Sanderson 1998; Grant 1998; Chiba 2004, reviewed in Leigh et al. 2007; Losos and Ricklefs 2009). On continents, it may be much harder to estimate ecological opportunity (although in some continental radiations, relatives interact particularly intensely, as in the North American wood warblers; MacArthur 1958; Rabosky and Lovette 2008). Of course, following mass extinctions, evolutionary recovery is often dominated by a small number of clades that radiate widely and rapidly—even in biogeographically large regions, such as continents (Erwin 2001). In such scenarios, the methods presented here may also detect the signature of declining opportunity in the phenotypic pattern of diversification.

Anoles provide an ideal system to test whether rates of phenotypic evolution exhibit a relationship with historical estimates of ecological opportunity in continental as well as in island radiations. In addition to radiating in the Caribbean, two anole clades have diversified in neotropical mainland habitats (Nicholson et al. 2005; Pinto et al. 2008). Although we presently lack the phylogenetic data necessary to adequately estimate ecological opportunity and rates of evolution in these clades, examination of these taxa is an exciting avenue for future investigation.

ASSUMPTIONS, POSSIBLE SOURCES OF ERROR, AND FURTHER DEVELOPMENT OF ECOLOGICAL OPPORTUNITY MODELS

A number of potential sources of error may influence the interpretation of results obtained using our method, but none of these are of particular concern to the present study. Here, we briefly detail two caveats associated with this method, and we provide a more detailed exploration of model assumptions and additional potential biasing factors in Appendix S5.

First, our methods do not directly account for extinction. For the lineage diversity model, our procedure provides an unbiased estimate of the lineage diversity at each node under a pure-birth process (i.e., no extinction), but the reconstructed lineage diversity at internal nodes will be biased downwards under more realistic

scenarios involving some degree of extinction. However, we evaluated the sensitivity of our method to extinction via simulation and found the method to perform well under a wide range of constant relative extinction rates (described in Appendix S2). In phylogenies in which the ratio of extinction to speciation was increased, our methods experienced a modest reduction in the power to detect the effect of ecological opportunity on diversification (i.e., increased Type II error), but did not tend to falsely select ecological opportunity models when data were evolved under pure Brownian motion (i.e., Type I error was not elevated appreciably by extinction). Apparently, constant extinction does not produce a phenotypic pattern resembling the signature of ecological opportunity, although at high levels, it may make such a signature more difficult to detect.

Second, we warn that our lineage diversity model only generates an estimate of ecological opportunity—one that assumes that the competitive factors influencing rates of evolution may be approximated using the lineage diversity of entire islands in the Greater Antilles. In reality, this may be an imprecise measure of local ecological opportunity because species diversity values in local communities were certainly not as high as on entire islands (each species does not occur everywhere on the island). It is difficult to obtain more accurate estimates of historical lineage diversity at the community level using comparative data, but one possible solution is to transform estimates of island lineage diversity so that they scale more closely with maximum community diversity estimates for each island. To do this, we log transformed lineage diversity estimates, which depresses large lineage richness values relative to small values. Such a transformation is appropriate, because maximum community richness increases with island size in Greater Antillean anoles, but with a much lower slope than island species richness (Losos 2009). Reanalyzing our data this way, we obtained similar results that further support the ecological opportunity hypothesis (see Appendix S5).

The lineage diversity model may be developed further in a number of ways. For example, the lineage diversity estimator might be modified to infer geographical location of lineages along branches rather than only at the nodes of the phylogeny to estimate contemporaneous diversity values at the time of occurrence of a focal node. The authors are currently exploring one potential branch-based approach in which stochastic character mapping methods (Bollback 2006) are used to reconstruct geographic history along branches. Also, future models may specifically consider whether rates of evolution are exceptional on the branches representing colonization of new regions (our current model assigns phenotypic diversification to the island of the ancestral node, even if one of the descendant lineages colonized another island; see Supporting Information for further discussion, including a test in which nodes associated with such events were removed). Nonetheless, the method presented herein is both highly tractable

and provides clear results showing a decrease in evolutionary rate with ecological opportunity in *Anolis*.

Conclusions

According to the ecological theory of adaptive radiation, ecological processes are responsible for generating many of the dominant patterns in the evolutionary history of life (Lack 1947; Simpson 1953; Schluter 2000). Here we report evidence for ecological controls on rates of phenotypic evolution—rates of body size and limb length evolution in *Anolis* lizards are a function of the diversity of competing lineages. The ecological pattern is strongest for body size, a trait with a well-established role in the structuring of ecological communities across metazoans (Hutchinson 1959; Peters 1983; Calder 1984; LaBarbera 1989), as well as in anoles.

Our results provide a phenotypic perspective on the study of diversification rates in species radiations, and support a model in which macroevolutionary diversification is bounded by ecological limits. Further testing of such limits, as well as exploration of how they shape diversity patterns in clades and regions, promises to be a rewarding avenue for future evolutionary research.

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Supporting Information

The following supporting information is available for this article:

Appendix S1. Description of the estimation of the variances of our maximum likelihood estimators.
Appendix S2. Extinction and method performance.
Appendix S3. Quantifying similarity of principal component axes among the phylogenies used in our analysis.
Appendix S4. The relationship between ecological opportunity and rates of evolution for trait axes PC II–IV.
Appendix S5. Discussion of additional model assumptions and potential biasing factors.
Appendix S6. Supplementary literature cited.

Supporting Information may be found in the online version of this article.

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