Morphological diversity and community organization of desert anurans

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ABSTRACT

Morphological approaches have been used extensively to understand assembly rules (species interactions, environmental filtering, and neutral processes) that structure ecological communities. Desert anurans cope with limited water by either being restricted to permanent water or becoming more fossorial, which should be reflected in their morphology. We examined morphological diversity of 16 frog species across six habitat types within the Chihuahuan Desert to investigate the relationship between species richness and morphological space. We measured 13 morphological traits associated with locomotion, habitat use, and feeding. Principal components analysis separated species into three ecomorphological groups: fossorial, terrestrial, and semi-aquatic species. Morphological diversity was analyzed and compared against a null model and revealed nonrandom community structure. The total assemblage morphospace increased in relation to species richness, though this relationship was not significant. Species were significantly packed within the morphospace exhibiting high morphological similarity while being less evenly dispersed, with increasing species richness, indicative of a response to an environmental gradient. Given the highly xeric nature of the Chihuahuan Desert, our results support the assumption that environmental filtering, rather than interspecific interactions, shapes assemblages' structure by favoring species with similar traits to co-occur more often within a given habitat type than expected by chance.

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1. Introduction

Ecological communities are structured as the result of the interaction between local and regional processes as well as biogeographical constraints (Ricklefs, 1987; Ricklefs and Schluter, 1993). Regional processes, such as abiotic factors, and the constraints set by historical biogeography tend to exert stronger influence at broad spatial scales, whereas local processes such as habitat heterogeneity, species interactions, and productivity exert greater influence on community structure at smaller spatial scales (Ricklefs and Schluter, 1993; Montaña et al., 2014). The roles these processes have in structuring a community can be inferred by studying the structure of species assemblages and the functional organization of species in relation to one another (Mouillot et al., 2007). In particular, functional organization on a trait-based approach has emerged as an important aspect to understanding community assembly rules and community functioning (Adler et al., 2013).

Many processes influence patterns of species richness and community structure at each spatial scale, but three main assembly rules have been proposed to explain these patterns: species interactions, environmental filtering, and neutral processes (Mouchet et al., 2013). Species richness and community structure can be influenced by biotic interactions via the principles of limiting similarity (MacArthur and Levins, 1967) and competitive exclusion (Hardin, 1960), with the underlying assumptions being that species are in competition with one another, that each niche is occupied by the competitively dominant species and that species possessing similar functional traits are unable to co-occur. Coexistence is promoted by assemblages of species possessing characteristics (i.e., functional traits) that are more dissimilar in relation to one another via complementarity or trait overdispersion. With the process of environmental filtering, abiotic factors sort species possessing

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similar suites of traits adapted to the environmental conditions of a given habitat (Zobel, 1997). Thus, the species persisting in a habitat filtered by such abiotic factors would be more similar to one another in their functional traits than would be expected by chance. Habitat features have been found to act as local filters regulating co-occurrence and distribution of species (Peres-Neto, 2004). In lentic fish assemblages, for example, stream flow influences community structure by filtering species in accordance with traits primarily associated with locomotion (Mouchet et al., 2013) whereas in anurans, local features such as microhabitat type and edaphic gradients filter performance traits associated with habitat use and reproduction (Moen et al., 2013; Menin et al., 2007). The neutral theory views species as being ecological equivalents with their coexistence and persistence independent of their biological traits (Hubbell, 2001), and the traits possessed by coexisting species being assembled in a random fashion. Quantifying the links between species' functional traits and surrounding habitats represents an important step in identifying the processes governing species distribution.

Morphological traits are useful predictors of niche dimensions, as the relationship between morphology, ecology, and assemblage structure has been well documented for many animal taxa, including birds (Ricklefs and Travis, 1980; Miles and Ricklefs, 1984), lizards (Ricklefs et al., 1981), fish (Gatz, 1979; Winemiller, 1991; Montaña et al., 2014), and insects (Silva and Brandão, 2010; Inward et al., 2011). Ecomorphological and functional morphology of anurans have been the subject of study at both the larval (Altig and Johnston, 1989; Wassersug, 1989) and post-metamorphic life stages (Zug, 1972, 1978; Emerson, 1976, 1978, 1985, 1988). The patterns of tadpole communities have been well-documented and the ecological processes causing these patterns have been tested through laboratory and field experiments (Wilbur, 1987; Werner, 1998) and more recently, ecomorphological approaches (Strauß et al., 2010). However, even less is known on the factors structuring post-metamorphic anuran assemblages; the majority of our understanding comes through studies focused on habitat use or diet (Wells, 2010). An ecomorphological approach to understanding the structure of these assemblages has yet to be applied, but could provide insights as to the ecological processes (i.e., limiting similarity, environmental filtering, or neutral processes) driving the observed patterns.

