



Body size distributions at local, community or taxonomic scales do not predict the direction of trait-driven diversification in snakes in the United States

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ABSTRACT

Aim We determine whether trait-driven diversification yields similar body size distributions for snakes in local, regional and phylogenetic assemblages.

Location United States, North America.

Methods Using total length and mass, we examine body size frequency distributions (BSFD) across 79 sites and respective biomes to determine if these areas represent random subsamples from the source pools of taxon body sizes. Using QuaSSE, we determine if the most probable model of trait-driven diversification in the three most common groups of snakes in North America, the ratsnakes, pitvipers and watersnakes, is similar to the predicted regional BSFD.

Results BSFD of snakes at the community, biome, regional and clade scales show symmetric distributions of body size. These patterns may simply be generated from random statistical subsampling. Speciation rates are not highest at or near the modal body size and simulations show that linear trait-driven models can still yield highly symmetric distributions of body size.

Main conclusions In this study region, processes such as competition due to size do not alter BSFD from one scale to the other. It is likely that rates of speciation are not highest at the mode in snakes and trait-driven diversification is not likely to account for a regional pool of body sizes from which local communities are drawn, although persistence of modal body sizes through time could yield regional BSFD.

Keywords

Biomes, body size frequency distributions, communities, snakes, trait-driven diversification.

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INTRODUCTION

Body size defines the basic ecology and physiological requirements for most organisms (Hutchinson & MacArthur, 1959; Peters, 1983; Gaston & Blackburn, 2000). Across body sizes for any group it is likely that there are more species in certain size classes than others. For example, in mammals and birds there are often many more species in the smaller size classes, thus giving rise to right (positive) skewing when determining body size frequency distributions (BFDS), particularly at higher taxonomic or continental levels (Brown & Maurer, 1989; Maurer *et al.*, 1992; Kozłowski & Gawelczyk, 2002; Allen *et al.*, 2006;

Clauset & Erwin, 2008). The distribution of body sizes at community, regional and lower taxonomic scales may differ, and the trend of right-skewed body sizes at the largest scales may disappear within regions of continents, biomes, communities or in orders or families (Gaston & Blackburn, 2000; Kozłowski & Gawelczyk, 2002).

Several broad explanations relevant at shallow and deep time scales may account for the distributions of body size (reviewed in Kozłowski & Gawelczyk, 2002; Allen *et al.*, 2006). At the deepest time scale, trait-driven diversification may yield skewed or unskewed pools of body sizes from which smaller areas or communities are drawn. For instance, if speciation rates are

highest at smaller sizes and extinction rates are highest at larger sizes then right-skewed distributions will occur at the broadest geographic scales (Maurer *et al.*, 1992). In contrast, at the shallowest time scales, local distributions of body sizes sampled from the regional pool of species may differ due to competition, ecological filtering, distribution of resources, increases in extinction for large taxa with small ranges or biogeographic barriers to dispersal (Kozłowski & Gawelczyk, 2002; Agosta & Janzen, 2005; Allen *et al.*, 2006; Rabosky *et al.*, 2011). For example, in North American mammals and African birds, BSFD are modal with a right skew (Brown & Nicoletto, 1991; Coetzee *et al.*, 2013) but show decreasing modality and skewing at smaller spatial scales. For these taxa, various explanations, including available energy at local scales or competition, may account for these patterns. In contrast, snakes in North America show very little skewing in BSFD at various spatial scales (Cox *et al.*, 2011). Therefore, a link between trait-driven modes of diversification at the phylogenetic scale, which provides the species for the source pool, and distributions of body size at local communities should exist unless competition or some other process restructures size distributions differently from the source or regional pool (McKinney, 1990; Kozłowski & Gawelczyk, 2002; Clauset & Erwin, 2008).

Trait-driven diversification has been explored where phenotype, particularly body size and complexity (Gittleman & Purvis, 1998; Adamowicz *et al.*, 2008; FitzJohn, 2010), is expected to have an impact on diversification rate (Vrba & Gould, 1986; Jablonski, 2008). It is possible that speciation rates are higher or extinction rates are lower in the size classes with the largest number of taxa. Conversely, extinction rates could be higher in those groups within size classes with the fewest taxa (Purvis, 2004). Therefore, body size among groups of closely related organisms may influence their evolutionary history and rates of speciation and extinction, which ultimately provides the source for the distribution of sizes in regional and local communities. Importantly, the distribution of body sizes on diversification can depend on a complex mixture of the intensity of trait-driven speciation and extinction, size at the origin of the group, the potential carrying capacity at different size classes and constraints on diffusion at the smallest sizes (Stanley, 1973; McKinney, 1990; Kozłowski & Gawelczyk, 2002; Clauset & Erwin, 2008). The hypothesis that groups of organisms evolve towards an optimal body size suggests that speciation rates should be highest or extinction rates lowest for lineages nearing that optimal value. For instance, a right skew in the body size distribution of birds was taken as evidence that the optimal size of birds is generally smaller than the mean and the possibility exists that elevated speciation or reduced extinction has promoted an abundance of species in this size class (Nee *et al.*, 1992). A direct connection between species richness and body size has not been found in mammals, birds and metazoans as a whole (Gardezi & da Silva, 1999; Owens *et al.*, 1999; Orme *et al.*, 2002; Isaac *et al.*, 2005); however, other studies, in rodents for example, have indicated that diversification increases with size, thus supporting Cope's rule (Avaria-Llautureo *et al.*, 2012). It is also unclear if there is a direct relationship between trait-driven

diversification and the representation of species distributed near the value of that trait in communities, regions or clades.

Here, we address questions of size-driven diversification across communities of snakes in the United States (US) distributed locally, throughout several biomes, and regionally. We first examine the patterns of the BSFD and relate these to potential processes accounting for skewing at several scales. Previous research has suggested that no skew exists for BSFD at local sites relative to regional samples and that optimal size theory cannot predict spatial scaling in snakes (Cox *et al.*, 2011). Given this unimodal distribution in snakes and a mean body length of 1 m, it is possible that this total length represents a physiological optimum in snakes at which diversification rates should be highest (Boback, 2003; Boback & Guyer, 2003). We first determine whether 79 well-surveyed local communities of snakes across North America show a signature of significant skewing or evenness (i.e. how adjacent pairs of body sizes are distributed) in BSFD from their respective biome (Fig. 1). Because dispersal and ecological gradients can affect community structure, and thus distributions of size, we determine if a measure of species turnover (beta diversity; Whittaker, 1972), which has been negatively correlated with dispersal ability (Josefson & Göke, 2013), is similar among biomes.

