Biological Journal of the Linnean Society, 2018, **124**, 308–318. With 1 figure.

Community structure in ecological assemblages of desert rodents

BADER H. ALHAJERI[1]* and SCOTT J. STEPPAN[2]

[1]*Department of Biological Sciences, Kuwait University, Safat, 13110, Kuwait*
[2]*Department of Biological Science, Florida State University, Tallahassee, FL 32306–4295, USA*

Received 14 March 2018; revised 4 May 2018; accepted for publication 4 May 2018

Global desert rodent communities were examined for evidence of phylogenetic and morphological community structure. Using geographical distribution data of desert rodents (within 15 assemblages), a composite molecular phylogeny and a geometric morphometric dataset of skulls, the mean pairwise distance and mean nearest taxon distance were calculated for each assemblage and compared with null communities. Community structure metrics detected phylogenetic clumping in two out of the 15 desert assemblages, indicating that co-occurring rodents were more closely related than expected by chance. No other assemblages showed a significant phylogenetic structure. Skull morphology had different structuring patterns, but overall, most examined desert assemblages were not significantly structured in skull morphology. Similar overall lack of community structure patterns was observed at the regional scale in both the phylogenetic and the body mass datasets. We also directly tested the association between phylogenetic and morphological structure and found it to be significant. The association between phylogenetic distance and increased diversity that we observed might indicate that niche partitioning facilities coexistence in diverse assemblages.

ADDITIONAL KEYWORDS: body mass – community phylogenetics – cranium –geometric morphometrics – mandible – morphological structure – skull – species coexistence.

INTRODUCTION

The main objective of community ecology is to understand the mechanisms that facilitate coexistence in local assemblages (i.e. community structure; Stevens *et al.*, 2012; Harmon-Threatt & Ackerly, 2013). A central question in this field is whether neutral or deterministic processes limit local assemblages to subsets of regional species pools (Cardillo, 2011). Traditionally, this question was addressed by determining whether species are non-randomly assembled into communities from regional species pools (lists of all species in the next-highest spatial scale) in terms of ecological traits and phylogenetic composition (Webb *et al.*, 2002). Phylogenies provide ecologists with improved estimation of species relatedness when addressing fundamental ecological questions (Cardillo, 2011). Interest in phylogenies in community ecology is also attributed to their usefulness as indirect measures of overall niche; phylogenetic proximity usually reflects ecological similarity because of phylogenetic niche conservatism (Webb *et al.*, 2002). Thus, phylogenetic trees provide an alternative to the difficult task of determining whether enough important characters have been measured to model Hutchinsonian niches adequately (Ricklefs, 2010). Although morphological traits can provide accurate estimates of resource use, phylogenetic information provides a more general estimate of niche that considers non-morphological axes of niche variation (Stevens *et al.*, 2012).

The first step in ecological studies that use the community phylogenetic approach of Webb (2000) and Webb *et al.* (2002) is often to determine whether focal communities are significantly structured or are randomly assembled from regional species pools (i.e. neutrally assembled; Hubbell, 2001). 'Null communities' are first estimated by repeatedly subsampling taxa from the regional species pool and thus calculating a null distribution of metrics of phylogenetic structure with which the observed community is compared (Webb, 2000; Webb *et al.*, 2002). If focal communities

*Corresponding author. E-mail: bader.alhajeri@ku.edu.kw

are significantly structured, then the dominant ecological force responsible can be determined. Phylogenetic clumping (or clustering) of communities (community members are more closely related to each other than expected by chance) is often attributed to environmental filtering (also known as habitat filtering), which selects for species with similar niche requirements inherited from their common ancestor (Webb *et al.*, 2002). On the contrary, phylogenetic overdispersion (or evenness) of communities, where community members are more distantly related to each other than expected by chance, is attributed to competitive exclusion (or species sorting; Grant, 1972) favouring the coexistence of species with divergent niches (Webb *et al.*, 2002). However, recent work has shown that it is difficult to establish a direct relationship between competition and overdispersed assemblages (Emerson & Gillespie, 2008; Cadotte & Tucker, 2017). Furthermore, competition is very difficult to test based on large-scale distributional data, because of habitat segregation and microallopatry (Whittaker & Fernández-Palacios, 2007).

Most studies in phylogenetic community ecology are performed at small or local spatial scales, although some have used this approach to investigate patterns at regional scales (e.g. carnivores, Cardillo, 2011; bumble bees, Harmon-Threatt & Ackerly, 2013; Australian desert vertebrates, Lanier, Edwards & Knowles, 2013; ruminants, Cantalapiedra, Fernández & Morales, 2014). At such large scales, historical processes may explain patterns of community structure better than ecological processes. Phylogenetic clumping at large spatial scales may be attributed to local diversification with no subsequent dispersal (owing to biogeographical barriers), whereas phylogenetic overdispersion may be attributed to colonization of species from distant origins (owing to recently formed habitat connections) (Cardillo, 2011; Brown, 2012).

The small spatial scales of most studies in community phylogenetics may be attributed to the disproportionate usage of taxa with limited mobility, such as plants and microbes. Vamosi *et al.* (2009) reviewed 24 studies in phylogenetic community structure and found that 22 were conducted on taxa that cannot move freely between local assemblages (Harmon-Threatt & Ackerly, 2013). Mobile taxa are expected to interact over much larger scales than those considered in community ecology (Cavender-Bares *et al.*, 2009) because they can overcome competition more easily through dispersal and therefore may appear to be assembled randomly at small scales (Weiher *et al.*, 2011). Therefore, in addition to historical forces, in mobile taxa, ecology may also direct community assembly at much larger spatial scales. For example, environmental filtering can be explained in terms of the abiotic range limits that lead to a discrepancy between fundamental and realized niches, which are in turn estimated by the range of the species (Cardillo, 2011). Likewise, interspecific competition can also be expanded to large spatial scale assemblages, as in studies showing that even in the absence of abiotic barriers to dispersal, interspecific competition can lead to stable geographical range limits (e.g. Case *et al.*, 2005; Price & Kirkpatrick, 2009).

