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Using phylogenetic trees to test for character displacement: a model and an example from a desert mammal community

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Abstract. The distribution of traits within communities is thought to provide information on the evolutionary and ecological forces that structure community composition. Ecological character displacement (evolutionary divergence among populations of interacting species within a community), as well as community-wide character displacement (even dispersion of species traits within a community via species sorting), have been widely reported and are typically interpreted as evidence for interspecific competition. However, defining an appropriate null distribution with which to assess the observed distribution of traits within a community has proved controversial. Phylogenetic methods provide an alternative approach to evaluating community structure, but such methods also require an appropriate null and have typically overlooked the potential for evolutionary dynamics within communities. Here, we present a novel phylogenetic framework that uses evolutionary expectations to generate a simple null model of the expected distribution of traits among co-occurring species. Using a stochastic Brownian motion model of trait change, we illustrate that the expected community-wide dispersion of traits varies with phylogenetic tree shape. We then use data on body mass for mammals to evaluate the accuracy with which phylogeny can predict the empirical distribution of traits and find a strong correlation between predicted and observed trait distributions. We suggest that deviations from phylogenetic expectations may therefore provide a useful tool for evaluating the role of competition in shaping community structure. Finally, we demonstrate the utility of our approach using empirical data on body mass and a phylogeny for a small community of terrestrial mammals in Yotvata, Israel, and reveal evidence consistent with ecological and community-wide character displacement. Our method unites ecological and evolutionary approaches, and it provides a novel framework for exploring community structure.

Key words: Brownian motion; character displacement; coexistence; competition; ecophylogenetics; environmental filtering; phylogenetic imbalance; Yotvata, Israel.

INTRODUCTION

Ecologists have long searched for rules governing the species composition of ecological communities. In particular, much effort has been invested in exploring evidence for limiting similarity in the distribution of traits among community members (Brown and Wilson 1956, Hutchinson 1959, Cody and Diamond 1975). Community-wide character displacement (here defined as even dispersion in ecological traits among community members through species sorting) and ecological character displacement (here defined as evolutionary divergence in ecological traits between interacting species) may be widespread (Dayan and Simberloff 2005), and have been interpreted as evidence for competition (Brown and Wilson 1956, Hutchinson 1959, Grant 1972). Traditionally, ecological character displacement is assessed by contrasting sympatric and allopatric populations of putatively competing species (but see Schluter and McPhail 1992). Evaluating evidence for community-wide character displacement is more challenging; typically, community-wide measures of trait dispersion are contrasted to a null distribution constructed by sampling species at random from the regional species pool (e.g., Strong et al. 1979, Gotelli and Graves 1996, but see Simberloff and Boecklen 1981). However, delineation of the appropriate regional species pool is problematic, and inferences can change depending upon both how the pool is defined and the details of the particular model used to sample from it (e.g., Harvey et al. 1983).

Recently, there has been growing appreciation that community phylogenetic structure might additionally

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provide valuable information for disentangling the various processes important in determining community composition (Webb et al. 2002, Emerson and Gillespie 2008, Cavender-Bares et al. 2009, Vamosi et al. 2009). However, this burgeoning field has developed, for the most part, independently from the large body of work that has focused upon ecological character displacement and the evidence for evolutionary divergence among interacting species (Dayan and Simberloff 2005; but see Davies et al. 2007). In addition, the influence of phylogeny on the expected distribution of traits of co-occurring species has been largely overlooked in the literature on character displacement (but see Colwell and Winkler 1984, and Cumming and Havlicek 2002).

Here we propose a novel phylogenetic framework to evaluate community structure using evolutionary expectations of trait dispersion, which allows us to consider both ecological character displacement via evolutionary divergence and community-wide character displacement via species sorting. We developed our approach in three stages. First, using simulations, we explored the relationship between phylogenetic tree shape and the expected distribution of traits at the tips of the phylogeny assuming a nondirectional, stochastic model of trait evolution. A close relationship between tree shape and trait distribution would suggest that the dispersion of traits within communities might vary even in the absence of general trends for directional or stabilizing selection, and may be explained simply by the shared evolutionary history of species (Colwell and Winkler 1984, Cumming and Havlicek 2002). Second, we evaluated the accuracy with which simulations match empirical data by comparing phylogenetic expectations with observed data on the distribution of body mass within mammal families. Our intention here was to demonstrate whether a stochastic model of evolution can replicate empirical patterns within clades, where species might be expected to interact less strongly than co-occurring species within communities (although some interspecific interactions between clade members are nonetheless likely). Third, we used evolutionary simulations to evaluate our approach for detecting evidence of ecological character displacement in an empirical data set of 21 terrestrial mammal species from Yotvata, Israel.

