Both traits and phylogenetic history influence community structure in snakes over steep environmental gradients

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Assemblages of closely related organisms are generated on axes of deep time diversification, biogeographic processes related to dispersal and habitat filtering, and competition. Using models that account for phylogeny, ecology, and traits, we examine how the interaction among biogeography, habitat filtering, and trait convergence influences community assemblage in Nearctic snakes. With 122 community surveys, environmental niche, trait data including size, diet, parity and habitat preference, and a nearly complete phylogeny of snakes from the United States, we ask 1) do phylogenetic species variability (PSV) and traits change in predictable and correlated ways given ecology and geographic distance, 2) are the measured traits variable within and across communities and how is this related to PSV at local scales, and 3) is there evidence of habitat filtering or trait divergence? Following a general trend of western to eastern North American origin and dispersal of major groups, we similarly show a significant decrease in PSV in this direction but unexpectedly with stable trait variance, showing that traits and phylogenetic variability are disconnected at the community level. We also demonstrate that trait variability and not PSV dominates local communities. Finally, regardless of phylogeny, we show that certain traits, such as reproductive mode (parity) frequency, change within communities in response to steep ecological gradients.

Biological communities are shaped by several interacting historical and ecological factors. At deep time and broad geographic scales, it is expected that speciation and dispersal produce the source pool of taxa available to local communities (Ricklefs and Schluter 1993, Webb et al. 2002, Cavender-Bares et al. 2009, Stephens and Wiens 2009). For example, high diversification or dispersal rates can provide an abundance of species from a particular group for regional source pools. However, if local communities are formed randomly from these source pools, then neutral processes drive the composition of local species assemblages (Ricklefs 2008, Cavender-Bares et al. 2009, Vamosi et al. 2009). Alternatively, at these shallower times scales, non-neutral processes such as habitat filtering or competition can influence both the composition of taxa found in regional pools and local communities. Habitat filtering can exclude taxa that do not have appropriate ecologically relevant traits, whereas competition may exclude species possessing similar traits in local communities (Darwin 1859, Cody and Diamond 1975, Lord et al. 1995, Cornwell et al. 2006, Webb et al. 2006, Kraft et al. 2007, Cavender-Bares et al. 2009, Vamosi et al. 2009). If traits are phylogenetically conserved, then both phenotypes and relationships among species should be either under- or overdispersed depending on if filtering or competition at the trait level is driving community composition. However, a certain trait shared among taxa may allow them to all exist in a particular environment while other traits may diverge reducing competition in local communities, or alternatively, several possible traits may permit a number of similar species to occupy the same habitat (multiple solutions to the same problem) and reduce competition.

Integrating ecological theory with phylogenetics has provided insight into how communities are assembled given that both deep (diversification and dispersal) and shallow-time processes (habitat filtering and competition) both play roles in this process (Webb et al. 2002, Ricklefs 2004, Helmus et al. 2007, Cavender-Bares et al. 2009). At large spatial scales, it is possible, given directional trends in colonization and diversification, that regional communities may only contain a subset of the diversity from the areas of origin. Therefore, newly colonized areas may have limited phylogenetic species variability (PSV; Helmus et al. 2007); communities composed of closely related species will have a lower PSV than communities with very unrelated taxa. Furthermore, traits found within taxa in communities may show regional trends as well, particularly if phenotypes are important for colonizing regions and forming communities. If PSV changes regionally and traits show significant phylogenetic signal then trait variance should also be associated with PSV at the community and regional levels. For example, if PSV declines in communities from areas most recently colonized, then a reduced pool of traits (lower variance) should be present. However, it is possible that traits may be highly variable within groups and match the ecological requirements of the newly colonized areas and, thus, trait variance should not decline with PSV.
Phylogenetic species variability can also change with respect to ecological gradients (Helmus et al. 2007, Pyron and Burbrink 2014). Therefore, if habitat filtering is driving the local assemblage of species and altering PSV, then it is also possible that trait convergence over these gradients will occur (Webb et al. 2002, Kraft et al. 2007, Hoiss et al. 2012, Harmon-Threatt and Ackerly 2013). In contrast, if competition is driving the local assemblage of species, then the signal of trait divergence should be apparent over these ecological gradients (Kraft et al. 2007, Pausas and Verdú 2010, Pillar and Duarte 2010). Finally, if phylogenetic and community turnover change with distance and not habitat gradients, then historical biogeographic processes related to the random probability of dispersal over large distances may primarily be responsible for how communities are assembled.

Variation within a community is composed of both phylogenetic and trait components, though it is generally unclear if traits and phylogeny provide complementary information about how communities are assembled over ecological gradients (Cadotte et al. 2013). Therefore, a single measure of the relative influence of trait versus phylogeny is important for understanding which variable makes the greatest impact in a community over large spatial scales and ecological gradients. For example, if the phylogenetic component is large when compared to the trait component (i.e. taxa are very distantly related yet have little variation among traits) this might suggest that the measured traits are not useful for understanding community assembly, that the organisms themselves are conserved morphologically, or that there has been repeated trait convergence that is necessary to exist in the given environment. The reverse is also possible; traits might remain highly variable relative to the phylogenetic component in a community, indicating that even closely related taxa are highly diverged with respect to ecologically relevant traits, as might be expected in an adaptive radiation (Schluter 2000).