Granivorous desert rodent communities are a classic model system in which to study community assembly patterns and have played a central role in the development of theories and approaches in animal community ecology (e.g. Bowers & Brown, 1982; Kotler & Brown, 1988; Brown, 1989). Most of the evidence indicates that interspecific competition is the dominant force in structuring heteromyid communities in North American deserts (e.g. Munger & Brown, 1981; Bowers & Brown, 1982; Brown & Munger, 1985; Heske, Brown & Mistry, 1994). However, other mechanisms that facilitate coexistence have also been considered, including disparate microhabitat selection and temporal variation in resource abundance (Brown, 1989). Although North American desert rodent communities have been relatively well studied, few studies have been done elsewhere to determine the importance of competition in community structure (Kelt *et al.*, 1996). Shenbrot & Krasnov (2002) provided direct evidence of the minor role of interspecific competition in Palaearctic desert rodent communities; this indicates that that patterns of community structure in small desert mammals derived from studies of North American deserts (that are generally structured by interspecific competition) are not generalizable to other deserts around the world. This difference might be attributed to the investigated traits (e.g. Leibold, 1998), which mostly dealt with body mass and locomotion; which although important in structuring granivorous desert rodent communities in North America, might not play a dominant role in mediating interspecific competition in the deserts of Africa, Asia and Australia (Kelt *et al.*, 1996; Weiher & Keddy, 2001; Shenbrot & Krasnov 2002). Given that other deserts include far fewer granivorous rodent species, coexistence might be facilitated more by dietary differences and other mechanisms than by differences in body mass and locomotion (Weiher & Keddy, 2001).

Stevens *et al.* (2012) recently examined phylogenetic community structure in rodent communities in the central Mojave Desert and found that communities in general were overdispersed in less productive habitats and clumped in more productive habitats. This pattern was interpreted as 'diversity begets diversity', facilitated by packing ecologically similar species in more diverse habitats (Brown, 2012). This result is concordant with studies that have used non-phylogenetic approaches and found a positive correlation between species richness and environmental

heterogeneity in desert rodent communities (e.g. Rosenzweig & Winakur, 1969; M'Closkey, 1976, 1978; Kotler & Brown, 1988).

In the present study, we assess the phylogenetic and morphological community structure of desert rodent assemblages. The primary objective of the study is to test the prediction that desert rodent species are assembled non-randomly from regional species pools and, more specifically, to determine whether these assemblages have similar structuring patterns. We also test the following predictions: (1) taxonomic diversity in assemblages is correlated with mean phylogenetic distance (i.e. more diverse communities are composed of phylogenetically distant relatives); and (2) phylogenetic and morphological community structure are correlated.

MATERIAL AND METHODS

Phylogenetic data

We calculated metrics of phylogenetic structure using community subtrees extracted from a composite chronogram of rodents that contained 2357 rodent species (2414 operational taxonomic units [OTUs]) based on Fabre *et al.* (2012) and Steppan & Schenk (2017). Details on the generation of this composite chronogram were discussed by Alhajeri (2014) and Alhajeri (2014). A pruned 289 species tree of desert rodents extracted from the composite chronogram is shown in the Supporting Information (Appendix S1, Fig. S1).

Assemblages and biogeographical regions

Species of desert rodents were assigned to one of 15 desert assemblages (Fig. 1A) based on overlapping geographical distributions within desert zones, as determined using the International Union for Conservation of Nature Red List website (www.iucnredlist.org; IUCN, 2013). The resulting 15 assemblages resemble the zoogeographical provinces of Shenbrot, Krasnov & Rogovin (1999), which were likewise based on desert rodent distribution data, but with two important differences. First, unlike Shenbrot *et al.* (1999), we include all the species whose range is found within the respective desert area (i.e. widespread species), even those whose range extends far beyond the focal assemblage (including non-endemic species), and thus our assemblages include more species than those in the aforementioned source. Second, Shenbrot *et al.* (1999) included only species that that they 'consider to belong to desert faunas', or species whose ranges are mostly located within deserts, whereas we include all species whose range, based on IUCN (2013), extends into each of the 15 desert regions.

Our changes were made because the provinces described by Shenbrot *et al.* (1999), which were based on a multistep process to determine whether to include a species in a desert province, might be overly conservative. Furthermore, the fact that they did not consider all rodent species, but only those that were 'desert-specific' is insufficient for our purposes, because non-desert-adapted species can still interact with other species in that assemblage. Species with narrow ranges or isolated on islands (e.g. *Peromyscus sejugis* and *Peromyscus stephani*) were excluded because their interactions with other species in those assemblages are minimal. Thus, for the remainder of the paper, we strictly use the term assemblage, not zoogeographical province, to differentiate our assembled rodent 'communities' from those of Shenbrot *et al.* (1999).

The regional species pools for the 15 desert rodent assemblages were determined by assigning assemblages to one of five desert regions, which correspond to biogeographical realms: (1) Nearctic; (2) Neotropical; (3) Australian; (4) Palaeotropical (Afrotropic); and (5) Palaearctic (Fig. 1B). The continental species pools for the five desert regions were determined by assigning all 2414 rodent OTUs in the composite phylogeny (see above) to one or more of the biogeographical realms. Following Schenk *et al.* (2013), North America (450 species) includes Central America southward to the Panamanian suture; South America (634 species) south of the Panamanian suture; Eurasia (444 species) includes the Middle East and North Africa; Southeast Asia (346 species) from southern India to the Philippines and Sulawesi; Sahul (164 species) includes Australia and New Guinea; Africa (413 species) south of the Sahara; and Madagascar (25 species). After the two biogeographical regions with no deserts (Southeast Asia and Madagascar) were dropped, the five remaining biogeographical regions resemble the desert regions of Shenbrot *et al.* (1999) (Palaearctic, Palaeotropical, Australian, Nearctic and Neotropical) with the exception that the horn of Africa is included in the Palaearctic desert region (which otherwise corresponds to Eurasia) and not in sub-Saharan Africa owing to its greater proximity to other deserts in that region. We adopt this scheme by including the horn of Africa in Eurasia (see Supporting Information, Appendix S1, Figs S2–S6). The IUCN (2013) species distribution maps, although very useful, are highly generalized; as such, they may contain errors that might affect our assignment of species to assemblages, but this is unlikely to influence the major trends that are the focus of this study.