Trait Distributions and Phylogenetic Topology

In a seminal paper, Hutchison (1959) suggested that a minimal size difference in ecologically relevant traits was needed for species coexistence. Although the existence of such rigid size ratios has been questioned (Simberloff and Boeklen 1981), the distribution of trait values among species is still thought to be important, and various indices that characterize these distributions have been proposed (Gotelli and Graves 1996). Here, we consider the variance in size ratios (VSR; Holmes and Pitelka 1968), calculated as the variance in the difference in natural log trait values between adjacent pairs of species ranked by their trait values (see also Rabosky et al. 2007 and Cornwell and Ackerly 2009 for a similar approach). We use this metric because it best encapsulates variance across all species in the pool, and its statistical properties are well understood (Pleasants 1994).

Large VSR indicates an uneven distribution of trait values, referred to here as clustering, and implies multimodality in size distributions such that some species cluster around similar trait values, but there are large gaps in the trait distribution. The community phylogenetics literature has typically considered clustering around a single optimum trait value; however, discontinuities in the trait distributions of species within an assemblage may be common (Holling 1992). In contrast, low VSR indicates an even trait distribution, sometimes referred to as "trait overdispersion," with equal spacing between species. If similar trait values reflect similar resource use, an even trait distribution should minimize competitive overlap among community members. Hence, constant size ratios (low VSR) are traditionally interpreted as evidence for interspecific competition (Hutchinson 1959, Grant 1972, Simberloff and Boecklen 1981).

Evaluating evidence for even dispersion is not straightforward. If sufficient data are available, observed VSR can be compared to a null distribution drawn from a more inclusive species pool (Strong et al. 1979, Gotelli and Graves 1996). However, such comparisons are inherently scale dependent, conditioned on the delineation of the species pool. Phylogeny might provide a useful alternative null distribution, given an appropriate model of character evolution. Although there are numerous models of trait evolution in the literature, none have been developed to explicitly model character displacement. The most common evolutionary model is the Brownian motion model, in which traits are inherited from a common ancestor, but diverge over time independently in a manner analogous to a random walk. Brownian motion is frequently assumed in phylogenetic comparative methods (Felsenstein 1985, 1988, Grafen 1989; but see Freckleton et al. 2002, Blomberg et al. 2003, Garland et al. 2005). We suggest that Brownian motion may also provide a useful null model for evaluating evidence for competitive character displacement.

Using simulations, we explored how phylogenetic tree shape influences the distribution of traits within an assemblage under a model of Brownian motion evolution. Tree shape may influence expected VSR even under a common Brownian process of trait evolution because changes in topology will alter the covariance structure among species. For our purposes here, we considered two axes of tree shape: imbalance and stemminess. Imbalance expresses the variation in the number of lineages between sister taxa (Shao and Sokal 1990). Stemminess captures the relative difference in internodal distances between divergences toward the tips of a

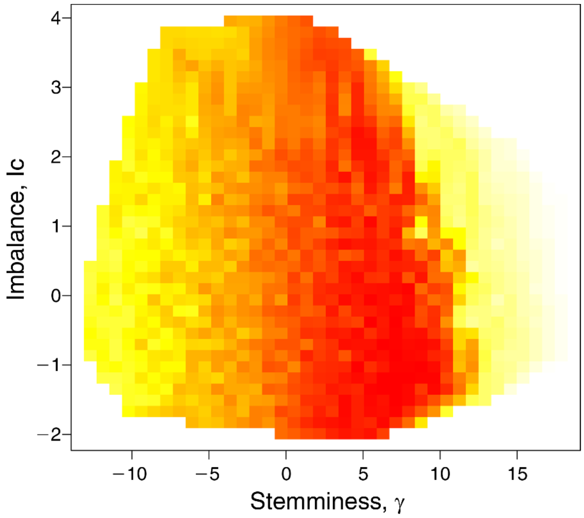

FIG. 1. Interaction between tree balance (Ic) and ”stemminess” (γ) on expected trait distributions (measured as median variance in size ratios [VSR] from 1000 simulated traits, $\mathrm{VSR}_{\mathrm{med}}$) assuming a model of Brownian motion evolution; VSR values vary from uneven (yellow-orange; minimum $\mathrm{VSR}_{\mathrm{med}} = 1.22$) to even (orange-red; maximum $\mathrm{VSR}_{\mathrm{med}} = 25.02$). Color intensity reflects interpolated values divided into 20 quantiles.

phylogenetic tree and those toward its root (Fiala and Sokal 1985, Mooers and Heard 1997): Trees with longer branches toward the root are “stemmy,” whereas trees with longer branches toward the tips are “tippy.”