In this paper, using a nearly complete phylogeny of snakes from the United States (US), taxon surveys of 122 sites covering all broadly defined ecoregions, and a comprehensive suite of ecologically relevant traits, we examine the influence of biogeography, phylogenetic species variability, trait variation, and environment to understand how communities of snakes are formed over large spatial scales. Snakes represent an important study system in this region for understanding how communities are assembled; with ~160 snake species present in the US, this large pool of taxa are highly variable with respect to traits and ecologies and span a wide range of shallow and deep divergences (Pleistocene to the Cretaceous). For example, as obligate carnivores, snakes in the US have substantially varied diets (ranging from specialists on insects, slugs, fishes, frogs, other snakes, or endotherms to generalists). Additionally, snakes here have body sizes that span greater than one order of magnitude (20–274 cm), feature two modes of reproduction (live bearing or egg laying), and have a range of habitat preferences (terrestrial, fossorial or aquatic).

Using models that integrate phylogeny, ecology, and traits, we examined how the interaction among biogeography, habitat filtering, and trait convergence influences community assemblage. Specifically, we ask 1) are there broad biogeographic trends across the US with respect to origin and dispersal, and similarly, does species richness, PSV, and traits change in predictable and correlated ways given changes in habitat variation and distance? Answering this will provide an understanding of whether PSV and traits respond similarly to broad biogeographic trends and changes in ecology or distance. We also ask 2) what are the relative contributions of phylogeny and traits within communities? Understanding this will help us determine if the measured traits respond to ecological change and if traits in communities are generally diverged (high trait variation) or converged (low trait variation) relative to phylogeny. Finally, with an understanding of trait and phylogenetic variation, we ask 3) is there evidence of habitat filtering or trait divergence over varying ecologies across the ecoregions of the US? Answers to this question will help understand how processes associated with historical biogeography, phylogeny, traits, and ecology interact at local and recent time scales to form communities.

Methods and material

Community data

We obtained species presence or absence from 122 well-surveyed communities of snakes across the US from published, unpublished, and our own surveys of two sites (Fig. 1, Supplementary material Appendix 1). All of these communities were cross-referenced with field guides and Herpnet (<www.herpnet.org>) to ensure that all species should occur locally. There is debate regarding the optimal size of area to survey given the space needed to incorporate the Darwin–Hutchinson zone, where competition structures communities. Although, it appears that plot area does not affect study outcome (Vamosi et al. 2009). For most survey studies on reptiles and amphibians, it is difficult to standardize size of area examined, because the primary objective is to survey all habitats types within a fixed locality in order to capture local habitat heterogeneity and properly estimate species diversity. To ensure that the difference in sizes of areas surveyed did not impact the probability of obtaining species we note that species numbers and area remain uncorrelated across all sites (Supplementary material Appendix 2; \( p = 0.08, p = 0.372 \)), and importantly no sites were large enough to contain all of the snakes found within the local ecoregion (Vamosi et al. 2009).

Phylogenetic data

To examine community composition with respect to phylogeny, we generated a tree of 144 species of snakes found within the Nearctic. Some rare species, which were found only in 6% of the total communities surveyed, were unobtainable for DNA sequencing forcing us to reduce 5 communities each by 1 taxon and another 3 communities each by 2 taxa.

We used 4 genes (cytochrome b, NADH2, NADH4, and cmos), with some species obtained from Genbank and the others sequenced here for cytochrome b and cmos (Supplementary material Appendix 3) using the protocol found in (Pyron and Burbrink 2009a). A dated phylogeny
Figure 1. Above, map showing localities with relative diameter indicating community size and color indicating phylogenetic species variability (PSV) with inset showing community turnover. Phylogenetic tree scaled to time showing relationships of taxa sampled through surveyed communities with * indicating node support below 95% posterior probability and insets showing the relationships between species richness and latitude and longitude using Bayesian correlation, where dark blue indicates 50% HPD (higher posterior density) and light blue indicated 95% HPD.
was produced with the most appropriate model of substitution (GTR +Γ) in BEAST using a relaxed phylogenetic technique and running the analysis for 30 × 10⁶ generations with 10 × 10⁶ discarded as burnin. Five fossil calibrations were applied with lognormal distribution priors accounting for the mean and 95% CI for the origin of the node (see Supplementary material Appendix 4 for additional details). The calibrations included the stem of Coluber/Masticophis (lognormal mean = 2.397; stdev = 0.1), the oldest member of Lampropeltini (lognormal 3.025; stdev = 0.3), the stem of Pituophis/Pantherophis (lognormal mean = 2.74; stdev = 0.3), the stem of Lampropeltis/Cemophora (lognormal 2.505; stdev = 0.3), and the stem of Thamnophis (mean = 2.77; stdev = 0.15). Using Tracer 1.5 (Rambaut and Drummond 2007), we estimated that the effective sample sizes were > 200 for all tree, substitution, and dating parameters.