Desert anuran assemblages are an ideal system to examine assemblage structure utilizing a morphological approach. Blair (1976) proposed that desert anurans cope with limited and unpredictable water availability in one of two ways: 1) becoming restricted to the vicinity of permanent waters in the desert, or 2) becoming highly fossorial. These adaptations are reflected in the morphological traits of anurans, particularly hindlimb length (Gomes et al., 2009), thus given that morphology partly reflects the evolutionary influences of environmental conditions, we would expect variation in morphological traits to be reflected amongst habitat types, especially in desert habitats where anuran occurrence appears correlated with physical conditions (e.g., vegetation, soils) of the habitats (Dayton et al., 2004; Boeing et al., 2013). These studies have primarily examined species diversity of Chihuahuan Desert anurans in relation to vegetation type (Boeing et al., 2013) or vegetation and soil type (Dayton et al., 2004). Dayton et al. (2004) hypothesized that the soil type was the most important predictor of an anuran species presence at a site. Soil type may act as a filter to species' occurrence within a given habitat because some species may lack the morphological traits to burrow or the water holding capacity may be too low causing the water to drain quickly, which limits available breeding sites and increases physiological stress for burrowing anurans (Dayton and Fitzgerald, 2006). If soil type acts as an environmental filter, it would be reflected in the morphological traits of co-occurring species within a habitat type.

In this study, we examined morphological diversity of 16 anuran species from six habitats within the Chihuahuan Desert ecoregion (Table 1) to infer ecological patterns of community assembly and structure among species occupying particular habitats. We were specifically interested in investigating whether or not Chihuahuan Desert anurans exhibited a non-random assemblage structure and whether the ecomorphological patterns followed the predictions proposed by one or more of the assembly rules (i.e., environmental filtering, species interactions, neutral processes). We examined the morphological community structure from known species—habitat associations (Morafka, 1977) to make inferences as to the mechanisms driving community structure of desert anurans across the ecoregion of the Chihuahuan Desert. We employed multivariate techniques to quantify the morphological space occupied for each species within these habitats, and used a null model to contrast observed patterns with those derived from randomly generated data. Given the harsh abiotic conditions of this ecoregion, and the broad spatial scale (i.e., habitat type) at which we were examining community structure, we predicted that the process of environmental filtering would be more likely to structure the post-metamorphic anuran assemblages of the Chihuahuan Desert, and expected that coexisting species within a given habitat would possess similar traits in relation to one another.

2. Methods

2.1. Selection of habitat associations and species within the Chihuahuan Desert

The Chihuahuan Desert spans over 350,000 km^2 across the West Texas—Mexico border (Morafka, 1989). Rainfall for the region averages 235 mm annually, 70% of which occurs in summer (May-—October) monsoon storms. Average annual temperature for the region is 18.6 °C (Schmidt, 1986). While the extent of the Chihuahuan Desert has been debated (Morafka, 1977, 1989; Schmidt, 1979), for the scope of this study we used the habitat delineations from Morafka (1977), as it is an attempt to designate formal biotic provinces using soil types and predominant vegetation formations (Morafka, 1977, 1989) and are still recognized as valid habitat types by recent studies (Pronatura Noreste, 2004; NatureServe, 2009). We recognize there are multiple definitions of the term "assemblage" in the literature; for the scope of this study, we follow the definition proposed by Fauth et al. (1996), where they define an assemblage as phylogenetically-related species occurring in the same place at the same time. To examine patterns of community organization and test whether in situ (i.e., habitat associations) ecological processes affect taxonomic diversity and morphological structure, we utilized the list of anuran species and their associated habitats (see Appendix A for the characteristics of each habitat) in the Chihuahuan Desert compiled by Morafka (1977). The species by habitat associations designated by Morafka (1977) were produced from extensive field surveys and were complimented by visiting specimen collections. HerpNet (http://www.herpnet.org) was used to search for specimens of 16 species of anurans reported by Morafka (1977) for the Chihuahuan Desert. We chose specimens from Brewster County, Texas, USA and the states of Nuevo Leon, Coahuila, and Chihuahua in Mexico (Appendix B), as the Chihuahuan Desert covers a large portion of each of those areas. In the cases when specimens were not available from those specific areas, we used specimens collected as near as possible to the study area. When possible, we measured at least five adult specimens of each species. Because body size can introduce allometric bias into morphological analysis, we focused on adult specimens similar in size; therefore, allometric influences should

Table 1
List of 16 anuran species found across six habitats of the Chihuahuan Desert included in this study. The species–habitat associations were taken from Morafka (1977). Taxonomy classification follows Frost (2014).

Family	Species	Desert riparian	Desert scrub barrial edaphic	Desert scrub alluvial	Chaparral	Pinyon juniper	Mesquite grassland ecotone
Bufonidae	*Anaxyrus cognatus*	x	x	x			x
	Anaxyrus debilis	x	x				x
	Anaxyrus punctatus	x	x	x			x
	Anaxyrus speciosus	x	x				x
	Anaxyrus woodhousii	x					x
	Incilius nebulifer	x					x
Craugastoridae	*Craugastor augusti*	x			x		x
Eleutherodactylidae	*Eleutherodactylus guttilatus*				x	x	
Hylidae	*Acris crepitans*	x					
	Hyla arenicolor					x	x
Microhylidae	*Gastrophryne olivacea*	x	x				x
Scaphiopodidae	*Scaphiopus couchii*	x		x			x
	Spea bombifrons						x
	Spea multiplicata	x	x	x		x	x
Ranidae	*Lithobates berlandieri*	x			x	x	x
	Lithobates tarahumare					x	

be negligible for interspecific comparison in which a restricted adult size class is chosen to represent a given species (Winemiller, 1991).