Phylogenetic simulations

To explore the interaction between tree shape and trait dispersion, we generated 1000 ultrametric, phylogenetic topologies of 128 taxa by randomly clustering the tips (function rcoal in the R library APE; Paradis et al. 2004). Next, we transformed branch lengths using Pagel's δ (Pagel 1999; function deltaTree in GEIGER, Harmon et al. 2008), where $\delta > 1$ increases the height of external nodes making trees increasingly tippy, and $\delta < 1$ increases the height of internal nodes increasing tree stemminess. To generate a suitable range of tree stemminess, we drew δ from a uniform distribution of between 0.1 and 100. For each tree topology, we then simulated 1000 independently evolving traits assuming Brownian motion, and estimated VSR. Our heuristic for simulating trees was largely ad hoc, and simply aimed at generating trees spanning a range of imbalance and stemminess.

On the simulated trees we summarized topological imbalance and stemminess using the rescaled Colless imbalance metric (Ic; Blum et al. 2006) and the γ statistic (Pybus and Harvey 2000), respectively. Both indices have an expected value of zero under a constant-rate pure birth (Yule process; Yule 1924) null model. Trees with $\mathrm{Ic} < 0$ are more balanced than predicted from a null model where all lineages have an equal probability of diversifying, and trees with $\gamma < 0$ are more tippy than predicted by the equal-rates null model. Our simulations show a predictable, but nonlinear relationship between VSR and the two axes of tree shape (Fig. 1 and Appendix: Fig. A1). There is a weak trend for lower VSR with more balanced trees (Spearman's $\rho = 0.06$). The correlation between VSR and stemminess is much stronger, with the highest VSR in stemmy ($\gamma > 5$) trees. We suggest that the variation in VSRs reflects the distribution of evolutionary distances separating tip taxa. For example, in trees with several species-rich clades separated by long internal branches (stemmy trees), species within each clade will be connected by short branches and, hence, tend to share similar trait values, but the larger distances separating clades will translate into large differences among their trait means, resulting in an overall uneven trait distribution.

Our results indicate that, under the Yule model of diversification (where $\mathrm{Ic} \approx 0$ and $\gamma \approx 0$), VSR will tend to be relatively low for traits evolving via Brownian motion. Real phylogenies, however, tend to be imbalanced (Mooers and Heard 1997), and negative γ's (tippy trees) may be common (e.g., McPeek 2008, Phillmore and Price 2008, Rabosky and Lovette 2009). Communities likely display similarly complex phylogenetic topologies (Heard and Cox 2007). We therefore suggest that, even in the absence of strong competition, many communities may a priori be expected to have relatively high VSR (see also Cumming and Havlicek 2002).

An empirical test using mammalian families

In our simulations, we demonstrate that expected VSR varies with tree shape under the simplistic assumption of Brownian motion. Here we evaluated whether a Brownian motion model can predict empirical VSR for the body sizes of mammal families (rather than communities). Taxonomic families provide a useful test case to compare with our simulations because interspecific competition within them is likely less prevalent than within guilds of co-occurring species. A close match between simulated and observed VSR would indicate that phylogenetic topology may strongly influence empirical VSR, and that Brownian evolution provides a reasonable null evolutionary model for predicting the distribution of body sizes for mammals. However, we note that even a close match between simulations and empirical data should not be interpreted as evidence that traits necessarily evolve in a Brownian fashion. We discuss the case where trait evolution departs significantly from Brownian motion.