Trait data

We obtained maximum body size, parity, average clutch size, diel pattern, and diet for all snakes in all communities from previously published sources (Supplementary material Appendix 5). Body and clutch size were log transformed and presence or absence was scored for viviparity or oviparity, nocturnal or diurnal diel patterns, and diet that includes mammals, birds, lizards, snakes, frogs, salamanders, arthropods, worms or gastropods. All of these traits have been considered ecologically relevant for snakes in previous contexts (Vitt 1987, Shine 1991, 1994, Rodriguez-Robles and De Jesus-Escobar 1999, Rodriguez-Robles et al. 1999, Boback 2003, Burbrink et al. 2012, Burbrink and Myers 2014).

Environmental data

For every site, we obtained 19 Bioclim variables at 30 degrees resolution, which defines variation in precipitation and temperature (Hijmans et al. 2005). In addition, we obtained net primary productivity (NPP) which defines the amount of solar energy converted to organic plant matter for all sites (Haberl et al. 2004, 2007, Ímhoﬀ et al. 2004). These variables have been used successfully to predict ranges and help define composition of snake communities on continents and islands (Pyron and Burbrink 2009b, 2014, Burbrink et al. 2011). To reduce variability in these datasets, we estimated 1st axis principal component (PCA) scores for temperature (Bioclim 1, 3–11) and precipitation (Bioclim 12–19), leaving NPP unaltered and used these axes for the remaining tests in this study.

Biogeographic tests

We assessed if there is a broad geographic trend regarding species and the phylogenetic composition of communities. First, we determined if there is an overall trend with regard to areas of origin and dispersal across the US, which may ultimately impact PSV and trait diversity. Previous publications indicated that for 96% of Nearctic (NA) snakes (Colubroidea), the New World was colonized from Asia through Beringia in 7 separate invasions (Burbrink and Lawson 2007, Wuster et al. 2008, Chen et al. 2012, Guo et al. 2012). Therefore, diversiﬁcation would necessarily have occurred west to east across the Nearctic. This might suggest that longitudinally there is a similar pattern of reduction in richness-independent measures of PSV for communities. To determine if this broad pattern holds, which ultimately inﬂuences source pools across the Nearctic, we ﬁrst estimated ancestral area of origin for our groups and determined if overall dispersal occurred from west to east. Terminal taxa were coded as occurring in three broad geographic Level 1 ecoregions (Commission for Environmental Cooperation 1997): eastern forested communities (ecoregions 15, 8), central grasslands (ecoregion 9) and western deserts and paciﬁc forests (ecoregions 10, 11, 12, 13). Similar geographic designations (east, central and western) have been successfully used for snakes in the Nearctic to test areas of origins (Pyron and Burbrink 2009b). With these regional designations, we estimated ancestral area and dispersal using the dated phylogeny of snakes with the maximum likelihood-based program Lagrange (Ree et al. 2005, Ree and Smith 2008). Dispersal among areas, initial extinction, and dispersal probabilities were left unconstrained (Supplementary material Appendix 6). We point out that our ancestral area reconstruction results could be compromised by not including the diversity of taxa from Mexico, Central and South America, though doing so is beyond the scope of this study given that the diversity of samples and community data needed are largely unavailable. However, these tests are used to assess overall support for a western NA origin of these groups as previously suggested.

Changes in species richness

To understand if and how species diversity in communities changes across NA, we ﬁrst tested if species richness can be predicted by latitude, longitude, temperature, precipitation, and/or NPP. Using Bayesian model averaging (BMA) we assess the relative importance of predictors over the entire model space (Raftery et al. 1997). The best-fit model with a combination of parameters was chosen as the one with the highest posterior probability distribution using the R package (R Core Team) BMS (Feldkircher and Zeugner 2009). Thus, we identiﬁed the most important ﬁrst- and second-order predictors to assess the relative importance of predictors over the entire model space (Raftery et al. 1997). We also determined if community turnover (beta diversity) is signiﬁcantly related to the predictors from BMA results using Mantel tests in Vegan (Dixon 2003). Additionally, we examined if turnover is caused by the loss of species and not replacement of taxa using the R package betapart (Baselga and Orme 2012). This is particularly important to test here, because it is likely that species richness is reduced at higher latitudes, and for snakes this turnover is generally not due to species replacement but simply loss. We used a Mantel test to determine if the parameters that most strongly predict species richness are correlated with changes in nested beta diversity.