2.2. Analysis of morphospace

Thirteen external morphological traits (Appendix C) were taken with dial calipers (precision: 0.1 mm) in a standardized manner on specimens obtained from museums. We chose measurements that reflect various facets of anuran trophic ecology, habitat use, and modes of locomotion (Emerson, 1976, 1978, 1985, 1988). Because fossoriality was proposed to be one adaptation by which anuran species could persist in desert environments (Blair, 1976), we were interested in examining the distribution of fossorial species across the six habitats. Fossoriality in anurans is reflected morphologically with a shortened tibiofibula (and thus overall reduction of the hindlimb); this increases the force generated by the metatarsal tubercle, which is used for digging (Emerson, 1976). Therefore, we looked at the ratio of the tibiofibula to total hindlimb length; a smaller ratio indicates a more fossorial lifestyle (Emerson, 1976). The original measurements were natural log-transformed before conducting the principal components analysis (PCA). We conducted a PCA to describe the morphological space occupied by each species assemblage and examine among-species differences in functional traits across habitat associations. Because we were interested in differences of shape variation among habitats, we removed the effect of size of the morphological measurements by calculating their residuals based on a generalized least squares linear regressions (Revell, 2009; Blackburn et al., 2013) of each measurement against snout-vent-length (SVL, measure of body size) using the software JMP Pro.10. We first conducted a PCA on the SVL and the 12 residuals to look at the effect of body size in the overall species distribution in the morphological space, as well as to identify patterns of correlation between morphology attributes and their habitat associations. SVL did not appear a significant trait in loadings of the first three PC axes (Appendices D and E); therefore, we ran a second PCA focusing only in shape (without SVL) and used it for comparisons of species distribution in morphological space. The PCA was performed in PC-Ord v.6 based on the correlation matrix of all species and traits. Interpretable PCA axes were selected using the broken-stick model (Jackson, 1993).

To examine whether the morphological traits of the frog assemblages varied among habitat associations, we performed a non-parametric Kruskal–Wallis test (K–W) on the average of each of the 13 morphological traits of each species assemblage among habitat associations. The Kruskal–Wallis test was followed by a post hoc analysis based on Bonferroni-corrected pairwise Mann–Whitney comparisons to determine which pairs of assemblages differ significantly. The coefficient of variation (CV) was calculated for each morphological trait within each frog assemblage, and allowed for inferences of frog morphological diversity among habitats. The higher the CV, the greater the variation of the trait. The non-parametric Kruskal–Wallis test, followed by a Mann–Whitney pairwise comparison were performed in both means and CVs because the data were not normal, even after transformation. Values were considered statistically significant at $p < 0.05$.

Morphological dissimilarity for every possible species pairing within each assemblage was estimated by calculating Euclidean distances among species pairs based on the PC scores for the retained PC axes. Sub-matrices containing species with their individual habitat association were compiled to test for generalizations about species similarity and community organization proposed by Ricklefs and Miles (1994) and Winemiller (1991). To perform this, we calculated three approaches based on the Euclidean distances between pairs of species in the assemblage. First, the average of nearest neighbor distance (mean-NND), which is an index of species packing in morphological space. Thus, the average between-species distance provides an estimate of ecological similarity among species (Winemiller, 1991). Second, the standard deviation of NND, an index of the evenness of species dispersion in morphological space (a lower SD indicates a more regular [i.e., even] dispersion pattern). Finally, the average distance to centroid, an index that provides an estimate of the total niche space or relative size of the morphospace occupied by an assemblage. Before calculating the indices of species' morphological dissimilarity, Euclidean distances were weighted to adjust for different amounts of variation modeled by each PC axis (Montaña et al., 2014). For each habitat association, assemblage average of NND, SD NND, and average of distance to the centroid were regressed (using linear regressions) against species richness using JMP Pro.10 for Windows.

To test the hypothesis that assemblage morphological structure differs from random when compared amongst habitat associations we ran a morphological null model using the computer program Sampler v.1 (Montaña et al., 2014). This program generates random species assemblages drawn from the observed species pool, and calculates the nearest neighbor distances and centroid distances. For smaller assemblages such as desert scrub barrial edaphic (DSBE,

6 species) and pinyon juniper (PJ, 5 species), the program generated all possible combinations (samples) from the original assemblage. For large assemblages such as desert riparian (DR, 12 species) and mesquite grassland ecotone (MGE, 13 species), the program generated 999 random samples of the simulated assemblages. To generate the random assemblages, species were chosen without replacement from the regional species pool. Because our null model assumes species without replacement, only four frog assemblages were considered for the randomization analysis: DR, DSBE, PJ, and MGE (all of them n ≥ 5 species). The null model also assumes that all species from the Chihuahuan Desert have equal probability to colonize an association type within this desert region. Observed values of mean NND, SD of NND, and mean centroid distance (CD) of natural assemblages were compared with values generated randomly for the same number of species as real assemblages. Using the null occurrence matrix and the observed distance matrix, we calculated the randomized statistic (e.g., mean and SD NND, and CD) for each simulated assemblage. For each of the statistics, we used one-tailed test to calculate the p-values and reject the null hypothesis because we are only interested in results that are greater or lower than the observed statistics, mean and SD NND, and CD, respectively (Manly, 1998).