Morphological data

Skull morphology was quantified in one to nine specimens of 234 desert rodent species, for a total of 956

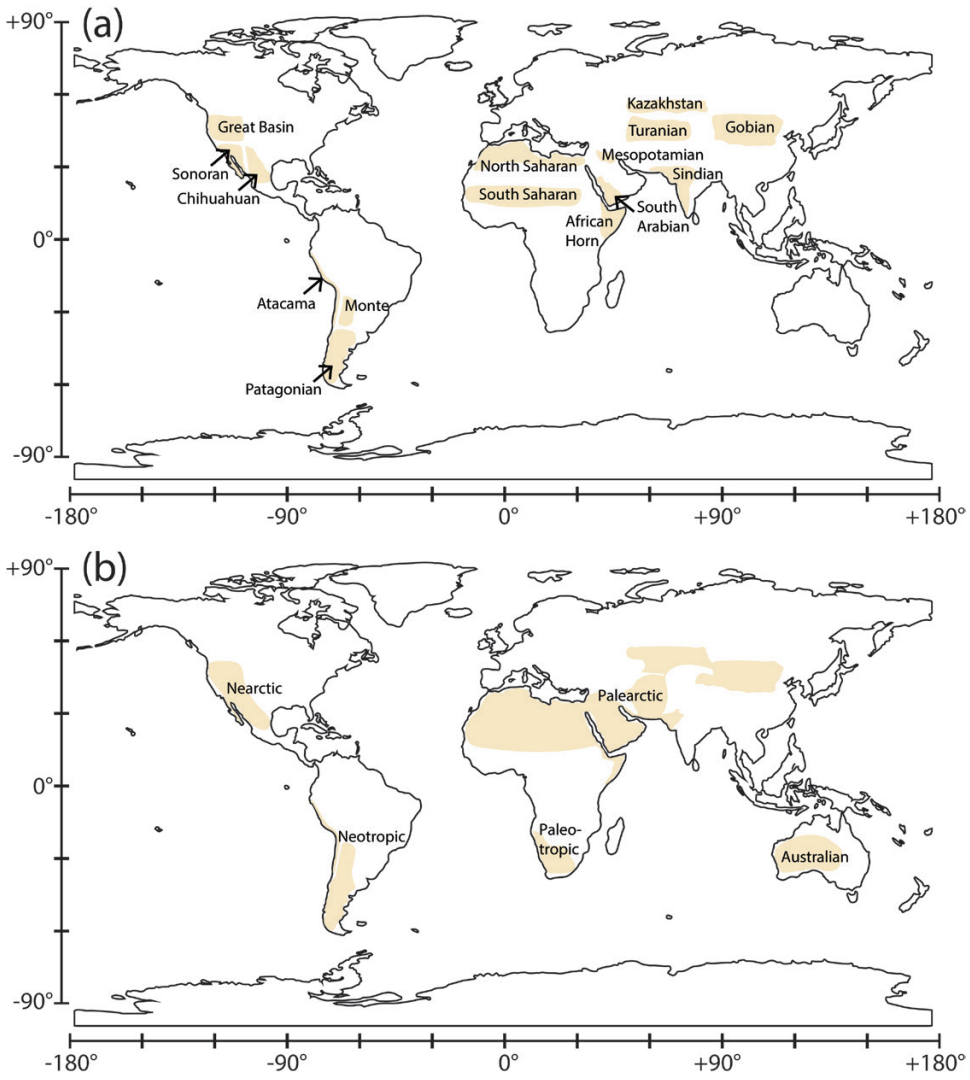

Figure 1. Maps of 15 desert rodent assemblages (A) and five desert rodent regions (B) used in the analyses. Assemblages and regions are not drawn to scale and are defined based on the distribution of rodent species, not the full extent of the deserts, and do not include all deserts.

specimens, and an average of four specimens per species (Supporting Information, Appendix S2, Table S1). Multiple specimens and equal representation of males and females were examined when possible to account for intraspecific variation and sexual dimorphism by calculating species averages.

We photographed skulls of voucher specimens of most available desert species in the American Museum of Natural History (AMNH), the Field Museum of Natural History (FMNH), the Museum of Vertebrate Zoology (MVZ), the United States National Museum of Natural History (USNM), the University of Florida Museum of Natural History (FLMNH), Laboratorio de Citogenetica Mamiferos, Universidad de Chile (LCM) and the Sam Noble Oklahoma Museum of Natural History (SNOMNH). Only wild-caught adult individuals were included, with adult status diagnosed by the basioccipital–basisphenoid epiphyseal fusion, as in the study by Robertson & Shadle (1954), and by the complete eruption of third molars to the occlusal surface (Steppan, 1997).

Cranial landmarks were digitized on photographs captured with a Nikon D3200 digital SLR camera using a Nikon 40 mm f/2.8G AF-S DX Micro-Nikkor Lens (Nikon, Tokyo, Japan) at 24 megapixels (resolution = 6016 × 4000; JPEG) in a standardized manner. Five photographs were taken per individual, to capture all the relevant orientations for landmark

digitization. A scale bar was included in each photograph. Landmarks were digitized on the left side of the skull except when the left side of the skull was damaged; in such cases, the right side was used after being reflected. Landmark digitization was conducted in TPSDIG (Rohlf, 2010).