At the deepest time scale, we have targeted the three most diverse groups of snakes among these sites, the pitvipers (Crotalinae), ratsnakes (Lampropeltini) and watersnakes (Thamnophiini), to examine the evolution of size distributions. In North America, the pitvipers, ratsnakes, and watersnakes each represent monophyletic groups, are ancient and diverse, co-occur in the same geographic area and comprise a substantial component of snake diversity in terms of species number, size and abundance (Gibbons & Dorcas, 2004; Burbrink & Pyron, 2010; Burbrink *et al.*, 2012a). Given that body size is one of the most important characters defining morphological and ecological variance in snakes (Pyron & Burbrink, 2009a), these groups provide an important model for examining the impact of size on diversification and community structure.

For the three groups of interest, we first determine if body size distributions are significantly skewed at the local, biome, regional or clade level. We then ask, given the distribution of body sizes at these different scales, if this is reflected in higher diversification rates at the mode using several models of trait-driven diversification. We also simulate trait-driven diversification to determine how often this will yield skewed or unskewed BSFD in regional communities. This study ultimately aims to determine if a link exists between trait-driven diversification and how these traits are distributed at various spatial scales.

MATERIALS AND METHODS

Size and mass

Following Cox *et al.* (2011) we use \log_{10} -transformed maximum total length (TL) to represent one measure of body size for all snakes used in this study; the measurements were taken from multiple literature sources and used for all sites, regions and taxa

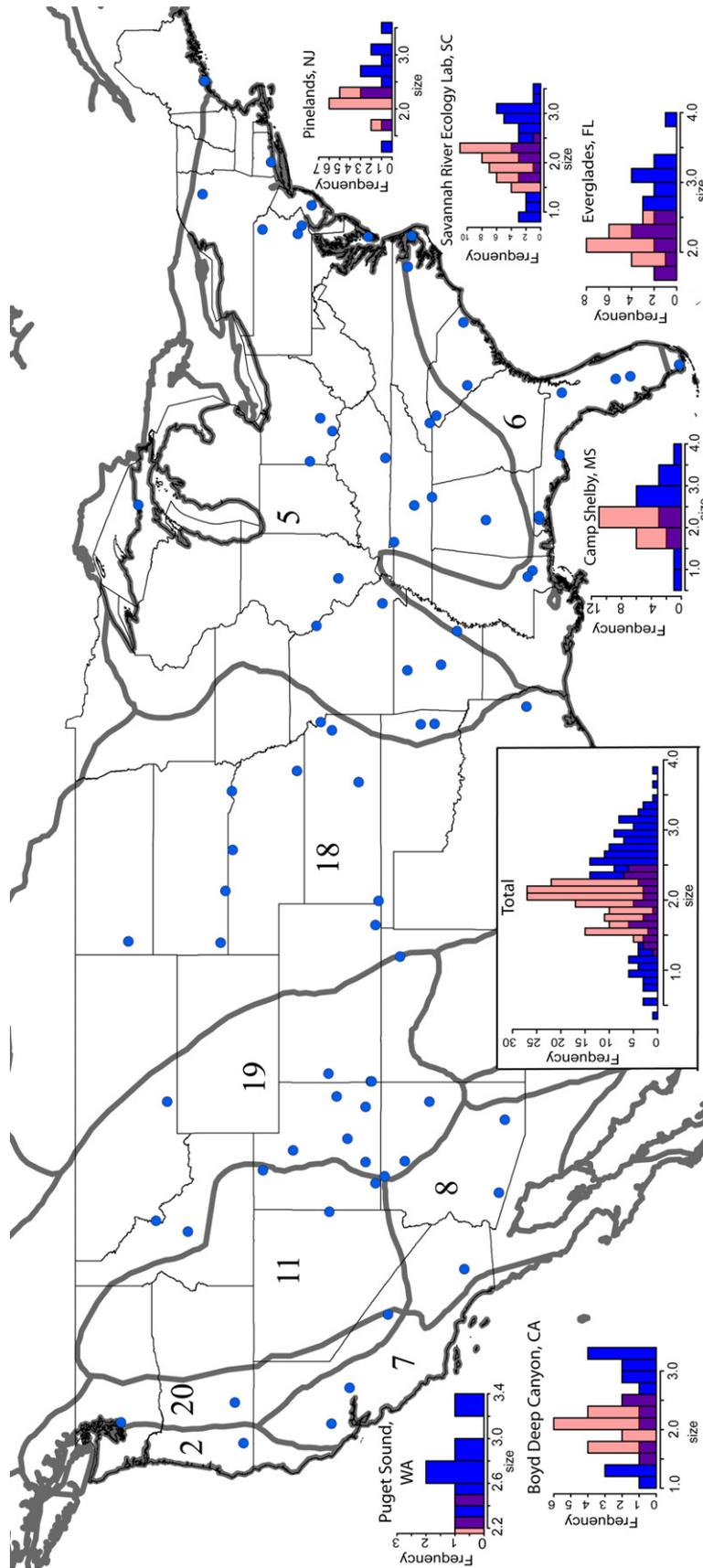


Figure 1 Map showing the location of sites and biomes (listed by number in their respective biome) in the United States. The histograms show the distribution of \log_{10} body sizes [blue, total length (cm); pink, total mass (g)] across all species and representatives of local communities examined in this study (Appendix S1). Map projection is Aitoff's equal area projection.

in the phylogeny (Appendix S1 in Supporting Information). Since mass may more approximately estimate body size in snakes, and has been the standard measurement of size in other vertebrates, we converted TL to mass using the equations in Feldman & Meiri (2013) because mass is not often reported for squamates. These equations convert total length to mass while accounting for phylogenetic differences and basic habitat differences (e.g. arboreal, terrestrial, fossorial or aquatic). All subsequent statistical analyses were conducted using both TL and mass.

Areas surveyed

We determined the taxonomic composition across 79 communities of snakes within the borders of the US. These sites were sampled by reviewing the literature for herpetofaunal surveys (Appendix S1). We chose these sites because they were all well surveyed, readily available in the literature, represented samples from a wide range of latitudes and longitudes and were similar in area to those successfully used for similar squamate studies in North America (Appendix S1; Cox *et al.*, 2011). Additionally, we have placed sites into their respective biomes based on the designation of North American biomes by Uvardy (1975) (Appendices S1 & S2).