To test further the null hypothesis of no significant correlation between phylogenetic relationships and morphological traits, a Mantel test was performed on the matrix of average morphological traits and matrix of morphological distances using PC-Ord, version 6. For the present study, a matrix of taxonomic distance was constructed by counting the number of nodes that separate each species in the phylogenetic tree (Winemiller et al., 1995; Silva and Brandão, 2010). Species assigned within the same genus were given a distance of 1, species within the same family had a distance of 2, and species in different families had a distance of 3. We used taxonomic levels as proxies for relative degrees of evolutionary divergence among anuran families present in our study region. An assumption for the use of taxonomic levels is that rates of evolutionary change are uniform for all branches between a given taxonomic level and the adjacent level, and this assumption would create bias in most cases. Thus, this method provides a coarse-scale, yet reasonably accurate, assessment of phylogenetic distances between species pairs. Our taxonomic classification and species relationships were based on a recent, large-scale phylogeny of amphibians (Pyron and Wiens, 2011).

3. Results

3.1. Ecomorphological gradients among habitat associations

Mean values for individual morphological features showed no significant differences overall (K–W test, $p = 0.98$; Appendix F). Likewise, the Mann–Whitney pairwise comparisons revealed no significant differences ($p > 0.05$) on the mean values of morphological traits between or among species assemblages occupying different habitat associations (Appendix G). Based on CV, we observed significant morphological variation overall (K–W test, $p = 0.007$; Appendix F). Consequently, Mann–Whitney pairwise comparisons showed significant variation of CV of individual trait values ($p < 0.05$) between five species assemblages including the DSA and CH, and DSA and DR; DSBE and CH, and DSBE and DR; and DSBE and MGE (Appendix G). The Mantel test did not reveal significant relationships between average morphological traits and phylogenetic distances ($r = 0.116$, $p = 0.12$).

Frog species were strongly differentiated on the basis of head shape and limb length. PCA resulted in two main axes (PC1-2) explaining 72.2% of the total variation in species morphology (Fig. 1, Appendix H), and separated species based on habitat use with
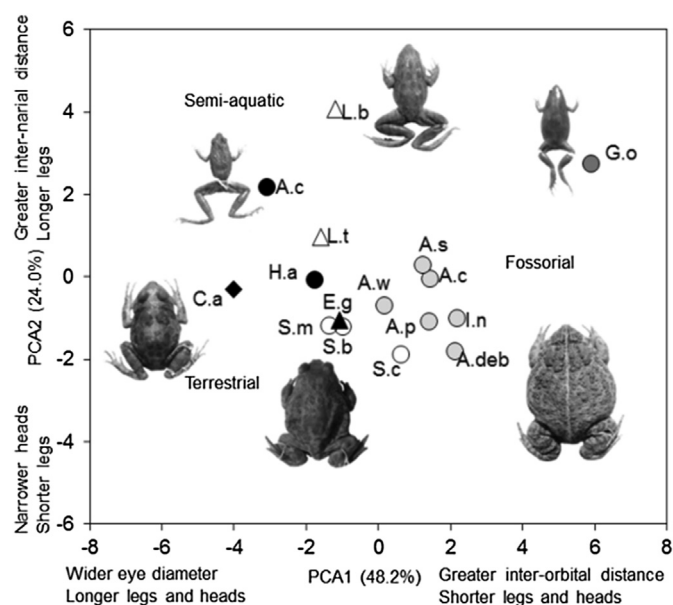

Fig. 1. Two axes of a PCA ordination of Chihuahuan desert frog species based on 12 morphological traits. Three ecomorphs (fossorial, non-fossorial, and semi-aquatic) were defined for the Chihuahuan Desert anuran assemblages (based on Gomes et al., 2009). Different shaped symbols correspond to the taxonomic family of each species. Species names are given in Table 1.

clusters of fossorial species (Bufonids, Scaphiophids, and the Microhylid *Gastrophryne olivacea*), terrestrial but non-fossorial (*Craugastor augusti* and *Eleutherodactylus guttilatus*), and semi-aquatic species (Hylids: *Acris crepitans*, *Hyla arenicolor*, and Ranids: *Lithobathes* spp.) (see Discussion below and Gomes et al. (2009) for further classification and explanation). PC1 described a gradient that reflected morphological differences in limb and head lengths. Species with positive scores in PC1 had relatively shorter limbs and shorter heads, but relatively greater inter-orbital distances (e.g., most species of Bufonidae and the Microhylid *G. olivacea*). Negative values on PC1 were associated with species having longer limbs and larger heads and a wider eye diameter (e.g., species in the family Hylidae and Craugastoridae [*C. augusti*]). Species with large and positive scores on PC2 had relatively longer limbs and greater inter-narial distance (e.g., species in the family Ranidae), whereas negative scores in the same axis were associated with relatively narrow heads and short limbs (e.g., most species of Scaphiopodidae and few species of Bufonidae).

On average, all the species considered to be fossorial (i.e., the Scaphiopodidae, Bufonidae, and Microhylidae) tended to have the lowest tibiofibula to total hindlimb ratio, with terrestrial species (*C. augusti* and *E. guttilatus*) having intermediate values, and semi-aquatic species (*Lithobathes* spp., *A. crepitans*, and *H. arenicolor*) having the highest values (Fig. 2a). However, examining the distribution of fossoriality among the species occurring in each of the six habitat associations revealed no differences in tibiofibula to total hindlimb ratio on average (Fig. 2b), though the chaparral habitat had the highest mean tibiofibula to total hindlimb ratio (Fig. 2b), while the desert scrub alluvial habitat had the lowest mean tibiofibula to total hindlimb ratio (Fig. 2b).