Phylogenetic species variability

Given changes in species richness and diversity among communities, we next determined if there is a trend in
community turnover correlated with distance that is independent of phylogeny using the pairwise dissimilarity in the phylogenetic community composition (PCDc) metric (Ives and Helmus 2012). We then see if biogeographic trends in dispersal and diversification are related to community level PSV, where dispersal to and diversification in the youngest communities would have lower PSV than older communities. We calculated the richness-independent measure of PSV (Helmus et al. 2007) in the R package Picante (Kemel et al. 2010) and determined if a significant trend in the reduction of PSV occurs longitudinally and latitudinally as predicted from the biogeographic areas of origin. Additionally we determined if PSV is related to ecological gradients using BMA. We also determined if any of these variables predict phylogenetic under- or overdispersion by randomizing members within all communities from the US pool of taxa but preserving species richness at each site and calculating null PSVs 1000 times for each community. We then compared our real community values of PSV against these simulations to assess how frequently (p < 0.05) our communities are over- or underdispersed.

Because these models do not account for spatial autocorrelation, we also used the conditional autoregressive model (CAR) in the program SAM (Rangel et al. 2010) to account for spatial autocorrelation across these sites when correlating PSV and location. Using the significant predictors from CAR, we estimated correlation probabilities using Bayesian correlation tests in the R package BayesianBandAid (<https://github.com/raskuas/bayesian_first_aid>). The Bayesian correlation test has the advantage of over the standard Pearson correlation tests by using a bivariate t-distribution to down weigh the influence of outliers.

**Trait variability**

If characters have a strong phylogenetic signal and community composition across the US is associated with changes in PSV, then it is expected that trait composition of communities should show a trend similar to PSV. We first determined if traits, and suites of traits (parity, clutch size, habitat preference, diet, and size) have significant phylogenetic signal using Blomberg’s K in Phytools (Revell 2012).

Next, we reduced traits to a single axis, from which we calculate mean, variance, and evenness using nonmetric multidimensional scaling and principal coordinates values in the programs vegan (Dixon 2003) and Ape (Paradis et al. 2004), respectively. Here evenness, referred to as SDND (standard deviation of nearest neighbor distances; or SDNDr if normalized by phenotypic range in each community; Kraft and Ackerly 2010), is defined as the standard deviation of the total distances between ordered states in each community normalized by state range. From these measures, we determined if SDND and SDNDr are clustered or overdispersed by site. Again we constructed 1000 randomly sampled communities, preserving richness at each site, to test if the traits in our real community are significantly over or underdispersed relative to the random communities.

We used BMA to examine the association between community composition with respect to morphological response variables (mean, variance, and SDNDr) and predictors: latitude, longitude, temperature, precipitation, NPP, and species richness. These tests were performed on all traits and subsets of traits, which included diet, size, habitat preference, and reproduction. Since no community models with respect to morphology accounted for species richness, we determined which of the predictor variables from the BMA remain significant by performing a Bayesian partial correlation in BayesMed (<http://cran.r-project.org/web/packages/BayesMed/index.html>) to control for species richness.

**Trait versus phylogenetic driven community assemblage**

Because community assemblage patterns based on phylogeny alone may not accurately represent how communities are assembled with respect to functional traits across environmental gradients, we determined the relative contribution of traits and phylogeny within communities. Using the method of Cadotte et al. (2013) we calculated functional-phylogenetic distance (FPDist) by examining phylogenetic distance (PDist) and trait functional distance (FDist), calculated as the Euclidean distance among taxa across all traits. Using the equation $FPDist = (\alphaPDist^p + (1-\alpha)Fdist)^{1/p}$ ($P = 2$) to assess the relative contribution of the phylogenetic (PDist) and trait functional (FDist) component via the tuning parameter $\alpha$, ranging from 0 (where $FPDists$ are dominated by functional trait distance) to 1 (where $FPDists$ are dominated by phylogenetic distance). Intermediate values reflect both a functional and phylogenetic contribution. Therefore, FPDist will decrease with an increase in $\alpha$ for diverged taxa in a community due to the decreasing contribution of traits and the increasing contribution of phylogeny. The metric will increase with $\alpha$ for convergent taxa due to an increasing contribution of phylogeny (see Fig. 1 in Cadotte et al. 2013), potentially indicating that none of the scored characters reflect real functional differences in these communities. For functional underdispersion, traits should be more similar (filtered) than expected, whereas for phylogenetic underdispersion with a lack of functional underdispersion, it is expected that taxa should be phylogenetically more closely related in a community than expected by random assemblage. For functional overdispersion in a community, traits reflect greater differences than expected, whereas for phylogenetic overdispersion with a lack of functional overdispersion, it is expected that taxa are phylogenetically less closely related than expected. A mixture of phylogenetic and functional over and underdispersion or null patterns are possible within a community. We determined, over 20 incremental increases of $\alpha$ from 0–1, if functional or phylogenetic under or overdispersion exists at any community. Also, we examined the relationship of $FPDist$ to environmental gradients and distance over 3 values of $\alpha$ (0, 0.47, and 1.0) capturing pure functional, intermediate, and pure phylogenetic distance. Lastly, we determined if $FPDist$ is predicted by temperature, precipitation, NPP, species richness, latitude, and/or longitude using BMA.
**Trait divergence and convergence**