Characterization of size distributions

To understand how size is distributed at local and regional sites for each of the following classes of data, we estimated BFSFD for: (1) all snakes in the US, (2) nine biomes, (3) each of the 79 sites, and (4) the three focal clades (Lamprodelphini, Crotalinae and Thamnophiini; Fig. 1). All computational approaches here used R (R Core Team, 2013) with existing packages or a new code available from F.T.B. Using the R package 'moments' we examined multimodality, skewing and kurtosis. For each of these classes of data we used Hartigan's dip test (Hartigan & Hartigan, 1985) to determine if multiple modes are present in the size distributions. We also used the D'Agostino (D'Agostino, 1970) and the Anscombe–Glynn (Anscombe & Glynn, 1983) tests to determine if kurtosis and skewing, respectively, were significantly different across each class of data. To further understand if BFSFD changes from local to regional scales, suggesting competition, we generated 1000 test datasets for each of these 79 sites by randomly choosing the same number of taxa found at each site from their respective biome pool of species and recalculated skew and kurtosis based on these 1000 new compositions. We determined if skewing or kurtosis was larger (more positive) or smaller (more negative) than each of these 1000 randomized datasets for each of the 79 sites or nine biomes.

To further understand how scale changes BFSFD, we examined how even the distribution of body sizes was at all 79 sites. Evenness is calculated as the variance of the log ratio across all adjacent body size pairs, where a low index of evenness demonstrates that TL and mass are evenly spaced and a large value indicates that size is spaced randomly (Gotelli & Entsminger, 2004; Cox *et al.*, 2011). If competition or some other process is structuring

these distributions at local sites, the values of evenness should be significantly lower than the values generated by resampling the same number of taxa found at each site from the total biome pool. We generated 1000 test datasets for each of the 79 sites by randomly choosing the same number of taxa from their respective biome pools and recalculating skew and kurtosis based on these 1000 new compositions.

Since it is possible that subsampling from a regional distribution of body sizes can change skewing or evenness when compared with the larger distribution by simply drawing a reduced and biased sample of small or large body sizes, which would not involve any ecological processes, we simulated regional skewed normal distributions in the R package 'sn' (Azzalini, 2013) using the same number of species as in our US dataset ($n = 162$), with position = 1.96 (yielding the same log mean as the real regional data), scale = 0.3 (generates the spread of the data) and shape = 10 (generates the shape of the skewed distribution). This yields a significantly positive skew with the same number of taxa for the total region, with the same position and a similar scale but with skewed shape. From this, we sampled sizes randomly from 13 species (our real average at any site), 38 species (our real maximum number of taxa at any site) and 100 species (to demonstrate that skew will be maintained at higher samples). For each of these subsample sizes, we repeated the simulation 1000 times and estimated the average and 95% confidence interval (CI) of significantly positively skewed sites. This was also repeated using the evenness statistic to determine if the variance for evenness is significantly lower than the full distribution of 162 taxa.

We also investigated the degree to which latitude, longitude and the number of taxa from the 79 sites affect skewing or kurtosis. For the 79 sites and the nine biomes, we also examined the spatial distribution of BFSFD in skewing and kurtosis by conducting a Mantel test with 9999 replicates. We assessed if spatial dependency for skewing or kurtosis is significant by calculating Moran's I in SAM 4.0 (Legendre & Fortin, 1989; Rangel *et al.*, 2010). We tested the significance of all Moran's coefficients for each distance using 9999 Monte Carlo permutations to generate P -values. Autocorrelation is expected if at least one of the coefficients is significant (Heikkinen *et al.*, 2004; Rangel *et al.*, 2010). Using the conditional autoregressive model (CAR) we examined the impact of the predictor variables, latitude or longitude and number of taxa on the response variables skewing and kurtosis separately, while accounting for spatial autocorrelation (Rangel *et al.*, 2010).

Finally, because evenness and skewing may be affected by the composition of taxa and their sizes at sites within regional biomes, we determine if each of the four most well-sampled biomes (5, 6, 18, 19) with respect to sites shows a similar signal of species turnover (beta diversity; Whittaker, 1972). Beta diversity has been shown to correlate negatively with dispersal ability (Josefson & Göke, 2013). Thus higher beta diversity may indicate lower dispersal ability or exclusion due to environmental filtering at each site and thus account for why certain biomes have a higher or lower proportion of sites showing significant skewing or evenness. Using the R package 'Vegan' (Dixon, 2003)

we assess beta diversity using the robust statistic β_{sim} (Koleff *et al.*, 2003) across all sites and within biomes. With these estimates we tested the multivariate homogeneity of the biome dispersions, which examines the average distance of the β_{sim} estimate for each site in a biome to the group centroid, using the function 'betadisper' originally described in Anderson (2006). We applied a single chi-square goodness of fit test to determine if skewing, evenness or kurtosis for TL or mass is significantly different among these biomes.

Phylogeny and divergence date estimation

We used the three most common monophyletic groups of North American colubroid snakes (Lampropeltini, Thamnophiini and Crotalinae; for the current taxonomy of these groups see Burbrink & Lawson, 2007; Wüster *et al.*, 2008; Pyron & Burbrink, 2009b; Guo *et al.*, 2012) to examine trait-driven diversification. These three groups were chosen because they represent a majority of the taxa at all sites (52%) and are extremely numerous in the US compared with the other clades (Leptotyphlopidae, Elapidae, Dipsadinae and non-lampropeltinine Colubrinae; for the taxonomy of these groups see Uetz, 2013). Following Burbrink *et al.* (2012a), we used the same multilocus data, taxa and Bayesian relaxed clock method in BEAST 1.6.2 (Drummond *et al.*, 2006) to infer dated trees using numerous internal fossil calibrations for Lampropeltini, Crotalinae and Thamnophiini (details are given in Appendices S3 & S4). We used the uncorrelated lognormal relaxed clock tree prior run for 5×10^7 generations twice to ensure consistency between runs, discarding the first 10×10^6 generations as burn-in and generating a consensus tree in TREEANNOTATOR (Drummond *et al.*, 2006) using the maximum clade credibility option. We ensured that effective sample size values were > 200 for all parameters.

