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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.

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