We used the R program SYNCSA (Pillar and Duarte 2010) to explicitly model trait correlation (filtering) or divergence (competition) across communities given phylogeny and ecology. The advantage of this method is that it applies fuzzy weighting of traits and phylogeny separately; using the Gower index to group taxa by phylogeny and traits without a priori designations. Traits can then be correlated to changes in ecology demonstrating habitat filtering using Mantel tests. Importantly, we can test for a model of trait divergence across communities by first fuzzy weighting traits and then removing the effect of trait correlation using a partial Mantel test, which is then correlated to environmental distances; significance indicates that traits diverge over environmental gradients (Pillar and Duarte 2010). We also determined if trait convergence or divergence assembly patterns are structured or independent of phylogeny, where the latter would indicate trait composition in communities is independent from phylogenetic history.

**Results**

**Phylogeny**

All effective sample sizes were > 200 for all tree, substitution, and dating parameters. The resulting topology and dates for the taxonomic groups of NA were similar to those found in larger, global phylogenetic studies of snakes (Burbrink et al. 2012, Pyron et al. 2013) with strong support for the following groups: Colubroidea (including Colubrinae, Dipsadinae, Elapidae, Lampropeltini, Natricinae, and Viperidae), Boidae, and Leptotyphlopidae. Similar to other studies (Chen et al. 2012, Pyron et al. 2013) with strong support for the following groups: Colubroidea (including Colubrinae, Dipsadinae, Elapidae, Lampropeltini, Natricinae, and Viperidae), Boidae, and Leptotyphlopidae. Similar to other studies (Chen et al. 2012), the crown ages of the Colubroid groups in the Nearctic were within the early Miocene (Fig. 1).

**Biogeography**

The global maximum likelihood for ancestral area reconstruction yielded a – lnL = 241.5, with dispersal rate = 5.239 and extinction rate = 0.513 (Supplementary material Appendix 6). The most likely ancestral area of origin for most groups was found in the western ecoregions (Lampropeltini, Colubrinae, Elapidae, Crotalinae, Boidae, and Leptotyphlopidae) but central or eastern for Dipsadinae and Natricinae. However, we note that competing area reconstructions for many nodes differed by less than a single likelihood unit (Supplementary material Appendix 6).

**Changes in diversity**

Species richness was most strongly predicted by latitude and NPP. Turnover in species composition by distance was significant (p < 0.001) and latitudinal gradients for both richness and beta diversity were also significant (p < 0.001). Additionally, nested beta diversity was significantly correlated with latitude and NPP (p < 0.001). However, because beta diversity may simply be driven by regional gamma diversity (Kraft et al. 2012), we randomized species composition of communities 1000 times, preserving richness, and tested these Mantel correlations with NPP and latitude against our real values. Only NPP remained significant (p < 0.001).

**Phylogenetic species variation**

The predictors for changes in PSV across the US were chosen using the model with the highest posterior probability prediction (Ppp) using BMA. Both temperature and precipitation variables were each reduced to a single principal component axis, with each capturing 99 and 95% of variance on the first axis respectively. The highest loadings for temperature was seasonality and for precipitation was annual precipitation and precipitation during the wettest, driest and warmest quarters. The top model (26% Ppp) included longitude (negatively correlated) and, more weakly, temperature (positively correlated) as predictors of PSV (Fig. 2). Additionally, over- or underdispersion in PSV was only associated with longitude, indicating that communities in the east were more likely to be underdispersed relative to the west (Fig. 2). Only 9 communities (7.3%) were significantly underdispersed and 3 (2.5%) were significantly overdispersed when tested against random community composition holding richness constant.

**Trait variation across communities**

Although Blomberg’s K was significant across all characters together and separately (k = 0.057–0.57; p < 0.001) except body size (k = 0.042, p = 0.1), the values were all less than 1.0, suggesting that closely related species resemble each other less than expected by Brownian motion. Similarly, mean values in morphology at each site were predicted by longitude, precipitation, temperature, NPP, and species richness (Ppp = 19.3%) and the posterior probability (Pp) for the existence of a partial correlation when controlling for species richness was 100% for NPP, longitude, and precipitation. Morphological variance was predicted by longitude, temperature, and precipitation (Ppp = 44.4%) in the absence of species richness. However, mean morphology was correlated with PSV yet variance was not (Fig. 2). When accounting for spatial autocorrelation, the CAR models also indicated similar predictor variables for both PSV and morphological responses (Supplementary material Appendix 7).