Body mass data were collected for all available rodent species in the 2414 rodent OTU tree (1411 out of 2414) using the PanTHERIA database (Jones *et al.*, 2009) following Alhajeri & Steppan (2016). Body mass for species with no data available (1003 out of 2414) was estimated using ancestral state reconstruction, as implemented in the PICANTE library (Kembel *et al.*, 2010) in R (R Development Core Team, 2013). Body mass data from the five sampled biogeographical regions (with deserts) was retained and $\log_{10}$-transformed before morphological structure analyses. Body mass, which is widely available in the literature, was used because this trait is extremely variable in rodents, and particularly in our dataset, where it ranges from 4.9 g in *Delanymys brooksi* to 47.5 kg in *Hydrochoeris hydrochaeris* (Jones *et al.*, 2009). Body mass is also a strong predictor of resource use (diet) in rodents (Alhajeri & Steppan, 2018) and mammals in general (Pineda-Munoz, Evans & Alroy, 2016). Variation in body mass in rodents has also been demonstrated in previous studies to be associated with environmental variation in a clinal fashion (Alhajeri & Steppan, 2016).

Morphological structure at the scale of assemblages was based on geometric morphometric analysis of skull shape. Like body mass, the skull is also highly associated with resource use in rodents, where dietary specialization is found to be associated with overall dental morphology (Martin, Alhajeri & Steppan, 2016) and with cranial morphology in general (Samuels, 2009). In addition to resource use, skull morphology also includes regions associated with environmental adaptation, such as the tympanic bulla, which has been shown to be associated with climatic variation in gerbils (Alhajeri, Hunt & Steppan, 2015) and in rodents in general (Alhajeri 2014). Skull morphology, which is perhaps a better proxy for niche than body mass, was not used at the regional scale because this trait must be quantified directly from museum specimens (and cannot be assembled from the literature). Skull landmarks were digitized from the aforementioned photographs; they were chosen to cover most of the important elements in the cranium and the jaw and are expected to be associated with overall ecology. Landmarks were used previously by Alhajeri (2018) and are illustrated in the Supporting Information (Appendix S1, Fig. S7) and described in the Supporting Information (Appendix S3).

A total of 302 out of the 956 digitized specimens had at least one missing landmark (Supporting Information, Appendix S2, Table S2) because of damage or being unidentifiable in the species. These missing landmark coordinates were estimated in the GEOMORPH library (Adams & Otárola-Castillo, 2013) in R, which conducts a thin-plate spline interpolation using landmarks common to complete specimens and specimens with missing data (Adams & Otárola-Castillo, 2013) using the process described previously by Alhajeri (2018). A detailed description of the geometric morphometric data process (Rohlf & Slice, 1990; Zelditch, Swiderski & Sheets, 2004) that was used to obtain shape variables for each species (following the method of Claude, 2008) to calculate the morphological structure below is described in the Supporting Information (Appendix S3) and follows Alhajeri (2018).

Estimation of phylogenetic and morphological structure

The phylogenetic structure of desert rodent assemblages was estimated using the PICANTE library in R. Ten subtrees were extracted from the 2414 OTU chronogram described above, one for each of the five desert regions (Palaearctic, Palaeotropical, Australian, Nearctic and Neotropical; Supporting Information, Appendix S1, Fig. S8) and one for each of the five biogeographical regions (North America, South America, Eurasia, Africa and Sahul; Supporting Information, Appendix S1, Figs S1–S5) and were used as the regional species pool for the assemblage-scale analyses (Supporting Information, Appendix S1, Figs S9–S11) and the desert region-scale analyses, respectively.

For each of the 15 desert assemblages and the five desert regions, the mean phylogenetic distance between all pairwise combinations of taxa (mean pairwise distance, MPD) and the mean phylogenetic distance between each taxon and its closest relative (mean nearest taxon distance, MNTD) were calculated (Webb, 2000; Webb *et al.*, 2002). The standardized effect sizes (SES) of the MPD and MNTD were calculated for each assemblage using all the available null models; however, as the results were largely concordant, we show the results only for the 'phylogeny pool' null community model, which randomizes the community data matrix by drawing species randomly with equal probability from the regional species pool (i.e. from the phylogeny or morphological distance matrix; Kembel *et al.*, 2010). The SES are measures of tree-wide (SES-MPD) or branch-tip (SES-MNTD) phylogenetic clumping or overdispersion, with a negative value indicating

clumping and a positive value indicating overdispersion, relative to null communities (Kembel *et al.*, 2010). The statistical significance of the SES values was calculated by comparing the observed data with data generated from a sample of 1000 simulated null assemblages drawn from regional species pools (*Z* values, calculated as the difference between the observed distance metric in the community and the mean of the distance metric in the 1000 null communities generated by randomizations divided by the standard deviation of the distance metric in the null communities; Kembel *et al.*, 2010). The *P*-values of the observed distance metric vs. the null communities were calculated as the rank of the observed distance metric vs. null communities divided by the number of randomizations +1 (=1001) (Kembel *et al.*, 2010). Significantly clustered assemblages were those with SES values ≤ −1.645 ($\alpha = 0.05$), and significantly overdispersed assemblages were those with SES values ≥ 1.645 ($P \geq 0.95$).

The SES mean pairwise distance (SES-MPD) and the SES mean nearest trait distance (SES-MNTD), the morphological equivalents of the phylogenetic metrics described above, were also calculated for each assemblage using the same methods described above, while substituting the phylogenetic distance with the Euclidean morphological distance between taxa. At the assemblage scale, these metrics were calculated using the five morphological (shape) datasets, whereas at the regional scale, these metrics were calculated using the log body mass dataset.

DATA ACCESSIBILITY

All data generated or analysed in this study are included in the Supporting Information.

RESULTS

PHYLOGENETIC AND MORPHOLOGICAL COMMUNITY STRUCTURE

Both phylogenetic structure metrics (SES-MPD and SES-MNTD) detected significant phylogenetic clustering in two out of the 15 desert assemblages; these assemblages occurred in each of the Palaearctic and Nearctic desert regions (Table 1; Supporting Information, Appendix S2, Table S3). The phylogenetically overdispersed assemblages (five based on SES-MPD and eight based on SES-MNTD) were all non-significant (Table 1; Supporting Information, Appendix S2, Table S3).