Size-driven diversification

To determine if size influences rates of species diversification in Lampropeltini, Crotalinae and Thamnophiini we used the whole tree likelihood methods of QuaSSE in R to examine continuous models of diversification (FitzJohn, 2010). For both TL and mass separately, we examined differences in the Akaike information criterion (AIC) among models that account for the following changes in speciation and extinction rate: constant (no relationship), linear (rate changes scale linearly with morphological change), sigmoidal (rate changes with morphology given a sigmoidal curve) and hump (highest rates are associated with median morphological values and declining symmetric rates as values diverge from the median). We also generated a novel inverted-hump-shaped trait-driven extinction model used in QuaSSE, where extinction rates increase for body sizes away from the mode. This model suggests that the modal body size simply persists longer through time and does not have a higher speciation rate, yet may account for why modal body sizes are common in extant clades. These tests will specifically determine, for example, if modal size generates the highest rates

of speciation. In addition, these models also included an estimate of drift and account for the percentage of missing taxa. Unfortunately, these models do not account for changes in species diversification rates from birth–death processes due to external factors associated with competition (e.g. diversity dependence; Rabosky & Lovette, 2008; Burbrink *et al.*, 2012a).

Since it is possible that the commonality of modal body size at local and regional scales is not due to higher rates of diversification but rather to persistence of that body size through time (Brown, 1995), we determined if the modal body size (with 5% error estimates around this measure) for each of the three extant snake clades persists through time in each of their groups. Using the 'ace' function in 'ape' (Paradis *et al.*, 2004), we estimated ancestral states using maximum likelihood with a Brownian motion model (Felsenstein, 1973) at all nodes and estimated mode using two methods: (1) calculating modes at 1 million year (Myr) intervals to the root or (2) using a sliding window taking the modes from three samples to the root. We determined if these ancestral modes overlapped with the extant modes given the 5% error around the extant estimates. Using a general linearized model (GLM), we determined if ancestral size is predicted by time, suggesting some directionality to body size evolution. Also, using a logistic regression with a binomial distribution, we determined if ancestral modes that overlap with the modes of extant species from the 1 Myr or sliding window approaches are clustered in time, yielding a significant relationship, or are constant through time, yielding no significant relationship.

Simulating size-driven diversification

We investigated if trait-driven diversification can yield distributions of extant body sizes through simulation. To determine if the chosen model for each group could yield clades where body sizes were not skewed, we simulated diversification in QuaSSE 100 times based on the range in body sizes in our datasets, the parameters for the model of diversification and the number of taxa. We then calculated how often this resulted in significantly skewed clades of extant species. In the case where diversification is linear, such that diversification rates are higher or lower at larger or smaller body sizes, we simulated trees under the same conditions as the groups examined here. To examine when significantly skewed distributions arise, we simulated a larger number of species from 50, 100, 200, 500 and 1000. We also increased the slopes of diversification, where speciation rates increase with smaller changes in body size. The parameters for diffusion, which models the stochastic elements of character change, and the breadth of body size ranges, using those recorded in mammals, were both also increased in these simulations (Blackburn & Gaston, 1994). We point out that these simulations are not exhaustive given the large number of parameters and combinations, but we have tried to replicate what is known from our real data to investigate the effects of several of these parameters. From these simulations, we determine how our likely linear models of diversification yield sig-

nificantly skewed body sizes and if this is related to rates of diversification, number of species or range in body size.

RESULTS

Community, biome and regional size structure

While some uncertainty remains regarding the appropriate measure of size for snakes (Feldman & Meiri, 2013), we find here that most results are similar using either TL or mass, although variance was quite different between measurements; the coefficient of variation was 0.15×10^{-2} and 2.6×10^{-2} for TL and mass, respectively (Fig. 1).

Multimodality was not significant ($P > 0.05$) at any site, biome, region or clade for snake TL or mass according to Hartigan's dip test. Additionally, none of these scales show significant skewing or kurtosis using the D'Agostino and Anscombe–Glynn dip tests, respectively, except for the Golden Spike, UT, site which is significantly platykurtic but composed of only four species.

When skewing and kurtosis are compared against 1000 random samples from the regional biome pool, we find that only two sites were significantly different with regard to skewing of TL and four for mass. For kurtosis, only two sites were significantly different for both TL and mass (Appendix S2). In contrast, we find that evenness was significantly lower than the regional biome pool at eight sites for TL and 12 sites for mass (Appendix S2). Using a chi-square goodness of fit test, we find that biomes do not differ significantly with respect to the number of sites showing significantly low evenness.

Our simulations of subsamples from a skewed regional distribution demonstrate that on average only 2.6 sites (95% CI 0–8) retained the significant skew for subsamples of 13 taxa, 15.6 sites (95% CI 0–46) for subsamples of 38 taxa, and 71.5 sites (95% CI 28–100) for subsamples of 100 taxa. Similar simulations using the evenness statistic showed that the regional distributions were not significantly less than the subsampled populations for the 13 or 38 taxa subsamples and were significantly less for only 0.6% of the 1000 simulations for the 100 taxa subsample.

The Mantel test indicates that the difference in skewing among communities is significantly and positively correlated with geographic distance for TL (observed = 0.20, $P = 0.0002$) and mass (observed = 0.110; $P = 0.0066$), such that skewing for both of these traits is more similar at sites separated by small distances, but kurtosis is not for either measure (observed < 0.04, $P > 0.11$). In addition, differences in the number of taxa per site and geographic distance are also significantly and positively correlated (observed = 0.121; $P = 0.003$). The first 2 out of 11 distance classes for Moran's I were significant ($P < 0.001$) for the degree of skewing associated with mass or length, and only the first distance class for kurtosis and mass. This suggests that spatial autocorrelation is present for these variables (Appendix S5). Therefore, taking into account spatial autocorrelation with the number of taxa sampled at a site, the CAR model indicates that the degree of skewing is significantly and positively associated with latitude for mass ($P < 0.001$) and