Evenness (SDND) was significantly correlated with latitude and temperature, however, when normalized to trait score range (SDNDr) these relationships became nonsignificant (Fig. 2). SDND was also correlated with species richness (p = 1 × 10−8), and most communities showing significant evenness, were smaller and not significant when normalized by trait score range. These real communities were not significantly different with respect to SDND from ones randomly generated from the entire species pool where community richness was held constant, although as expected, variance in the difference between real and simulated values of SDND was significantly higher in smaller communities when regressed against species richness (p = 2.2 × 10−16).
Figure 2. Results from (A) Bayesian model averaging (BMA) showing cumulative probabilities for the environmental, geographic or species richness model predictions for phylogenetic species variability (PSV), trait mean, variance, and scaled evenness (SDND). Each predictor variable is scaled by their posterior model probabilities, where blue indicates a positive relationship and orange negative with PSV, trait mean or SDND. (B) Bayesian correlations are also shown for particular variables where dark blue indicates 50% HPD (higher posterior density) and light blue indicated 95% HPD. We indicate for the scaled environmental variables directionality of precipitation or seasonality.
For overall morphology, species richness only predicted SDND, and no variables predict SDNDR. Additionally, SDNDR for reproductive traits only (parity and clutch size) was predicted by latitude and species richness, however, the variables were only partially correlated at 74% Pp when controlling for richness. Similarly, evenness in size was predicted by both species richness and longitude, yet partial correlation is only 73% Pp when controlling for species richness.

Functional-phylogenetic distances

A diverged pattern at all communities was estimated, where high variation in phenotype relative to lower variation in phylogeny accounts for most of the functional-phylogenetic differences (FPDist) in communities (Fig. 3). Given that most of the variance was concentrated within functional and not phylogenetic distances, it can be concluded that the reverse situation was not present (i.e. variance in FPDist being dominated by phylogenetic distances suggesting that unknown functional traits were not sampled).

With regard to over or underdispersion against null simulations, 67% of sites were not statistically significant, with only 13% being functionally underdispersed, 4.9% functionally overdispersed, 6.5% phylogenetically underdispersed and 1.6% phylogenetically overdispersed. Only 7% of the total communities were significantly underdispersed when considering intermediate values of α (where both functional and phylogenetic distances contribute both to FPDist). Also, similar to the morphological analyses, mean FPDists were correlated with changes in temperature and precipitation among communities, even when accounting for species richness (Fig. 3).

Trait divergence and convergence

Our tests of community assembly using traits, phylogeny, and environmental variables in the SYNCSA framework indicated some signal for trait convergence (r0TE: 0.293; p = 0.05) in communities with regard to environmental gradients. There was also evidence for trait divergence (after fuzzy weighting and removal of trait convergence) in communities with regard to environmental gradients (r0XE,T: 0.235; p = 0.01). While the phylogenetic signal in traits was significant (r0BF: 0.174; p = 0.001), there was no evidence for a correlation of phylogenetically structured assembly patterns to these environmental gradients (r0PE: 0.100; p = 0.405). Significant trait convergence was found for clutch size (0.251; p = 0.037), diel pattern (0.281; p = 0.029), endothermic diets (0.310; p = 0.009), and nearly so for parity (0.196; p = 0.098; Fig. 4). Gower indices may be inappropriate for grouping single binomial traits like parity, therefore we alternatively tested and found significant correlation for parity frequency and temperature and latitude (p = 0.005). Moreover, both latitude (positively) and precipitation (negatively) at the highest Ppp (67%) in the BMA models predict the frequency of live birth in communities. Finally, trait divergence in ectothermic diets was significant along environmental gradients (p = 0.012).

Discussion

Community assemblage likely reflects processes associated with diversification, historical biogeography, habitat filtering or competition (Cavender-Bares et al. 2009). For snake communities across the US, we demonstrate that distinct biogeographic trends linked to phylogenetic species variability and trait variability drive community composition, while competition as traditionally defined as limiting similarity, is hardly detected. This research demonstrates the need to understand biogeographical process in relation to phylogenetic diversity at regional scales that yield source pools for local communities. Additionally, across extreme changes in climate, there is some evidence of habitat filtering.