Overall, out of the 15 desert assemblages, the dorsal cranium was significantly clustered in only one assemblage and significantly overdispersed in two to four assemblages; the lateral cranium was significantly clustered in one to three assemblages and significantly overdispersed in one ot two assemblages; and the ventral cranium was not significantly clustered in any assemblage and significantly overdispersed in one to three assemblages (Table 2; Supporting Information, Appendix S2, Tables S4, S5). In the lateral mandible dataset, there was significant clustering in three out of the 15 desert assemblages, and significant overdispersal in one assemblage, whereas the occlusal mandible was not clustered in any assemblage and was significantly overdispersed in one to three assemblages (Table 2; Supporting Information, Appendix S2, Tables S4, S5). There were no apparent differences in the patterns of community structure among desert regions (Table 2; Supporting Information, Appendix S2, Tables S4, S5).

At the regional scale, based on the phylogenetic dataset, out of the five desert regions, only one was

Table 1. Summary of phylogenetic structure metrics (using the 'phylogeny pool' null model) for the three desert regions that encompass the 15 desert rodent assemblages

	SES-MPD		SES-MNTD	
	Clustered	Overdispersed	Clustered	Overdispersed
Palaearctic	7 (1)	2 (0)	3 (1)	6 (0)
Nearctic	2 (1)	1 (0)	2 (1)	1 (0)
Neotropical	1 (0)	2 (0)	2 (0)	1 (0)
Overall	10 (2)	5 (0)	7 (2)	8 (0)

Abbreviations: MPD, mean pairwise distance; MNTD, mean nearest taxon distance; SES, standardized effect size. The numbers of clustered (SES < 0) or overdispersed (SES > 0) assemblages are shown (based on MPD/MNTD), with the numbers in parentheses indicating significantly clustered/overdispersed assemblages. SES ≥ 1.645 ($P \geq 0.95$) indicates significant phylogenetic overdispersion; SES ≤ −1.645 ($P \leq 0.05$) indicates significant phylogenetic clustering. A full output of the results appears in the Supporting Information (Appendix S2, Table S3). The Palaearctic region includes the following assemblages: North Saharan, South Saharan, South Arabian, Mesopotamian, Sindian, Turanian, Kazakhstan, Gobian and African horn. The Nearctic region includes the following assemblages: Great Basin, Sonoran and Chihuahuan. The Neotropical region includes the following assemblages: Atacama, Monte and Patagonian. The Australian and Palaeotropical deserts were omitted because the species lists in the regional species pools are equivalent to species lists of the assemblages.

Table 2. Summary of morphological structure metrics (using the 'phylogeny pool' null model) for the three desert regions that encompass the 15 desert rodent assemblages

	SES-MPD		SES-MNTD	
	Clustered	Overdispersed	Clustered	Overdispersed
Palaearctic				
Dorsal cranium	5 (0)	4 (3)	4 (0)	5 (0)
Lateral cranium	6 (3)	3 (2)	5 (1)	4 (0)
Ventral cranium	6 (0)	3 (2)	8 (0)	1 (0)
Lateral mandible	8 (0)	1 (0)	6 (2)	3 (0)
Occlusal mandible	8 (0)	1 (0)	6 (0)	3 (0)
Nearctic				
Dorsal cranium	1 (1)	2 (0)	1 (1)	2 (1)
Lateral cranium	2 (0)	1 (0)	1 (0)	2 (1)
Ventral cranium	2 (0)	1 (1)	1 (0)	2 (1)
Lateral mandible	1 (0)	2 (1)	2 (1)	1 (1)
Occlusal mandible	2 (0)	1 (1)	2 (0)	1 (0)
Neotropical				
Dorsal cranium	1 (0)	2 (1)	1 (0)	2 (1)
Lateral cranium	1 (0)	2 (0)	1 (0)	2 (0)
Ventral cranium	1 (0)	2 (0)	1 (0)	2 (0)
Lateral mandible	0 (0)	3 (0)	0 (0)	3 (0)
Occlusal mandible	1 (0)	2 (2)	0 (0)	3 (1)
Overall				
Dorsal cranium	7 (1)	8 (4)	6 (1)	9 (2)
Lateral cranium	9 (3)	6 (2)	7 (1)	8 (1)
Ventral cranium	9 (0)	6 (3)	10 (0)	5 (1)
Lateral mandible	9 (0)	6 (1)	8 (3)	7 (1)
Occlusal mandible	11 (0)	4 (3)	8 (0)	7 (1)

See legend to Table 1 for more information. A full output of the results appears in the Supporting Information (Appendix S2, Tables S4, S5).

Table 3. Phylogenetic and morphological structure metrics for five desert regions (Palaearctic, Nearctic, Neotropical, Australian and Palaeotropical) within five biogeographical regions (Eurasia, North America, South America, Sahul and Africa) using the 'phylogeny pool' model

	SES-MPD		SES-MNTD	
	Clustered	Overdispersed	Clustered	Overdispersed
Phylogenetic	1 (0)	4 (0)	2 (1)	3 (1)
Morphological	3 (1)	2 (1)	2 (1)	3 (1)

See Table 1 for more information. A full output of the results appears in the Supporting Information (Appendix S2, Table S6).

significantly clustered and one was significantly overdispersed (Table 3; Supporting Information, Appendix S2, Table S6). Likewise, using the morphological dataset (body mass), only one out of the five desert regions was significantly clustered, and one was significantly overdispersed (Table 3; Supporting Information, Appendix S2, Table S6).