We examined a range of tree topologies by extracting the subtree for all monophyletic mammal families with more than four species from a published phylogenetic supertree for mammals (Bininda-Emonds et al. 2007, 2008). For each family, we then estimated empirical VSR using data on body mass from the PanTHERIA database (Jones et al. 2009), and contrast the observed VSR values with expected VSRs estimated from the phylogeny and assuming a Brownian motion model of trait evolution. Species with no body mass data were pruned from the tree prior to analysis. Because families varied in their average body sizes, we rescaled simulated traits to the maximum and minimum extent of observed body sizes within each family. Importantly, by rescaling tip values, our results are insensitive to differences in the Brownian rate parameter, σ^2.

Mammal families differ greatly in species richness, phylogenetic resolution, and trait distribution (Appendix: Table A1). However, phylogeny accurately predicted empirical VSR for most clades (regression of empirical VSR against median values from simulations, slope = 1.03, $t = 20.13$, intercept = not significant, $r^2 = 0.83$, model $P \ll 0.01$, $n = 83$ for all families; Fig. 2), and the difference between empirical and predicted VSR was not significantly different from zero, although results were marginal ($P = 0.06$, paired t test). Poor phylogenetic resolution will tend to bias tree shape toward increased tippiness, potentially skewing our estimates of predicted VSR. We therefore re-examined trends for families with ≥75% of internal nodes resolved, and found that the relationship between empirical and predicted VSR was qualitatively unchanged (slope = 1.02, $t = 9.79$, intercept = not significant, $r^2 = 0.82$, model $P \ll 0.01$, $n = 23$; Fig. 2).

Our analysis demonstrates that Brownian motion can predict the empirical distribution of traits among species, summarized using VSR, with a high degree of accuracy using only information on their phylogenetic relationships. When the model of trait evolution departs from Brownian motion, inferences derived from the phylogenetic structure of communities may be confounded (Kraft et al. 2007). However, we show that, even for clades where trait evolution is not strictly Brownian (Appendix: Table A1), simulations assuming Brownian motion still perform well. This finding indicates that our methods are robust to differences in the model of trait evolution. Nonetheless, if an alternative evolutionary model is known a priori to provide a better fit to a clade, it would be relatively straightforward to generate expected trait distributions using this model.

TREE SHAPE, TRAIT EVOLUTION, AND SPECIES COEXISTENCE

If competition is strong among coexisting species and relevant traits are evolutionarily labile, such that they can evolve rapidly, interspecific interactions might shape their evolutionary trajectories (Losos 1992, Schluter and McPhail 1992, Losos et al. 1998, Tofts and Silvertown 2000), and ecological character displacement is predicted among sympatric species. In the absence of evolutionary character displacement, competition might structure ecological communities by restricting coexistence to species with previously evolved niche differences via species sorting (Grant 1972, Davies et al. 2007), evident as community-wide character displacement. Alternatively, fit to the environment might determine species coexistence, such that species in communities would be predicted to share similar traits (phenotypic attraction or clustering; Webb 2000, Webb et al. 2002). For example, traits might converge on local adaptive optima (Butler and King 2004), or particular environments may act as geographical attractors for specific lineages (Wiens and Donoghue 2004). Where there are multiple alternate adaptive peaks, we predict a more uneven trait distribution, as species sharing similar traits cluster around each local optima. However, we note that if species are filtered into, or converge on, a single ecological niche (i.e., species fall within a single guild), there is no a priori expectation of any relationship between VSR and filtering, but rather the trait range may be truncated (Kraft and Ackerly 2010).

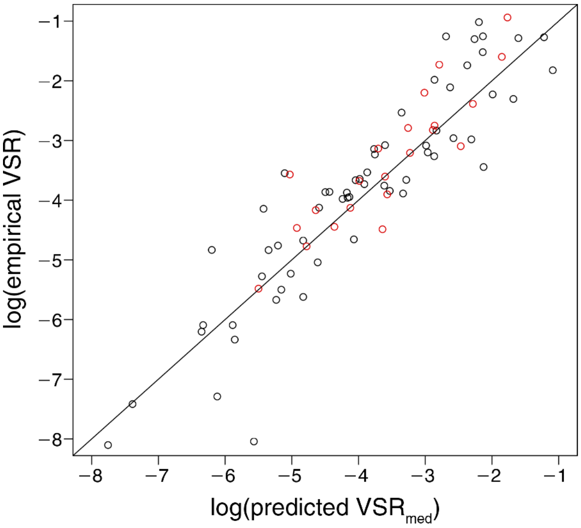

FIG. 2. Comparison of empirical VSR vs. predicted (median variance in size ratios, VSR$_{med}$) for mammalian families. The black line represents the 1:1 line. Red symbols represent families with ≥75% of nodes resolved. Empirical VSR correlates strongly with predicted values from simulations ($r^2 = 0.83$, $n = 83$; and $r^2 = 0.82$, $n = 23$, from the regression of all families combined, and families with phylogenetic resolution >75%, respectively). VSR was log-transformed as this best met model assumptions of normal errors and constant variance. The difference between empirical and predicted VSR was not significantly different from zero ($P = 0.06$, paired t test).