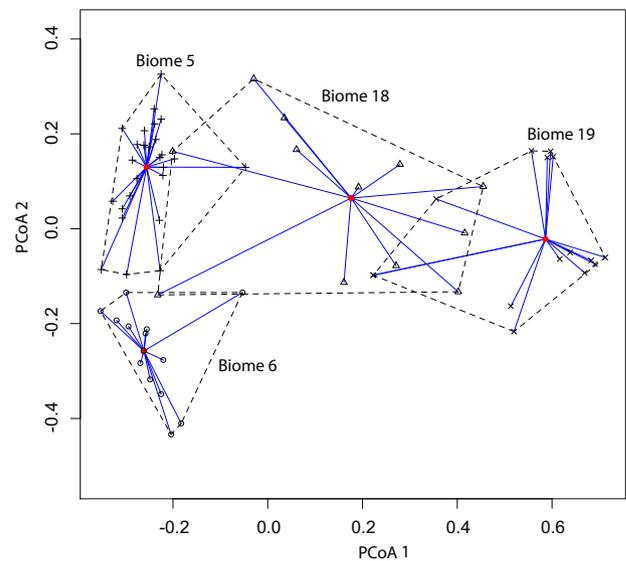


Figure 2 Differences in beta diversity among the largest four biomes examined for snakes in the United States. Illustrated here are the locations of group (biome) centroids (red dots) and distances of sites within their respective biomes to the centroid (blue lines) for the first two principal coordinates generated using the analysis of multivariate homogeneity of group dispersions.

nearly so for TL ($P = 0.052$), whereas neither measurement is significant for longitude (Appendix S5). In contrast, latitude does not significantly predict kurtosis for length, but it is negatively and significantly correlated with mass (0.02) and neither length nor mass is significant for kurtosis.

Estimates of beta diversity using β_{sim} were not significantly different among the biomes with the largest number of sites (biomes 5, 6, 18, 19) according to either the ANOVA of multivariate dispersions or the permutation test for homogeneity of multivariate dispersion (Fig. 2). Turnover is moderate among all biomes examined, with averages and variance for each as follows: biome 5 = 0.64 (0.07), biome 6 = 0.35 (0.04), biome 7 = 0.64 (0.07), biome 11 = 0.64 (0.07), biome 18 = 0.64 (0.07), biome 19 = 0.65 (0.07), biome 20 = 0.64 (0.07). These are similar to mean estimates of β_{sim} across all sites (0.68, var = 0.06). In addition, the chi-square goodness of fit tests indicates that biomes do not differ in their proportion of sites that show significant skewing, evenness or kurtosis for TL or mass ($P > 0.3$).

Phylogeny and trait-driven diversification

Among the seven models of trait-driven diversification, we find that linear models were preferred across all three groups of snakes (Table 1). The direction of trait-driven diversification was positively correlated with increasing size in the Crotalinae and Thamnophiini but negatively correlated within Lamproleptini (Fig. 3). We find little support for either the hump-shaped or the inverted-hump-shaped trait-driven extinction model, indicating that speciation rates are not highest at the mode and extinction rates are not highest away from the mode.

Table 1 Akaike information criterion values for the different models of trait-driven diversification (λ = speciation, μ = extinction) using the traits total length (TL) or mass and the phylogenies for the three snake groups examined here. The lowest AIC values are indicated in bold and with an α . If a second model falls within two AIC units of the best model then these are marked with a β .

Model	Crotalinae	Crotalinae	Lampropeltini	Lampropeltini	Thamnophiini	Thamnophiini
	TL	mass	TL	mass	TL	mass
Constant λ μ	462.9	663.6	218.7 ^{β}	288.2 ^{β}	254.1	348.7
Linear λ	461.0	661.4	220.2	290.2	255.6	350.0
Sigmoidal λ	466.2	662.2	224.3	293.6	259.6	346.8
Hump λ	462.0	661.3	223.1	292.4	259.3	344.2 ^{β}
Linear drift λ	427.3^{α}	627.0^{α}	217.1^{α}	286.4^{α}	248.8^{α}	343.4^{α}
Sigmoidal drift λ	444.4	631.4	219.5	293.5	253.6	348.4
Hump drift λ	434.3	635.0	220.1	289.7	251.2	345.8
Linear μ	464.8	665.4	220.7	290.2	256.0	350.7
Sigmoidal μ	483.6	665.4	224.7	294.3	260.0	354.7
Hump μ	NA	669.6	NA	NA	NA	NA
Inverted hump μ	468.8	661.20	220.4	293.3	260.0	353.6
Linear drift μ	466.8	667.4	222.6	292.2	257.9	352.7
Sigmoidal drift μ	471.5	671.6	226.6	296.1	261.9	356.7
Hump drift μ	NA	656.0	NA	295.6	NA	352.4
Inverted hump drift μ	470.5	658.8	220.7	294.3	261.9	355.3

For both Lampropeltini and Thamnophiini we see no significant association between time and ancestral character size or clustering of extant modal sizes in time ($P > 0.59$; Table 2). However, the mode of TL is significant and negatively correlated with time using either the 1 Myr time slice or sliding window approaches. In addition, a large number of ancestral nodes for TL overlapped with extant modes in all three groups (18.8–46%) but less so for mass (6.5–18.6%).

Simulations parameterized on the morphological range in these snakes using models of linear speciation, drift and diffusion show that obtaining skewed distributions at the clade level is unlikely, even though rates of speciation increase linearly with decreasing or increasing sizes (Fig. 4). We investigated the impact of taxon number on skewed distributions and found that clades are more likely to be significantly skewed with increasing numbers of species ($P < 0.01$). Still, even for 1000 taxa, fewer than 50% of the replicate clades are significantly skewed. This holds when the slope of speciation is increased relative to trait values. When examining the effect of morphological spread by increasing the range of body sizes to be equivalent to that of extant mammals (\log_{10} 4.7–8.23) we find the same trend. However, given the unlikely conditions when the slope of speciation is 10 times higher than the predicted values from our snake clades and diffusion (Brownian motion) is increased 10- or 100-fold, then skewed distribution of body size is greater than 50% at 100 taxa and 90% at 1000 taxa (Fig. 4).