Our broadest findings indicate that community turnover in snakes is significant longitudinally across the United States, while richness remains relatively stable across longitude. This indicates that community sizes are relatively similar across the US, given latitude, regardless of habitat type, which is in contrast to other groups of organisms in the Nearctic where transitions through forested, grassland, and desert ecoregions changes species richness (Fig. 1; Rosenzweig 1995, Badgley and Fox 2000). Related to this turnover, community composition responds to long-range geographic distances in two ways: 1) richness-independent phylogenetic species variability decreases with increasing longitudes and 2) community morphology with respect to variance but not evenness changes with longitude and latitude (Fig. 2). This demonstrates that historical biogeographic processes are important for understanding phylogenetic composition of communities in North America, given that all colubroids in the New World dispersed through Beringia (Chen et al. 2012) and originated in the Western Nearctic. Therefore, communities of snakes in the US are necessarily composed of lineages that diverged earlier at higher longitudes yielding a similar directional trend in PSV in spite of stable species richness. Additionally, the oldest groups of snakes, scolecophidians and boids, are only found at sites in the west or central ecoregions, and thus inflate the values of PSV in these regions. While colubroids in the New World originated in the west during the early Miocene or late Oligocene (Supplementary material Appendix 6), it is possible, though not detected, that extinction and recolonization from the east to the west could eliminate a pattern of west to east dispersal. Also, the high PSV found in the southwestern US may be the result of divergent taxa from the Neotropics and Mexico in these communities, although tests of regional tropical influence in the Nearctic requires additional sampling of communities and taxa from lower latitudes (Fig. 1). Other studies have also demonstrated local underdispersion above large spatial scales (Harmon-Threatt and Ackerly 2013), suggesting that significant niche filling by particular clades may be responsible for lowered phylogenetic diversity (Cardillo 2011). In the eastern ecoregions where phylogenetic diversity is generally lower than the western ecoregions, the watersnakes (Natricinae) and ratsnakes (Lampropeltini) each respectively account for 33 and 30% of the total species, whereas the western ecoregions are dominated only by a single lineage of Colubrinae, which represent 33% of taxa, indicating that niche filling is likely occurring among only a few groups.
Figure 3. Above, mean functional-phylogenetic distances ($FPDist$) relative to the alpha tuning parameter (where low values indicate purely functional distances and high values indicate phylogenetic distances) for all communities showing the diverged pattern (Cadotte et al. 2013). Below, results from Bayesian model averaging (BMA) showing cumulative probabilities for the environmental, geographic or species richness model prediction for functional-phylogenetic distances. Bayesian correlations are also shown for particular variables where dark blue indicates 50% HPD (higher posterior density) and light blue indicated 95% HPD. We indicate for the scaled environmental variables directionality of precipitation or seasonality.

While phylogenetic diversity may show strong trends at large geographic scales, this does not provide a complete picture as to what causes specific turnover among communities and across regions, particularly when traits reveal different patterns from the phylogeny. We find that snake communities in the Eastern Nearctic generally have similar or higher trait variance than those communities found in the Western Nearctic, despite having overall lower phylogenetic diversity (Fig. 2). Interestingly, suites of characters, excluding size, show significant phylogenetic signal, which is important if traits and phylogenetic diversity at the community level are filtered along environmental gradients (Graham et al. 2009, Baraloto et al. 2012, Jacquemin and Doll 2014). However though, closely related taxa resemble each other for these
traits less than expected, which supports the opposing trend between PSV and trait variance locally. If trait variance and phylogenetic diversity are therefore not tied locally, then phylogenetic structure alone may be unhelpful for understanding how communities are formed (Cavender-Bares et al. 2009, Vamosi et al. 2009, Mayfield and Levine 2010). These trends hold here even when we examine them for subsets of characters such as body size, parity, habitat preference, or diet. Other studies have also demonstrated disconnection between trait variance and phylogenetic diversity at the community level, interpreted as the outcome of competition among closely related taxa (Graham et al. 2012).

Despite stable trait variance across communities with declining phylogenetic diversity, we find little evidence in snakes for competition with respect to how phenotypes diverge in communities. Ectothermic diets show a weak signal of trait divergence, where these diets do not overlap among snakes within communities over changing ecologies, though caution is warranted when interpreting this as competition (Mayfield and Levine 2010). Similarly, we also find no evidence for significant evenness among traits in communities, where this measure has often been used as a signal of competition (Cavender-Bares et al. 2004, Kraft and Ackerly 2010), though we note extreme values of low or high evenness may be generated randomly in smaller communities when not normalized by richness (Fig. 2). Furthermore, the outcome of competition on traits in communities using evenness is not correlated with latitude, longitude or environmental variables when species richness is taken into account, where richness in snake communities appears to be dictated by latitude and seasonality in temperature (Fig. 1). It is possible then that competition among species of snakes is simply not influencing community assemblage, at least using the phylogenetic and phenotypic metrics and traits applied herein. Alternatively, local community composition may rarely be at a long-term equilibrium and therefore the signal of competition may be too weak or is non-existent. As noted by Mayfield and Levine (2010), it is possible that competition will not produce an even or diverged distribution of traits in communities, but rather yield single directional trends (clumped) as species compete for similar recourses.