Here, we have attempted to more closely match community phylogenetic approaches with evolutionary expectations derived from models of character divergence and present a novel framework (Table 1) that provides some simple predictions generated from our simulations. Broadly, we suggest that where trait evolution is more or less nondirectional when averaged over time, processes shaping community composition may be reflected in the evolutionary relationships among constituent species (i.e., the shape of the community phylogenetic tree). However, when traits are subject to strong selection pressure, for example, through interspecific competition or abiotic forces, assembly processes might be apparent in the departure of the community-wide trait distributions from expected trait distributions

TABLE 1. Phylogenetic framework inspired by Webb et al. (2002), describing expected phylogenetic tree shapes and trait distributions for communities assuming alternative evolutionary and ecological processes.

	Evolution of ecological traits	
Ecological force	Nondirectional (Brownian)	Directional
Competition	a) Sorting for evolutionary divergent species with low observed VSR: Community phylogeny relatively balanced and "stemmy" ($0 < \gamma < 10$).	b) Evolutionary divergence (ecological character displacement): Low observed VSR relative to expectations from Brownian motion evolution.
Environment†	c) Sorting for clusters of species sharing similar functional traits and high observed VSR: Community phylogeny relatively imbalanced and either "tippy" ($\gamma < 0$) or extremely "stemmy" ($\gamma > 10$).	d) Evolutionary convergence: High observed VSR relative to expectations from Brownian motion evolution.

† Assuming multiple local optima (niches).

under a nondirectional model of evolution, such as Brownian motion.

Non-Brownian evolution

Our method provides a novel approach for detecting ecological character displacement without reference to some more inclusive species pool. Instead, we derived a null expectation from the phylogenetic topology connecting the species within the community using a model of Brownian motion evolution. We have focused on a Brownian motion model because it is commonly assumed in the comparative literature (Freckleton and Harvey 2006) and its properties are well described (Felsenstein 1985). We show that a simple Brownian model performs well, even when the true model of trait evolution deviates from strict Brownian motion. Nonetheless, we recognize that trait evolution can depart significantly from Brownian expectations, and that models of evolution may vary among traits, clades, and taxonomic ranks (e.g., Gittleman et al. 1996, Hansen 1997, Böhning-Gaese and Oberrath 1999, Blomberg et al. 2003, O'Meara et al. 2006, Thomas et al. 2006, Cooper and Purvis 2010, Harmon et al. 2010). Other models of trait change could easily be substituted for Brownian motion within our framework to generate an expected distribution of VSR if these models were known to provide a better fit to the observed data. The fit of alternate models can be evaluated using information criterion (Burnham and Anderson 2002). Generating an appropriate null distribution when the underlying model of trait change is unknown might be considered a greater challenge.

We believe that, even when the precise mode of trait evolution is unspecified, a Brownian motion model of evolution may be informative. Critically, we suggest alternate models of evolution will generally elevate VSR (resulting in a less even distribution of traits), except where competition drives trait differences between close relatives. As an illustration, we compared predictions from Brownian motion to another commonly used model of evolution: the Ornstein-Uhlenbeck (OU) model, which approximates stochastic evolution with a constraining force due to stabilizing selection (Hansen 1997). In the OU model, trait divergence approximates a random-walk model with a central tendency, so that phenotypes are pulled back toward some optimal trait value (Hansen 1997). Assuming a single-trait optimum, the OU model predicts higher VSR than Brownian motion (Appendix: Fig. A2), and we would expect a multi-optima OU model to further elevate VSR. Because Brownian motion predicts lower VSR, it is the more conservative model for evaluating evidence for competition. Nonetheless, in certain cases, a Brownian motion model might perform poorly if rates shift through the tree. Specifically, a recent speed-up in evolutionary rates, which can be conceptualized as stretching the tip branch lengths in the tree (Blomberg et al. 2003), will return low VSR, biasing us toward inferring evidence for character displacement. A variable rate model could be evaluated under such circumstances. However, we note that a more common trend for trait evolution would seem to be a slow-down in rates toward the present (Harmon et al. 2010). Brownian motion, therefore, provides a sensible model choice for evaluating evidence for competition in the absence of evidence pointing to alternative models.