Two series of plots involving the first two PCs from pooled-habitat data sets clarified the relative positions in the morphological space occupied by assemblages and frog species (Fig. 3). The total multidimensional space occupied by CH and DSA assemblages was smaller than those of other faunas. The DR and MGE occupied greater morphological space and spanned comparable assemblages of morphological space. Although assemblages' boundary shapes
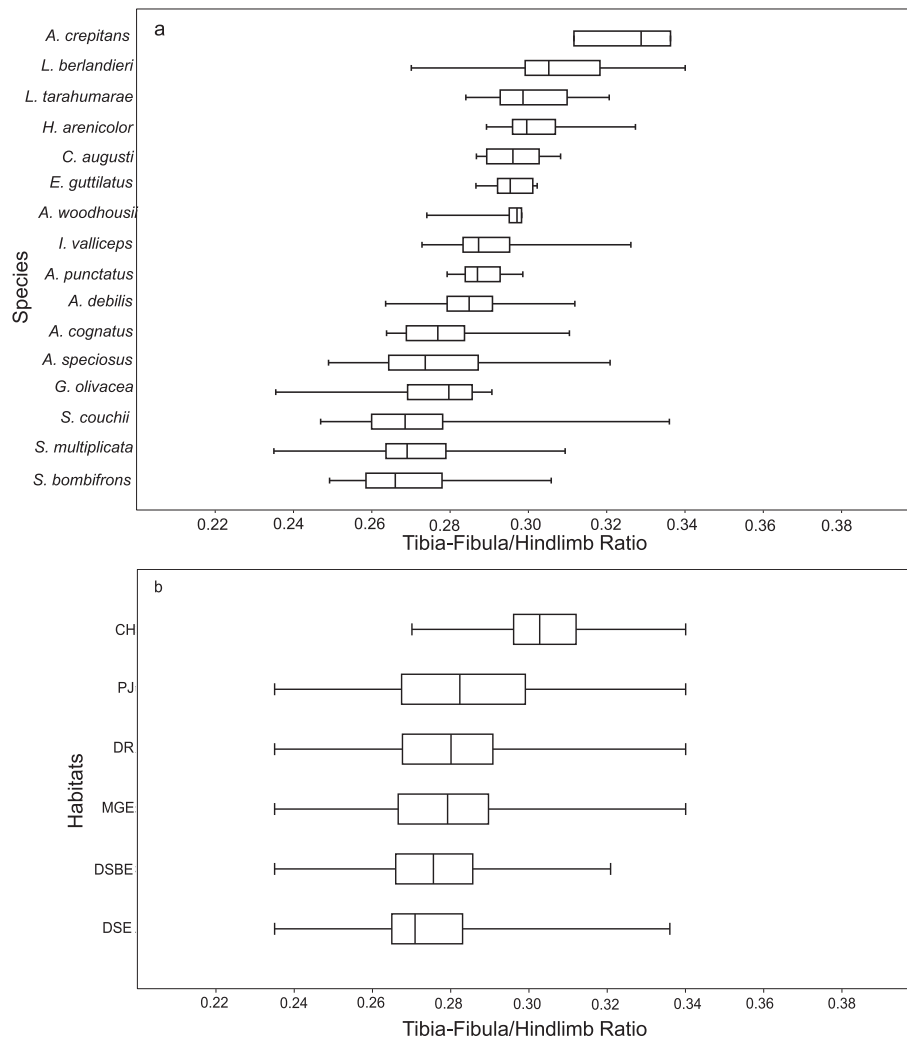
Fig. 2. Boxplots of the ratio of the tibiofibula to total hindlimb length for a) each of the 16 anuran species occurring in the Chihuahuan Desert, and b) the anurans occurring in each habitat within the Chihuahuan Desert. A smaller ratio indicates a more fossorial lifestyle. Whiskers represent the minimum and maximum range of values.

and patterns of dispersion within morphological space varied among habitat associations, the general centroids of assemblage hypervolumes in morphological space did not vary significantly (Fig. 4).

3.2. Morphological similarity within local assemblages

Total assemblage morphological space measured by average Euclidean distance to the assemblage centroid appeared to increase in relation to species richness (Fig. 4). Mean values of NND significantly decreased with increasing number of species (Fig. 4a), whereas SD-NND values significantly tended to increase with increasing number of species, indicating high morphological similarity among species occupying the morphospace (Fig. 4b). Mean values for the centroid distance (CD) significantly increased with increasing species richness (Fig. 4c).