DISCUSSION

Community and regional size processes

Ecological processes at various spatial and temporal scales can influence patterns of local BSFD. Our results demonstrate that

both TL and mass, when examined for local communities, biomes, regions and clades, remain symmetric across most scales. At least at the continental scale this is generally in contrast to what is seen for some other large groups of vertebrates such as mammals and birds, where a reduction in skewing is recorded from larger to smaller spatial scales or where multiple modes exist at regional scales (Brown & Nicoletto, 1991; Bakker & Kelt, 2000; Kelt & Meyer, 2009; Coetzee *et al.*, 2013). For both measures of size used here, we find no difference in the evenness statistic at different scales. These results are similar to those found by Cox *et al.* (2011) for snakes and do not require special processes that alter BSFD across scales, as has been discovered in other vertebrates which often show discordant patterns of skewing at different scales, indicating signals of competition, constraints on the lower range size for large taxa, limitations on the distribution of energy and available resources, or physiological restrictions at local levels (Brown & Maurer, 1989; Brown & Nicoletto, 1991; Kozłowski & Gawelczyk, 2002; Agosta & Janzen, 2005; Allen & Gillooly, 2006). Local communities examined here generally show no signature of significant positive kurtosis, indicating that environmental filtering is not affecting BSFD.

Ultimately these results may suggest that body size has no impact on competition or other factors that could potentially structure snake communities, yet this character greatly influences basic ecology and physiology for most organisms (Hutchinson & MacArthur, 1959; Peters, 1983; Blackburn & Gaston, 1994). Cox *et al.* (2011) suggested that the energy requirements of squamates (including snakes) are reduced relative to mammals and thus competition may be weaker, particularly when species richness is low at the community level. Physiological requirements may result in a single modal optimal body size in some groups (Brown *et al.*, 1993; Kozłowski, 1996; Boback & Guyer, 2003). This suggests that species selection

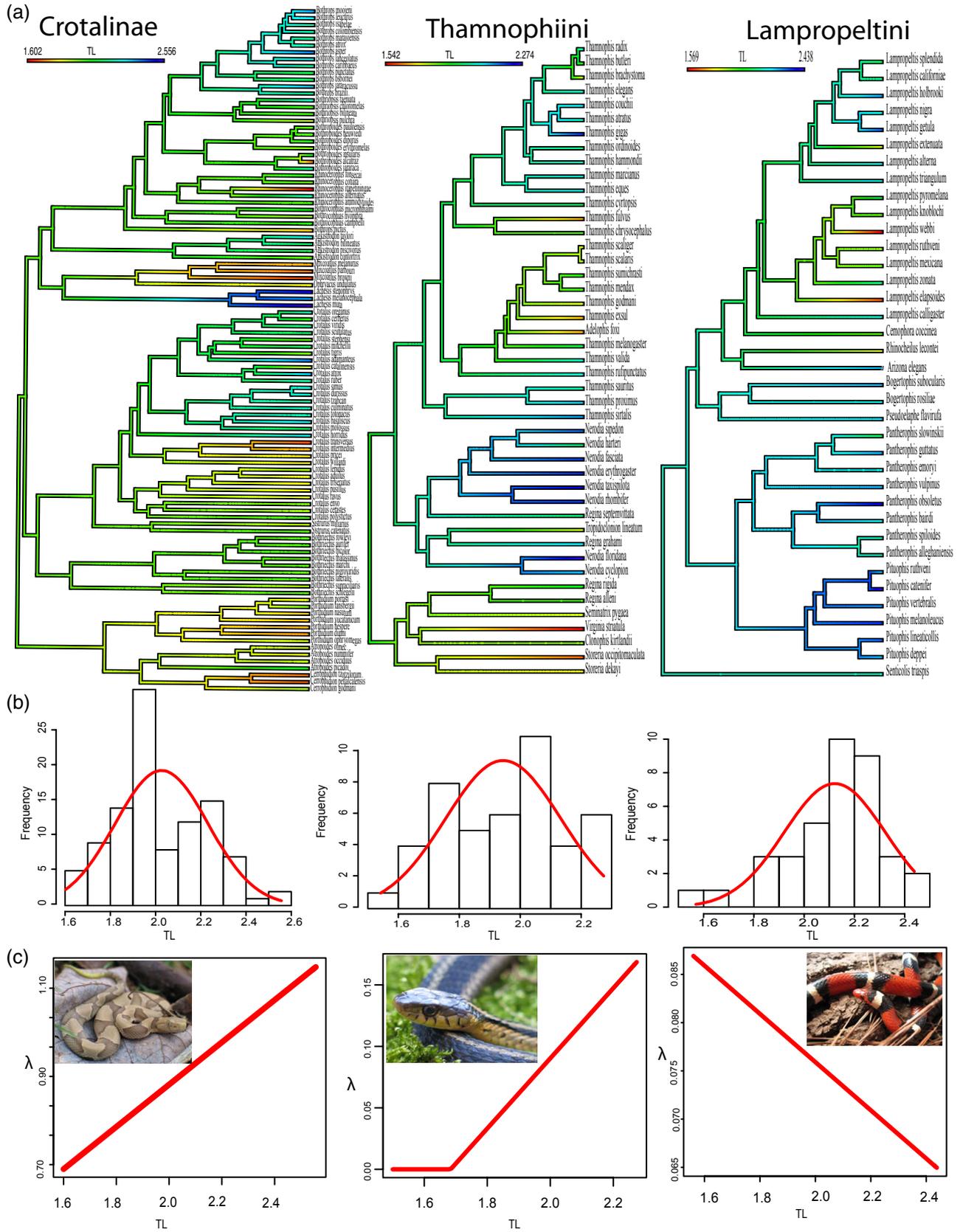


Figure 3 The evolution of body size in the three focal groups of snakes illustrated in each column. (a) Phylogenies are shown with colours indicating quantitative values for body size (log(cm); where TL is total length) generated in the R package phytools (Revell, 2012). (b) Histograms (with normal curve in red) of TL for extant snakes. (c) The preferred models of body size-driven diversification, showing linear increases or decreases in speciation (λ) with increasing TL (photo courtesy of Sara Ruane).

Table 2 The percentage of ancestral modes for body size (TL) or mass that overlap with the extant species in the three groups of snakes examined phylogenetically. Two techniques to estimate mode from ancestral states either group ancestral state and take mode at (1) 1-million-year time slices or (2) from a sliding window.

Taxon	Mode at time slices – TL	Mode at time slices – mass	Sliding window – TL	Sliding window – mass
Crotalinae	46.2**	15.4	37.8**	15.3
Lampropeltini	42.9	14.3	37.1	17.1
Thamnophiini	18.8	6.5	34.9	18.6

**Significant logistic regressions ($P < 0.001$), which demonstrates that ancestral states matching extant modes are clustered in time.