Phylogenetic structure vs. diversity and morphological structure

The observed mean phylogenetic distance between the desert assemblage species showed a significantly positive correlation with log species richness for the MPD metric ($R^2 = 0.24$, $P = 0.0276$) but not the MNTD metric ($R^2 = 0.02$, $P = 0.401$; Supporting Information,

Appendix S1, Fig. S12A). For both MPD and MNTD, we found a significant positive correlation between the mean phylogenetic distance and mean morphological distance based on the dorsal cranium (MPD, $R^2 = 0.65$, $P < 0.0001$; MNTD, $R^2 = 0.66$, $P < 0.0001$; Supporting Information, Appendix S1, Fig. S12B), the lateral cranium (MPD, $R^2 = 0.75$, $P < 0.0001$; MNTD, $R^2 = 0.51$, $P = 0.0008$; Supporting Information, Appendix S1, Fig. S12C), the ventral cranium (MPD, $R^2 = 0.87$, $P < 0.0001$; MNTD, $R^2 = 0.53$, $P = 0.0005$; Supporting Information, Appendix S1, Fig. S12D) and the lateral mandible (MPD, $R^2 = 0.42$, $P = 0.0030$; MNTD, $R^2 = 0.23$, $P = 0.0308$; Supporting Information, Appendix S1, Fig. S12E). For both MPD and MNTD, the mean phylogenetic distance was not significantly correlated with the mean morphological distance based on the occlusal mandible (MPD, $R^2 = 0.18$, $P = 0.0525$; MNTD, $R^2 = 0.02$, $P = 0.434$; Supporting Information, Appendix S1, Fig. S12F).

DISCUSSION

Community structure in desert rodent assemblages

This study is the first to use the community phylogenetics approach (*sensu* Webb *et al.*, 2002) to examine the structure of desert rodent assemblages across continents. Community phylogenetics is commonly studied in immobile organisms, including plants (see Emerson & Gillespie, 2008), and the greater vagility of mammals provides a complement and a contrast to those studies, as the ability to disperse and interact over very large spatial scales may lead to unique patterns of community structure (Harmon-Threatt & Ackerly, 2013).

We found that at both the assembelage and the regional scales, the overwhelming majority of desert rodent assemblages do not show a significant phylogenetic structure and seem to be assembled in a neutral manner (Tables 1, 3). We also found that most desert rodent assemblages were not significantly structured in skull morphology at the assemblage scale (Table 2) or in body mass in the regional scale (Table 3). Thus, the general pattern seems to be that of neutral assembly of assemblages from species pools, regardless of the dataset (phylogenetic vs. morphological) and the scale used (assemblage vs. region). Taken together, these results also indicate that no generalizations can be made about community structure patterns in desert rodent assemblages at the spatial scales examined.

Our results are in contrast to recent evidence compiled on mobile taxa that show a pattern of clumping, which the authors mostly interpret in terms of such mechanisms as environmental filtering, or localized rapid speciation and/or reduced extinction (e.g. carnivores, Cardillo, 2011; bumble bees, Harmon-Threatt & Ackerly, 2013; Australian desert vertebrates, Lanier *et al.*, 2013; ruminants, Cantalapiedra *et al.*, 2014). However, our results do seem to be in accordance with Stevens *et al.* (2012); they likewise found a high degree of variation in the phylogenetic structure of rodent communities in the Mojave Desert (most of which are not significantly structured). They point to habitat specificity as a potential explanation for the lack of pattern and argue that the pattern of overdispersion in body mass observed in many of the North American deserts (e.g. Brown, 1973; Brown & Kurzius, 1987; Ernest *et al.*, 2008) might be the exception rather than the rule (Stevens *et al.*, 2012).

Association between phylogenetic structure and diversity

The prediction that more diverse desert assemblages are composed of phylogenetically distant relatives that may overlap less in niche space was supported by the significant positive correlation between the observed mean phylogenetic distance and log species richness (Supporting Information, Appendix S1, Fig. S12A). The fact that there was a positive correlation in MPD but not MNTD suggests that this positive correlation is associated with the addition of distant relatives that presumably differ more in niche and not the addition of sister taxa (Webb *et al.*, 2002). Interestingly, this result is the opposite of what Stevens *et al.*, (2012) found when they examined this association at much smaller community scales. This may indicate that this pattern is scale dependent, where the increase in diversity at small spatial scales is associated with more clumped communities, and the increase in diversity at large spatial scales is associated with more overdispersed assemblages.

Additional insights that can be drawn from the results include the striking difference in diversity of the examined assemblages, which could not be attributed to the absolute size of the assemblage (e.g. the Sonoran assemblage is the most diverse, yet it is smaller than the least diverse assemblage, the Australian assemblage; Fig. 1; Supporting Information, Appendix S1, Fig. S12A). The high diversity in the Sonoran assemblage can be attributed to greater resource diversity and an increase in heterogeneity, which could allow more species to coexist (as evidenced by the associated increase in phylogenetic distance; Supporting Information, Appendix S1, Fig. S12A) and exploit the different resources facilitated by the increase in niche space (MacArthur & MacArthur, 1961; Stevens & Tello, 2011).

Association between phylogenetic and morphological structure

The results strongly support the prediction that phylogenetic and morphological structure indices are correlated in desert rodent assemblages, with a significant positive correlation between mean phylogenetic distance and the mean morphological distance (for both MPD and MNTD) for all skull regions, except the occlusal mandible (Supporting Information, Appendix S1, Fig. S12B–F). The association between phylogenetic and morphological structure generally supports the contention that using the phylogeny and metrics of phylogenetic structure as a surrogate for niche does capture this concept well in desert rodent communities. Harmon-Threatt & Ackerly (2013) found the same in bumblebees, a highly mobile taxon, which they interpreted as attributable to the examined traits having a strong phylogenetic signal or convergence of community members owing to shared resources.

Despite the association between phylogenetic and morphological structure indices (MPD and MNTD), many assemblages differed in statistical support for phylogenetic and morphological structure, which might simply reflect habitat specificity, where different traits differ in importance in different habitats (i.e. whether differentiation in skull morphology is advantageous depends on the resources available in the focal community). Moreover, discordance between the significance of phylogenetic and morphological structure indices might indicate that the phylogeny is capturing other non-morphological aspects of niche/phenotype that may be important for structuring the focal community and are not captured by the examined morphological traits, or that the morphological dataset is capturing non-phylogenetically conserved traits that may be important for structuring certain assemblages. These hypotheses may provide a fruitful avenue to peruse in a more spatially focused research endeavour.