We compared these three morphological distances against a null model to infer which ecological processes are organizing these frog assemblages. Results from comparisons of observed data with randomized data from the null model indicated non-random distribution within morphological space of frog assemblages in the Chihuahuan Desert, as most of the observed data were greater than predicted at random (Appendix I). Assemblages in all four habitats

had mean NND greater than expected at random suggesting that species packing within these habitats are more likely to be less similar to each other in morphological space than expected by chance, but we did not find any statistical support (Table 2). In all four assemblages, species appeared less evenly dispersed than expected by random (i.e., observed SD-NND was significantly greater than expected at random; Table 2) and the general trend of the SD-NND increased with increasing species richness suggesting greater morphological similarity within the morphospace. The mean distance to the assemblage centroid was greater and statistically significantly different than expected at random for all other habitats except the DSBE, indicating expansion of the assemblage morphospace (due to the addition of more convergent morphologies) (Table 2).

4. Discussion

The Chihuahuan Desert anuran assemblages have a nonrandom organization at the local habitat scale; species became more similar to one another on average, packing within the morphospace as species richness increased. A pattern emerges in communities with non-random organization, whereby species' functional traits are increasingly correlated with habitat characteristics as a response to
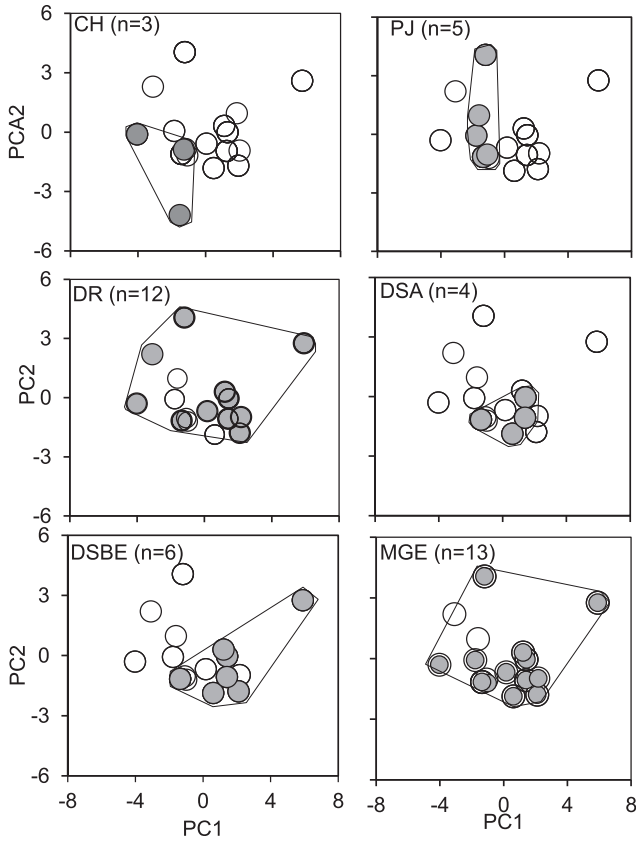
Fig. 3. Scatter plots of the first two principle components axes based on 13 morphological traits and a pooled species data set for the six habitats included in this study. Species present at each named habitat are highlighted (grey circles) and bounded (lines). Numbers of species by habitat are in parentheses. Habitat abbreviations: Ch: chaparral, PJ: pinyon juniper, DR: desert riparian, DSA: desert scrub alluvial, DSE: desert scrub barrial edaphic, MGE: mesquite grassland ecotone.

Table 2
P-values of observed versus random generated data of three morphological dispersion metrics (mean and standard deviation of nearest neighbor distance and mean distance to centroid) for anuran assemblages in four habitat types in the Chihuahuan Desert. Differences in the means of observed versus random generated samples were significant at $p < 0.05$.

Habitat association	Mean NND	Standard deviation NND	Mean CD
DR	0.080	0.020	0.026
DSBE	0.075	0.001	0.125
MEG	0.155	0.012	0.040
PJ	0.066	0.066	0.001

Species occupying the same habitats may have similar morphology in response to adaptations to physical environments (Grant, 1972), or they may have divergent morphology as response to interspecific competition (Brown, 1971). Assemblages with high taxonomic and morphological similarity among coexisting species may reflect a lack of niche specialization (Winemiller, 1991). We observed that the total assemblage morphological space (i.e., CD) of Chihuahuan Desert anurans tended to increase in relation to increasing species richness for every habitat association, though the relationship was not significant. As anuran species were added to local assemblages, the mean NND tended to decrease slightly, but significantly, suggesting that species are packing closer together in morphological space and are similar morphologically to one another (Mouillot et al., 2007). As indicated by the SD-NND, species tended to be less evenly dispersed within the morphological space, increasing in their morphological similarity with increasing species richness. This may appear to conflict with the observation of increasing niche space (i.e., CD) with increasing species richness, but increased species packing is likely due to the disproportionate addition of morphologically similar species (e.g., Bufonids) to a habitat, while the addition of a few morphologically distinct species (e.g., *G. olivacea*) drove the trend of increasing the overall morphospace.