Related to the high variance in traits across communities, most of the variation existing within snake communities in the US can be attributed to differences in phenotype relative to phylogenetic divergence. This supports a diverged model using the $FPDist$ metric, where trait variance among species in communities is always higher than their expected phylogenetic distances (Fig. 3). Similarly, we also found using the SYNCA method (Pillar and Duarte 2010) that while traits appear to be significantly clustered across changing environments, there is little phylogenetic structure associated with either these changing environments or with the traits in communities. Across the US, mean $FPDist$ is higher in areas with greater precipitation and greater seasonality (Fig. 3) and might suggest that the combination of trait diversity is highest in wetter regions, though a mechanism for this bears further exploration. Similarly, when examining the predictors for the greatest component of mean $FPDist$, functional changes ($\alpha = 0$), seasonality and precipitation are strongly associated with increased functional distances. This indicates that while species richness decreases with increased seasonality, phenotypic variation is still maximized, which demonstrates that a variety of different snake traits are still able to exist in extreme climates. Specifically though, we estimated that the frequency of viviparous taxa in communities increases with greater seasonality at higher latitudes (Fig. 4). Globally this trait is associated with diversification at higher latitudes (Pyron and Burbrink 2014) and it is at least manifested at the community level in this study regardless of phylogenetic relationships. Additionally, endothermic diets appear to increase with latitude, which may also be important for existing at extreme latitudes. A parallel change in community body size across ecological gradients, where size usually increases with endothermic diets (Rodriguez-Robles and De Jesus-Escobar 1999, Pyron and Burbrink 2009c, Hamilton et al. 2012), was not detected.

Snake communities in North America also show the typical significant latitudinal species diversity gradient noticed in other taxa (Rosenzweig 1995), where richness in some northern communities is reduced by 92% of taxa found in communities at lower latitudes. Most of the change in richness correlated with latitude is due to the loss
of species and not replacement; only NPP is correlated with this measure of nested beta diversity. Causes for latitudinal gradients have been discussed in detail elsewhere (Rohde and Heep 1998, Willig et al. 2003, Kozak and Wiens 2007, Pyron and Burbriink 2009b) but generally fall into categories of ecological (dispersal and survival is limited at northern latitudes), evolutionary (speciation is higher at lower latitudes or extinction is greater at higher latitudes), or biogeographic (southern regions were occupied earlier or more often; Willig et al. 2003, Mittelbach et al. 2007). Snakes communities in the US generally experience a loss of taxa at higher latitudes and not replacement, therefore species found in the north are a subset of those same taxa in the south having extended ranges. This might suggest that speciation is likely concentrated in the south or extinction is so high in the north given that few unique species are found there. Though parsing out the specific cause for this gradient is beyond this study, it is possible that speciation rates (evolutionary mechanisms) are much higher in the south and ecological factors limit ranges at higher latitudes. Given the correlation between richness and NPP, it is likely that some aspect of ambient energy is involved. This suggests that a lack of environmental stability or increased seasonality and harshness decreases population sustainability for most species of snakes (Willig et al. 2003), which has also been demonstrated in various animal and plant groups (Currie 1991). Our results for snakes in the Nearctic indicate that these latitudinal trends are not strongly associated with changes in PSV, though phylogenetic community composition is weakly correlated to temperature seasonality, though adaptations to northern regions are generally not associated with any single taxonomic group. Detailed studies on thermal tolerance, hibernation, dietary breadth, and reproductive mode are needed to further determine the specific causes for species dropout towards the poles.

Finally, we note that some additional considerations for community assembly may be useful in future studies. First, it is difficult for most methods to separate the affects of ecological and evolutionary processes, for example, in cases where sister taxa do not co-occur simply because of recent allopatric speciation and not competition (Warren et al. 2014). In turn, methodologically separating macroevolutionary processes (e.g. speciation, extinction and historical biogeography) from more recent ecological interactions (e.g. filtering or competition) is likely artificial given that community assembly may be fluid among these scales (for additional arguments see Warren et al. 2014). Second, studies of local variation within species (e.g. diet and morphology) along with the development of new models that allow traits to vary within species among different communities would be useful to confirm patterns and address important adaptations to local ecologies. Third, the continued delimitation of species in this region (Burbrink et al. 2011, Myers et al. 2013, Ruane et al. 2014) and the use of species trees may have important effects on downstream phylogenetic community analyses as has been shown in comparative phylogenetic studies (Burbrink and Pyron 2011). Ultimately though, for a species rich group of predatory vertebrates, our results highlight important traits for structuring communities along ecological gradients while accounting for phylogenetic history and underscore the need for more detailed studies of adaptation to harsh climates.

Acknowledgements – We are grateful for the following individuals and institutions for donating tissue samples for this project: Carol Spencer and Jimmy McGuire at the Museum of Vertebrate Zoology, David Blackburn and Jens Vindum at the California Academy of Sciences, Chris Austin, Robb Brunfield and Donna Dittmann at Louisiana State Univ. Museum of Natural Science, Janet Braun at the Oklahoma Museum of Natural History, Don Shepard, Dan Mulcahy, Kenny Wray, Dustin Wood, Phil Frank, Trip Lamb, and Notah Howe. We also thank J. Boundy, T. Anton, T. Kahn, and K. Krysko for providing community information. We also thank M. Cadotte for providing R code. This project was supported in part by L. Clampitt, D. Rosenberg and S. Harris and a US National Science Foundation Grant (DEB 1257926) to FTB.

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