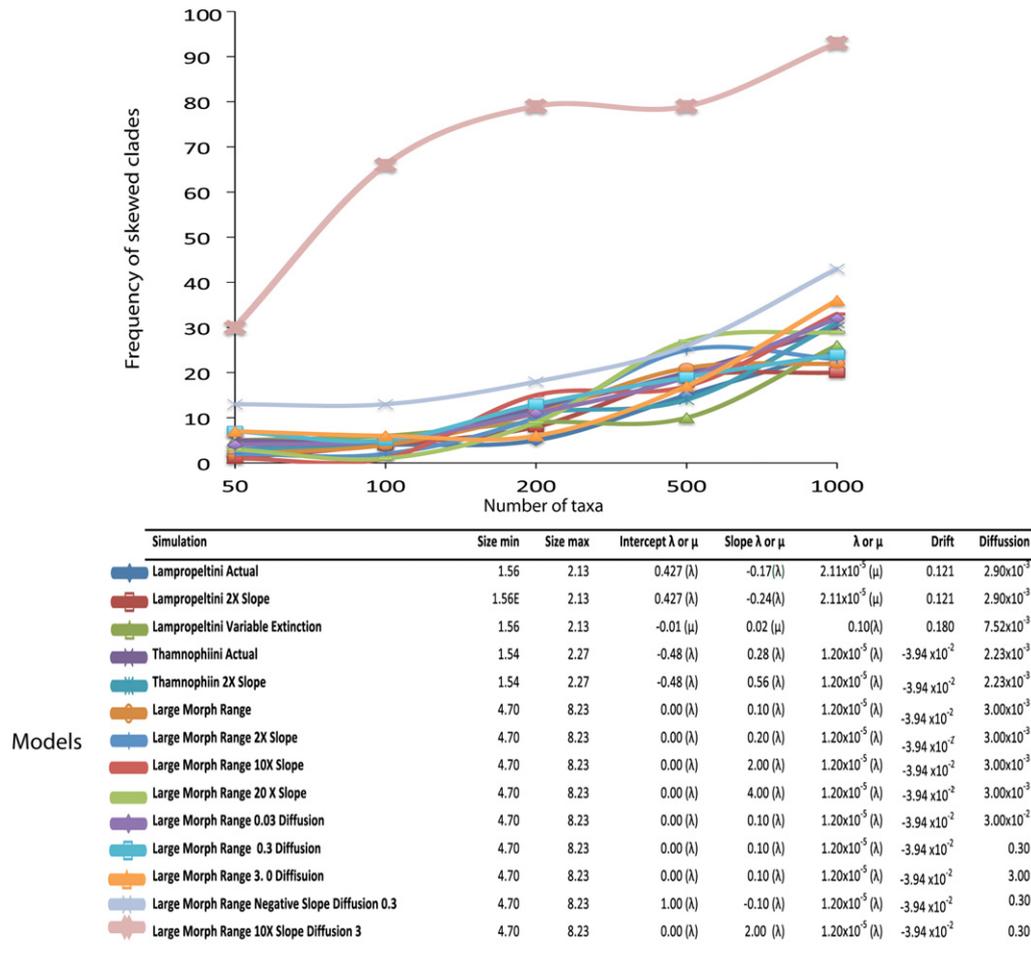


Figure 4 Simulations of trait-driven diversification using QuaSSE showing how often groups are generated that produce skewed distributions of a trait for different numbers of taxa (50–1000) per model. Colours of lines on the graph correspond to the description of models (in the first column of the table). The naming of these models reflects the parameters used in the simulation. Here the range of log-transformed body sizes examined for Lampropeltini and Thamnophiini as well as those taken from a larger morphological range (the log-transformed range recorded in extant mammals) are simulated under various values for (1) slope of speciation or extinction given the trait value, (2) changes in the sign of the slope, (3) drift and (4) diffusion.

should generate higher rates of diversification at the optimal body size, thus providing regional and local communities with a source of body sizes centred on this optimum (Monroe & Bokma, 2009; Rabosky & McCune, 2010). However, we find no evidence for a higher rate of diversification at a single mode (Fig. 3; see below). This does not suggest that community com-

position overall within a biome or across US biomes is random for snakes. We do find turnover among sites, yet beta diversity is not significantly different among biomes (Fig. 2). Given that competition has been found among closely related species of snakes in the south-eastern US (Steen *et al.*, 2013), it is possible that competition is occurring on some other axis (e.g. diet,

abiotic niche) or local predation and trophic structure are important for structuring community assemblages (Lynch & Shapiro, 1981; Ayal, 2007).

From a functional point of view, it seems unlikely that a unique body size across unrelated species with different ecologies and diets would evolve and be stable over time in communities (Kozłowski & Gawelczyk, 2002; Bokma, 2004). Other aspects such as dispersal and biogeographic limitations may account for these unimodal distributions. Under the universal neutral theory of biodiversity, Etienne and Olff (2013) constructed a hypothesis such that within a guild having a particular size it is expected that taxa compete in a similar way for resources, which should yield different speciation rates and dispersal capacities among guilds. Here, species richness will be highest at an intermediate body size as a result of the contrasting effect between allometric scaling laws that reduce speciation rates and increase dispersal capacity in the larger size classes. While we find no support for increased diversification at the modal body size, we do see in two of the three clades an increase in the rates of diversification at larger body size (Fig. 3). Although snakes as a group may have similar physiological requirements, many species within a community or biome having the same body size may not be considered part of the same guild, given that dietary and habitat requirements are very different among watersnakes, pitvipers and ratsnakes of similar size (Campbell & Lamar, 2004; Gibbons & Dorcas, 2004; Pyron & Burbrink, 2009c).

While we find no evidence for changes in symmetry or evenness across the scales examined here, we stress that while many studies demonstrate actual changes (see Coetzee *et al.*, 2013) some differences may be statistical artefacts (Greve *et al.*, 2008). For example, we modelled a skewed normal distribution after the number of species and range of body sizes recorded across our regional pool and randomly subsampled communities equivalent to the number of species at our local sites. The majority of these subsampled communities were symmetrically distributed; indicating that random and small subsamples from a larger skewed distribution can generate different distributions unrelated to local competition or other ecological processes. Therefore, it is important for researchers conducting such studies on other groups to generate similar tests to contrast expectations from competition against a null model.