Studies in aquatic and terrestrial environments have corroborated the hypothesis that an organism's ecomorphology is related to environmental pressures (i.e., abiotic and biotic factors) (Winemiller, 1991; Keddy 1992, Silva and Brandão, 2010; Moen et al., 2013; Mouchet et al., 2013). Although at a much smaller scale, our findings are consistent with other findings in freshwater fish communities where species tend to join to the periphery of the morphological space as species richness increases and
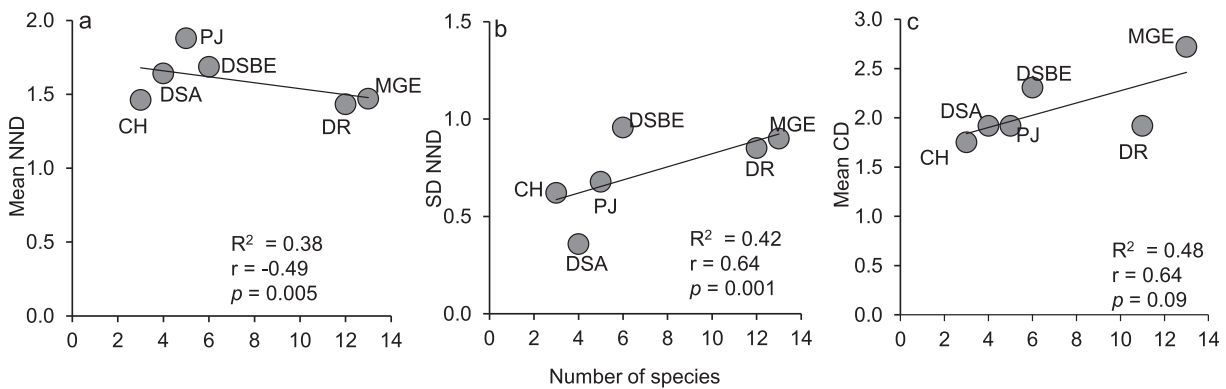
biotic interactions or abiotic filters (i.e., community assembly processes; Weiher et al., 1998). We predicted that the harsh abiotic conditions in the Chihuahuan Desert ecoregion would cause frogs trait clustering compared to the range of traits represented in the regional pool. Species within these anuran assemblages appeared to have sorted into local habitats based on their trait combinations, indicating a strong response to environmental filters.

Fig. 4. Three measures of morphological distances between species in the morphospace plotted as a function of number of species in habitat of the Chihuahuan desert: a) nearest neighbor distance (Mean-NND; an index of species packing in morphological space), b) standard deviation of NND (SD NND; an index of the evenness of species dispersion in morphological space), and c) average distance to centroid, (Mean CD; an index of the estimate of the total niche space or relative size of the morphospace occupied by an assemblage).

morphological similarity increases or remains constant (Mouchet et al., 2013). The Chihuahuan Desert anuran assemblages were less even in species dispersion within the morphospace, a pattern suggesting species response to an environmental gradient. Although a pattern indicative of competitive interactions (via limiting similarity) was not observed at the broad habitat scale, we cannot exclude competition as another mechanism affecting the co-occurrence of these species within a habitat, as it may be observed at a much smaller (e.g., mesohabitat or microhabitat) scale. This has been demonstrated in the larval life stage of some of these Chihuahuan anuran species in the region; tadpoles almost never co-occur in breeding ponds and larval *Scaphiopus couchii* are so competitively dominant that they outcompete co-occurring heterospecifics (Dayton and Fitzgerald, 2001). Similar patterns have been observed in freshwater fish assemblages; competitive interactions occurred between some functionally similar fish species at the macrohabitat (e.g., channel and lagoon, Mouchet et al., 2013) and habitat patch scale (Montaña et al., 2014). Given the highly xeric nature of the Chihuahuan Desert, environmental filtering apparently shapes assemblage structure by favoring species with similar traits to co-occur more than expected by chance. This finding is also supported by the fact that morphological space of desert anurans was significantly overdispersed, but without having a total assemblage morphospace significantly greater than expected by chance.

For anurans, the variation in anuran jumping ability is strongly linked to their habitat use and niche diversification (Emerson, 1976, 1978; Gomes et al., 2009). Species with both short heads and limbs have the lowest jumping performance and tend to be fossorial, whereas those species with longer limbs and heads tend to be semi-aquatic (Gomes et al., 2009). Non-fossorial species (referred to as terrestrial species in this study) are intermediate in these morphological traits as well as their performance when compared to fossorial and semi-aquatic species (Gomes et al., 2009). Within the Chihuahuan Desert anuran assemblage, species morphological traits tended to vary across habitat type with species segregating in the morphospace on the basis of head shape and limb lengths across the six habitat types.

In general, we observed no differences in the distribution of fossoriality (determined by the species' tibiofibula/hindlimb ratios) across the six habitat types in the Chihuahuan Desert as many of these habitats contained species that ranged from fossorial to semi-aquatic species. Our lack of variation in the distribution of fossoriality is likely due to the broad scale (habitat type) in which our study was conducted. Two adaptations that allow anurans to persist in desert environments include becoming fossorial or becoming restricted to the vicinity of permanent waters (Blair, 1976); those non-fossorial species are likely utilizing different mesohabitats (e.g., streams) than the fossorial species they co-occur with in a given habitat type, which would be more evident at a smaller spatial scale. We did not find evidence to support this; however, we did observe some difference in the fossoriality values among the habitat types. The chaparral has the highest average value of the tibiofibula/hindlimb ratio, due to the absence of fossorial species from that habitat, whereas the lowest tibiofibula/hindlimb value in the desert scrub alluvial habitat was due to the absence of terrestrial and semi-aquatic species in that habitat. Understanding the distribution of fossoriality amongst habitats could serve as a useful metric to understand the structure of other anuran assemblages, especially at smaller habitat scales.