THE TERRESTRIAL MAMMALS OF YOTVATA, ISRAEL

Yotvata is a small settlement distant from major urban centers in the southern Negev Desert in southeast Israel. It lies in a flat desert region, with little vegetation, low mean annual precipitation (~30 mm, all in winter) and high mean annual temperatures (+30°C in summer). The fauna is mostly Saharo-Sindic in origin, with some tropical elements reaching north along the Rift Valley, and some Mediterranean species reaching southwards. The mammal community is comprised of 13 species of bat, plus ~21 species of non-volant mammals. We use this small non-volant mammal community as an illustration for our methods, comparing the empirical size distribution for body mass to expectations from phylogeny.

The Yotvata terrestrial mammal community provides an ideal test case, as it is small enough to be easily tractable, but with representatives from each of several major clades, including Carnivora (eight species) and

Rodentia (eight species). Species can be broadly grouped into three functional types or guilds: carnivores (Carnivora), omnivores (omnivorous rodents: spiny mice [*Acomys cahirinus*], gerbils [*Gerbillus* sp.], and jirds [*Meriones crassus*], plus Ethiopian hedgehogs [*Hemiechinus aethiopicus*]), and herbivores (gazelles [*Gazella* sp.], Cape hares [*Lepus capensis*], fat sand rats [*Psammomys obesus*], porcupines [*Hystrix indica*], jerboas [*Jaculus jaculus*], and nesokia [*Nesokia indica*]). The phylogeny for these species (Appendix: Fig. A3) is well resolved (95% nodes resolved), and body mass data was collected from specimens within the locality (111 measured specimens from the Tel Aviv University Museum of Natural History, Tel Aviv, Israel; S. Meiri, *unpublished data*).

Methods and results

The phylogeny for the Yotvata community (Appendix: Fig. A3) is imbalanced (Ic = 0.31) and marginally stemmy ($\gamma = 0.03$). We generated a null distribution of community-wide trait dispersion using 1000 simulated traits evolved along the branches of the phylogeny assuming Brownian motion, and compared this to the observed VSR from empirical data on species mean body mass. Observed VSR was significantly lower than simulated values (VSR = 0.07 vs. 0.16, empirical vs. median from Brownian simulations, respectively, $P = 0.034$, one-tailed test from simulations; Fig. 3). To evaluate whether our results were sensitive to our choice of evolutionary model, we repeated the simulations assuming an OU, rather than a Brownian motion, model of evolution. We estimated parameters for the OU model from the data using the OUCH R library (Butler and King 2004) and assuming a single evolutionary optima. Results were similar to the Brownian model (VSR = 0.07 vs. 0.17, empirical vs. median from OU simulations, respectively, $P = 0.038$, one-tailed test from simulations; Fig. 3), and fit of the two models did not differ (AIC = 85.07 vs. 84.35 for fits of the data to an OU vs. Brownian model, respectively), which is reflected in the low maximum likelihood estimate of the constraint parameter, α, in the OU model ($\alpha = 0.007$, vs. expectation $\alpha = 0$ under unconstrained Brownian motion).

Our analysis used the published phylogenetic supertree of mammals from Bininda-Emonds et al. (2007, 2008) assuming the best estimate of node ages. Although we believe our method is relatively robust to phylogenetic error, a bias toward inferring overly stemmy or tippy phylogenies would shift our null distribution of VSR (see Fig. 2). We therefore explored alternative dated topologies (best, lower, and upper date estimates; from Bininda-Emonds et al. [2007, 2008]). The γ statistic varied among tree topologies ($\gamma = 0.03$, 0.31, and -0.35 for the best, lower, and upper date estimates, respectively), and *P* values from simulations were also somewhat variable: For the lower dates, $P = 0.038$ and 0.051, for Brownian and OU models, respectively; and for the upper dates, $P = 0.037$ and 0.046, for Brownian and OU models, respectively.