Finally, we find that the skewing becomes significantly more positive with increased latitude, even when controlling for spatial autocorrelation and the number of taxa per site. This may at least suggest that skewing and the composition of communities, which is reduced in overall taxon size at higher latitudes, are susceptible to changes over area. Therefore, community size composition may not be a completely random process of subsampling from larger regional pools. Studies on other vertebrates have found a significant relationship between community skewing and latitude, albeit a negative one (Knouft, 2004; Griffiths, 2012). At least at the community level, smaller-bodied snakes may have a selective advantage for rapid warming in colder latitudes, alternatively the resource base at higher latitudes may not be able to support larger snakes. This

interspecific selection for smaller body sizes with increasing latitude, the inverse of Bergmann's rule (Bergmann, 1847), has also been found within species of snakes (Ashton & Feldman, 2003).

Trait-driven diversification

Even though unimodal symmetric distributions are maintained at all scales, including taxonomic category, we demonstrate that rates of diversification are not highest at the modal size for either TL or mass (Table 1). For two of the groups, Crotalinae and Thamnophiini, diversification is higher at larger body sizes (Fig. 3), evidence of Cope's rule (Cope, 1887; Avaria-Llautureo *et al.*, 2012). In Lampropeltini, species diversification increases with smaller body sizes (Fig. 3). These models are all supported over null or alternative trait-driven diversification models (Table 1). Such results are not entirely expected. In some organisms, such as primates, all extant species have a single symmetric mode in body size and also have rates of speciation that are highest at the modal body size (FitzJohn, 2010). In contrast to what we found with US snakes, altophiine snakes in the West Indies did not show trait-driven diversification (Burbrink *et al.*, 2012b). It is possible that combinations of taxonomic groups with multiple trends in trait-driven diversification could yield a source pool with a unimodal BSFD similar to what we see in the US. Another possibility is that mode has remained the same for these groups through time, regardless of trends of trait-driven diversification (Brown & Maurer, 1989; Brown, 1995). For the groups examined here, we show that the extant modal body size is maintained and not clustered in time, particularly for Lampropeltini and Thamnophiini (Table 2). This could suggest that extinction rates for modal body sizes are reduced and thus regional BSFD are influenced by the persistence of these sizes at or near the mode through time. However, we found little support for our inverted-hump-shaped model of trait-driven extinction in QuaSSE, which tests persistence of modal sizes by increasing extinction rates towards the tails of the size distribution while not increasing speciation rates at the mode (Table 1). We acknowledge though that estimating proper extinction rates using molecular phylogenies alone is notoriously difficult (Rabosky, 2010). Finally, our analyses use only data from extant taxa, which could bias model outcomes given that ancestral character estimation improves when combining fossil data and molecular phylogenies (Oakley & Cunningham, 2000; Webster & Purvis, 2002; Pyron & Burbrink, 2012; Slater *et al.*, 2012). When including fossils for a reduced sample of Lampropeltini, diversification rates are predicted to be constant regardless of change in body size, but still do not support a hump-shaped model (Pyron & Burbrink, 2012).

Interestingly, for groups with similar number of species and rates of diversification, our simulations of linear trait-driven diversification agree that the production of skewed extant taxon BSFD is unlikely (Fig. 4). Production of skewed BSFD extant species does, however, increase in all cases where communities/regions support larger numbers of species. For the size of the

groups examined here, it is unlikely that the distribution of extant taxa would be skewed. Further, this pattern is maintained even at larger group sizes, larger ranges in body size disparity, higher rates of speciation and greater morphological diffusion. Our results show that the distribution of body sizes with respect to skewing is actually similar from the deepest (phylogenetic) to the shallowest (community) time scales in US snakes despite diversification models indicating that either larger or smaller body sizes increase rates of speciation. We also note that trait-driven diversification can give rise to skewed distributions of extant taxa in smaller clade sizes, but only under more extreme conditions. Other authors have described a model of size-driven diversification with a reflecting barrier that enforces a gradually decreasing probability of survival or diversification at smaller size classes (McKinney, 1990; Kozłowski & Gawelczyk, 2002). These models, particularly for small-sized taxa, can yield positively skewed distributions of species. However, if a reflecting barrier is limiting diversification in the three snake groups examined here, the effect is hardly noticeable given that the distributions of size in these clades are symmetric.

The three groups examined here are members of the advanced snakes (Colubroidea) that arrived in the New World at similar times (Burbrink & Lawson, 2007; Wüster *et al.*, 2008; Burbrink *et al.*, 2012a; Guo *et al.*, 2012) and show similar diversity-dependent modes of species diversification. However, patterns of body size evolution are different among the three groups. Therefore, it is likely that selection or drift is acting differently on size in Lampropeltini than in Crotalinae and Thamnophiini. Furthermore, even though the model of trait-driven diversification may be the same in some groups, differences may still exist as to why we see the same trend in diversification in pitvipers and watersnakes. For instance, dietary, habitat or predation pressures may differ between these groups, yet produce similar directional trends in size-driven diversification. Future studies on trait-driven diversification should include more information from these types of data to tease apart the effect of the differences in the natural history of these organisms that account for differences in diversification rates.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Community sites, taxon composition, body size (TL), mass, biome and references.

Appendix S2 Local community statistics for total length (TL) and mass which include (A) location of sites, mode, mean, number of taxa, values for skewing and kurtosis and (B) significance for skewing, kurtosis and evenness and biome.

Appendix S3 Species and genes obtained from GenBank for the three snake groups (Lampropeltini, Thamnophiini, and Crotalinae) examined here.

Appendix S4 Description of taxa used and tree fossil placement for inference of dated phylogenies from Lampropeltini, Crotalinae and Thamnophiini.

Appendix S5 The first four tables show statistics for Moran's *I* for significant autocorrelation in skewing and kurtosis across communities of snakes in North America for mass and total length. The next four tables show the results from the CAR (conditional autoregressive model) analyses for skew and kurtosis for mass and total length and latitude, while accounting for

number of taxa. The last four tables show the results from the CAR analysis for skew and kurtosis for mass and total length and longitude, while accounting for number of taxa.

BIOSKETCHES

Frank T. Burbrink examines processes of diversification, historical ecology, phylogenetics and phylogeography of reptiles and amphibians across the world and is a connoisseur of fine punk rock vinyl.

Edward A. Myers is a doctoral student interested in phylogeography, species delimitation and diversification of herpetofauna.

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