The size and type of prey that can be consumed are influenced by anuran skull shape and body size (Toft, 1980; Emerson, 1985). Anurans with extremely wide mouths and body sizes are capable of consuming large-bodied prey such as vertebrates (Emerson, 1985; Schalk et al. 2014), whereas smaller-bodied species with smaller mouths tend to consume smaller-bodied prey such as ants (Emerson, 1985). The three ecomorphs occurring in the Chihuahuan Desert exhibited high morphological similarity in relation to one another. The notable exception was the Microhylid *G. olivacea*, which is considered to be a fossorial species, but possesses a very distinct head shape and is a dietary specialist, feeding primarily on ants (Conant and Collins, 1998; Lannoo, 2005), causing it to not be clustered with any species. Though some of the larger species (e.g., *Lithobates* spp.) have been documented to consume small vertebrates, the Chihuahuan anurans lacked traits associated with consuming vertebrates, as the other species present in these assemblages are usually considered to be generalist invertivores (Lannoo, 2005). These species lack the distinctive morphologies (i.e., extremely narrow or wide mouth width) associated with specialized feeding (Emerson, 1985). Given the lack of morphological specialization associated with diet in the majority of Chihuahuan Desert anurans, the occurrence of species across their respective habitats is likely a response to the environmental gradients associated with habitat type. Creusere and Whitford (1976) suggested that food is not a limiting factor around breeding sites, where juvenile and adult anurans tend to be most abundant. When scaling up to a broader spatial scale, as in this study, it is unlikely that the distribution of species is driven by the distribution or abundance of prey. Finally, it is also important to note that we did not observe a correlation between phylogeny and species' morphology in the Chihuahuan Desert. This is likely due to the extreme environment of the Chihuahuan Desert and the strong environmental filters imposed on the anurans occurring in this ecoregion. For example, only three ecomorphs (fossorial, terrestrial, and semi-aquatic) were observed in the Chihuahuan Desert anuran assemblages. In fact, 10 of the 16 species from three families (Bufonidae, Scaphiopodidae, and Microhylidae) possessed morphologies indicative of a fossorial lifestyle. The only hylid species present (*H. arenicolor*) is not considered to be an arboreal ecomorph, but actually a semi-aquatic ecomorph based on its jumping performance (Gomes et al., 2009). The predominance of the fossorial ecomorphs across three families is likely to be the reason we failed to find any correlation between phylogeny and morphology.

At broader spatial scales (i.e., macrohabitat and mesohabitat), the composition and distribution of frog assemblages has been linked to abiotic factors, such as topographic and edaphic gradients, climate, and vegetation type (Duellman 1999, Dias-Terceiro et al., 2015; Dayton et al., 2004; Menin et al., 2007; Dias-Terceiro et al., 2015). At the habitat scale, anuran assemblage structure is influenced by edaphic gradients, species-specific responses attributed to prey abundance or suitable breeding sites (Menin et al., 2007; Dias-Terceiro et al., 2015; Watling, 2005. Frogs of the Chihuahuan Desert region exhibit strong associations between species presence and the soil and vegetation type (Dayton et al., 2004; Boeing et al., 2013). Dayton et al. (2004) hypothesized that the soil type was the most important predictor of an anuran species presence at a site; those species that exhibit fossorial behaviors are more likely to occur in habitats with soils that retain moisture better due to the risk of desiccation during the dry winter months. Mesquite scrub is an important habitat component for desert anurans not only because it provides shelter, but also because it increases soil surface moisture and temperature for burrowing species, and increases the abundance of food availability within these habitats. Despite the broad habitat classifications in this study, our results appear to support the hypothesis by Dayton et al. (2004), in which species' morphological traits respond to environmental factors in determining which amphibian species are able to inhabit a given habitat association. The fossorial species occupied a wide range of habitat associations in the Chihuahuan Desert, yet these species were

notably absent in chaparral, a habitat containing rocky, well-drained soils (Morafka, 1977). The terrestrial ecomorphs (*E. guttatus* and *C. augusti*) found in the chaparral do not burrow, but rather are able to utilize spaces between rocks to overwinter and are direct developers (*E. guttatus* and *C. augusti*), whereas the semi-aquatic *Lithobates berlandieri* has strong ties to streams. The physiological ecologies of many of these Chihuahuan anurans are known (Shoemaker, 1988), therefore transplant experiments of species across different soils would provide additional insights into the interplay between soil type, functional traits, and physiological ecology in the community organization of these arid-adapted anurans. This would be of particular use to better predict how this community would respond to disturbances, such as drought due to climate change, as even a change small in magnitude would have substantial effect in this water limited system (Brown et al., 1997).

Our results suggest that species morphological traits are important indicators of habitat use and niche specialization in anuran assemblages, and a useful framework to understand the organization of anuran communities. In particular, this framework would be useful to understand the consequences of alterations to environmental conditions (e.g., climate change, habitat fragmentation) on anuran functional diversity (Carey and Alexander, 2003; Blaustein et al. 2010). Given that the strength of biotic and abiotic processes is scale-dependent, it would be useful to examine how these ecological processes interact at different scales to affect functional diversity and in turn, provide a more comprehensive understanding as to how these communities are organized and how they respond to perturbations in their environments.

Acknowledgments

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.jaridenv.2015.06.019.

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