ACKNOWLEDGEMENTS

This research project would not have been possible without the help of the museum curators and collection managers, who provided us with access to their collections: AMNH (Darrin Lunde and Eileen Westwig); FMNH (Lawrence R. Heaney, William Stanley, John Phelps, Julian C. Kerbis-Peterhans and Bruce D. Patterson); MVZ (James L. Patton and Chris Conroy); USNM (Kristofer Helgen, Darrin Lunde, Helen Kafka and Michael D. Carleton); FLMNH (Candace McCaffery and David Reed); LCM (Angel Spotorno and Laura Walker); and SNOMNH (Michael Mares, Janet K. Braun, Hayley Lanier and Brandi S. Coyner). Earlier versions of this manuscript benefited from comments by Gregory Erickson, Joseph Travis, Thomas Miller and William Parker. We also thank John Allen and three anonymous reviewers for their helpful comments. Financial support for this work was provided by a fellowship from Kuwait University to B.H.A. and a grant from the National Science Foundation to S.J.S. (DEB-0841447).

REFERENCES

Adams DC, Otárola-Castillo E. 2013. geomorph: an R package for the collection and analysis of geometric morphometric shape data. *Methods in Ecology and Evolution* **4:** 393–399.

Alhajeri BH. 2014. *Adaptation, diversification, and desert ecology of the most diverse order of mammals (Mammalia, Rodentia)*. Unpublished PhD Thesis, Florida State University.

Alhajeri BH. 2018. Craniomandibular variation in the taxonomically problematic Gerbil Genus Gerbillus (Gerbillinae, Rodentia): assessing the influence of climate, geography, phylogeny, and size. *Journal of Mammalian Evolution*: **25:** 261–276.

Alhajeri BH, Hunt OJ, Steppan SJ. 2015. Molecular systematics of gerbils and deomyines (Rodentia: Gerbillinae, Deomyinae) and a test of desert adaptation in the tympanic bulla. *Journal of Zoological Systematics and Evolutionary Research* **53:** 312–330.

Alhajeri BH, Steppan SJ. 2016. Association between climate and body size in rodents: a phylogenetic test of Bergmann's rule. *Mammalian Biology – Zeitschrift für Säugetierkunde* **81:** 219–225.

Alhajeri BH, Steppan SJ. 2018. Ecological and ecomorphological specialization are not associated with diversification rates in muroid rodents (Rodentia: Muroidea). *Evolutionary Biology*. 1–19. doi:10.1007/s11692-018-9449-8

Bowers MA, Brown JH. 1982. Body size and co-existence in desert rodents: chance or community structure? *Ecology* **63:** 391–400.

Brown JH. 1973. Species diversity of seed-eating desert rodents in sand dune habitats. *Ecology* **54:** 775–787.

Brown JH. 2012. The role of phylogeny in desert rodent community assembly. *Journal of Animal Ecology* **81:** 307–309.

Brown JH, Kurzius MA. 1987. Composition of desert rodent faunas. *Annales Zoologici Fennici* **24:** 227–237.

Brown JH, Munger JC. 1985. Experimental manipulation of a desert rodent community: food addition and species removal. *Ecology* **66:** 1545–1563.

Brown JS. 1989. Desert rodent community structure: a test of four mechanisms of co-existence. *Ecological Monographs* **59:** 1–20.

Cadotte MW, Tucker CM. 2017. Should environmental filtering be abandoned? *Trends in Ecology & Evolution* **32:** 429–437.

Cantalapiedra JL, Fernández MH, Morales J. 2014. The biogeographic history of ruminant faunas determines the

phylogenetic structure of their assemblages at different scales. *Ecography*, **37:** 1–9.

Cardillo M. 2011. Phylogenetic structure of mammal assemblages at large geographical scales: linking phylogenetic community ecology with macroecology. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366:** 2545–2553.

Case TJ, Holt RD, McPeek MA, Keitt TH. 2005. The community context of species' borders: ecological and evolutionary perspectives. *Oikos* **108:** 28–46.

Cavender-Bares J, Kozak KH, Fine PV, Kembel SW. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters* **12:** 693–715.

Claude J. 2008. *Morphometrics with R*. New York: Springer.

Emerson BC, Gillespie RG. 2008. Phylogenetic analysis of community assembly and structure over space and time. *Trends in Ecology & Evolution* **23:** 619–630.

Ernest SK, Brown JH, Thibault KM, White EP, Goheen JR. 2008. Zero sum, the niche, and metacommunities: long-term dynamics of community assembly. *The American Naturalist* **172:** E257–E269.

Fabre PH, Hautier L, Dimitrov D, Douzery EJP. 2012. A glimpse on the pattern of rodent diversification: a phylogenetic approach. *BMC Evolutionary Biology* **12:** 88.

Grant PR. 1972. Convergent and divergent character displacement. *Biological Journal of the Linnean Society* **4:** 39–68.

Harmon-Threatt AN, Ackerly DD. 2013. Filtering across spatial scales: phylogeny, biogeography and community structure in bumble bees. *PloS One* **8:** e60446.

Heske EJ, Brown JH, Mistry S. 1994. Long-term experimental study of a Chihuahuan desert rodent community: 13 years of competition. *Ecology* **75:** 438–445.

Hubbell SP. 2001. *The unified neutral theory of biodiversity and biogeography*. Princeton, NJ: Princeton University Press.

IUCN. 2013. *IUCN red list of threatened species. Version 2013.1*.