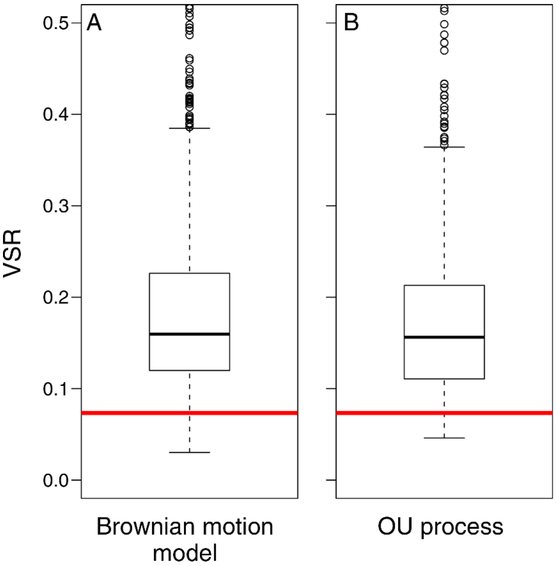

FIG. 3. VSR for the non-volant mammal community of Yotvata, Israel. Observed VSR is indicated by the red horizontal bar, and expected VSR from simulations assuming (A) a Brownian motion model of trait evolution and (B) a bounded Ornstein-Uhlenbeck (OU) process. Observed VSR values are significantly lower than expected VSR values from both models ($P = 0.034$ and $P = 0.038$, respectively).

We show that the distribution of body sizes for the non-volant mammal community of Yotvata is more even than expectations obtained from two commonly assumed evolutionary models (Brownian motion and OU), although the exact degree to which this is true varies somewhat with tree topology. Our results are consistent with ecological character displacement and the evolutionary divergence of traits to minimize niche overlap. Our findings agree with evidence from more traditional studies that have suggested competition is a significant force structuring mammal community assembly in this region (e.g., Dayan et al. 1989, 1990, Yom-Tov 1991). We considered the community of all non-volant mammals, but it is unlikely that there is direct competition for resources among species falling within very different functional guilds (e.g., carnivores vs. herbivores). However, within each guild or clade, competition might be strong (e.g., within carnivores [Dayan et al. 1989] or rodents [Yom-Tov 1991]).

SUMMARY

We illustrate that the expected community-wide distribution of traits varies with phylogenetic tree topology. Although multiple processes are likely to be important in shaping the evolution of traits within clades, using data on mammalian families, we show that the distribution of traits among species maps closely to phylogenetic expectations assuming a simple Brownian motion model of evolution. These results demonstrate that we are able to generate useful predictions of the expected trait distribution for a set of species given their phylogeny. When traits are evolutionarily labile, interspecific competition may drive evolutionary divergence, resulting in a more even trait distribution than predicted by a nondirectional model of stochastic evolution. Alternatively, species may be sorted into communities based upon their pre-evolved niche similarities or differences. We suggest species sorting might be reflected in the topology of the phylogenetic tree that links them. We did not explore fully these predictions because evaluating topological patterns would require additional information on phylogeny for the regional species pool, whereas we feel the strength of our simulation approach is that it frees us from the constraint of having to define the regional pool.

It remains possible that apparently "non-Brownian" communities might also represent species sorting, with selection for species whose traits have evolved in a random walk toward more even dispersion. One approach for teasing apart these two mechanisms would be to explore the phylogenetic depth at which lineages diverge: Species sorting might be more likely to reflect trait variation that arose deeper in the phylogeny, assuming evolutionary character displacement occurs within the context of the contemporary community, whereas sorting operates on pre-evolved trait differences. In addition, if species sorting is the primary force shaping trait distributions, then we might expect species within clades to be more or less exchangeable; for example, a fox is a fox, and fills the fox niche within a community. However, if evolutionary divergence shapes the trait distribution, it is possible that the "fox niche" can only be filled by the "correct" fox from that particular locality. Of course, it is more than likely that both processes are important in shaping community structure (Cornwell and Ackerly 2009). Furthermore, different traits might illustrate different patterns within the same communities; for example, lineages might be sorted on traits delimiting species' environmental niches, but demonstrate evolutionary divergence within traits important in direct or interference competition.

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Supplemental Material

Appendix

A table reporting phylogenetic statistics for clades representing mammal families included in Fig. 2, figures showing variation in size ratios (VSR) with tree stemminess and under an Ornstein-Uhlenbeck process, and a figure depicting the phylogeny for the mammal community of Yotvata, Israel (*Ecological Archives* E093-177-A1).