Jones KE, Bielby J, Cardillo M, Fritz SA, O'Dell J, Orme CDL, Safi K, Sechrest W, Boakes EH, Carbone C, Christina Connolly C, Cutts MJ, Foster JK, Grenyer R, Habib M, Plaster CA, Price SA, Rigby EA, Rist J, Teacher A, Bininda-Emonds ORP, Gittleman JL, Mace GM, Purvis A. 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. *Ecology* **90:** 2648. doi:10.1890/08-1494.1

Kelt DA, Brown JH, Heske EJ, Marquet PA, Morton SR, Reid JRW, Rogovin KA, Shenbrot G. 1996. Community structure of desert small mammals: comparisons across four continents. *Ecology* **77:** 746–761.

Kembel SW. 2009. Disentangling niche and neutral influences on community assembly: assessing the performance of community phylogenetic structure tests. *Ecology Letters* **12:** 949–960.

Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD, Blomberg SP, Webb CO. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics (Oxford, England)* **26:** 1463–1464.

Kotler BP, Brown JS. 1988. Environmental heterogeneity and the coexistence of desert rodents. *Annual Review of Ecology and Systematics* **19:** 281–307.

Lanier HC, Edwards DL, Knowles LL. 2013. Phylogenetic structure of vertebrate communities across the Australian arid zone. *Journal of Biogeography* **40:** 1059–1070.

Leibold MA. 1998. Similarity and local co-existence of species in regional biotas. *Evolutionary Ecology* **12:** 95–110.

M'Closkey RT. 1976. Community structure in sympatric rodents. *Ecology* **57:** 728–739.

M'Closkey RT. 1978. Niche separation and assembly in four species of Sonoran Desert rodents. *The American Naturalist* **112:** 683–694.

MacArthur RH, MacArthur J. 1961. On bird species diversity. *Ecology* **42:** 594–598.

Martin SA, Alhajeri BH, Steppan SJ. 2016. Dietary adaptations in the teeth of murine rodents (Muridae): a test of biomechanical predictions. *Biological Journal of the Linnean Society* **119:** 766–784.

Munger JC, Brown JH. 1981. Competition in desert rodents: an experiment with semipermeable exclosures. *Science (New York, N.Y.)* **211:** 510–512.

Pineda-Munoz S, Evans AR, Alroy J. 2016. The relationship between diet and body mass in terrestrial mammals. *Paleobiology* **42:** 659–669.

Price TD, Kirkpatrick M. 2009. Evolutionarily stable range limits set by interspecific competition. *Proceedings of the Royal Society B: Biological Sciences* **276:** 1429–1434.

R Development Core Team. 2013. *R: a language and environment for statistical computing*. Available at: http:// cran.r-project.org

Ricklefs RE. 2010. Evolutionary diversification, coevolution between populations and their antagonists, and the filling of niche space. *Proceedings of the National Academy of Sciences of the United States of America* **107:** 1265–1272.

Robertson RA, Shadle AR. 1954. Osteologic criteria of age in beavers. *Journal of Mammalogy* **35:** 197–203.

Rohlf FJ. 2010. *tpsDig. Version 2.16*. Department of Ecology and Evolution, State University of New York, Stony Brook, NY. Available at: http://life.bio.sunysb.edu/morph/soft-dataacq.html

Rohlf FJ, Slice D. 1990. Extensions of the Procrustes method for the optimal superimposition of landmarks. *Systematic Biology* **39:** 40–59.

Rosenzweig ML, Winakur J. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. *Ecology* **50:** 558–572.

Samuels JX. 2009. Cranial morphology and dietary habits of rodents. *Zoological Journal of the Linnean Society* **156:** 864–888.

Schenk JJ, Rowe KC, Steppan SJ. 2013. Ecological opportunity and incumbency in the diversification of repeated continental colonizations by muroid rodents. *Systematic Biology* **62:** 837–864.

Shenbrot G, Krasnov B. 2002. Can interaction coefficients be determined from Census data? Testing two estimation methods with Negev desert rodents. *Oikos* **99:** 47–58.

Shenbrot GI, Krasnov BR, Rogovin KA. 1999. *Spatial ecology of desert rodent communities*. Berlin, Heidelberg: Springer-Verlag.

Steppan SJ. 1997. Phylogenetic analysis of phenotypic covariance structure. I. Contrasting results from matrix correlation and common principal component analyses. *Evolution; International Journal of Organic Evolution* **51:** 571–586.

Steppan SJ, Schenk JJ. 2017. Muroid rodent phylogenetics: 900-species tree reveals increasing diversification rates. *PLoS One* **12:** 1–31.

Stevens RD, Gavilanez MM, Tello JS, Ray DA. 2012. Phylogenetic structure illuminates the mechanistic role of environmental heterogeneity in community organization. *Journal of Animal Ecology* **81:** 455–462.

Stevens RD, Tello JS. 2011. Diversity begets diversity: relative roles of structural and resource heterogeneity in determining patterns of community structure. *Journal of Mammalogy* **92:** 387–395.

Vamosi SM, Heard SB, Vamosi JC, Webb CO. 2009. Emerging patterns in the comparative analysis of phylogenetic community structure. *Molecular Ecology* **18:** 572–592.

Webb CO. 2000. Exploring the phylogenetic structure of ecological communities: an example for rain forest trees. *The American Naturalist* **156:** 145–155.

Webb CO, Ackerly DD, McPeek MA, Donoghue MJ. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* **33:** 475–505.

Weiher E, Freund D, Bunton T, Stefanski A, Lee T, Bentivenga S. 2011. Advances, challenges and a developing synthesis of ecological community assembly theory. *Philosophical Transactions of the Royal Society B: Biological Sciences* **366:** 2403–2413.

Weiher E, Keddy P. 2001. *Ecological assembly rules: perspectives, advances, retreats*. Cambridge, UK: Cambridge University Press.

Whittaker RJ, Fernández-Palacios JM. 2007. *Island biogeography: ecology, evolution, and conservation*. Oxford, UK: Oxford University Press.

Zelditch ML, Swiderski DL, Sheets HD. 2004. *Geometric morphometrics for biologists: a primer*. London, UK: Elsevier Academic Press.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's website:

Appendix S1. Supplementary figures.
Appendix S2. Supplementary tables.
Appendix S3. Description of landmarks and geometric morphometric process.