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Processes structuring amphibian assemblages along a subtropical arid gradient

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ABSTRACT

Biotic assemblages are organized according to multiple factors, including environmental filtering and species interactions. However, the roles of abiotic and biotic factors in the organization of amphibian assemblages in arid regions are still not completely understood. Here, I examined the distribution patterns of seven species of amphibians that occur in Tunisia (north-western Sahara Desert) and the composition of 328 amphibian assemblages, including their meta-structural organization. The species showed different responses to environmental gradients, predominantly the aridity and vegetation gradients. The assemblages in xeric regions were composed of nested subsets of the species present in mesic regions. Most of the significant species associations were explained by shared environmental responses, indicating that they can be largely attributed to environmental filtering. The only exception was between two species of generalist bufonids, *Bufotes boulengeri* and *Sclerophrys mauritanica*, which showed a residual correlation greater than their shared association with the gradient. In this case, phylogenetic and morphological similarities could favour patterns of mutual exclusion in habitats such as desert oases, where the resources are limited.

1. Introduction

The diversity of biotic communities is influenced by multiple factors, including environmental characteristics and species interactions (Miller et al., 1997). Harsh climatic conditions, such as those found in deserts and polar regions, exert a pronounced effect on species richness (Currie, 1991; Hawkins et al., 2003). Amphibians are particularly influenced by the balance of water and energy because they require high environmental moisture in several phases of their life cycles (Rodríguez et al., 2005; Wells, 2007). For this reason, the amphibian assemblages in deserts include small numbers of species and these are usually relegated to the few habitats that include permanent or intermittent water (Bradford et al., 2003; Lannoo, 2005). The compositions of amphibian assemblages in deserts are largely explained by environmental filtering, but competitive exclusion could also play a role, at least at the level of breeding habitats (Dayton and Fitzgerald, 2001; Escoriza and Ben Hassine, 2017). However, it is unknown whether exclusion patterns are also detectable on large spatial scales and whether they prevail over abiotic factors.

Here, I investigated the organization of the amphibian assemblages at the margins of a subtropical desert and analysed the variations in the assemblage compositions along an ecotonal strip of 400 km. The study region was Tunisia, which is located on the north-western edge of the Sahara Desert. Seven species of amphibians occur in this region, and are unevenly distributed, with the highest diversity of amphibians in a narrow humid area at the extreme north of the country (Ben Hassine and Nouira, 2012). I assessed the possible influences of both the environment and species' interactions on the compositions of the assemblages. To quantify the biotic interaction strengths, I examined the species occurrences, testing whether the species associations were spatially structured. To do this, I used a null-model approach (Peres-Neto, 2004), which when combined with a multivariate analysis of the assemblage compositions and environmental data should reveal whether the environment alone or the environment and interspecific interactions determine the local occurrences of species (Greenwald et al., 2016).

I also evaluated broad spatial patterns of organization of the amphibian assemblages (Baselga, 2012). Nested subset patterns of species composition (i.e., when biotas in species-poor habitats are subsets of those found in species-rich habitats) can be expected in regions with harsh climates, where assemblages are mainly composed of vagile and abundant species (Rezende et al., 2007; Hortal et al., 2011). For the reasons previously given, I anticipated that the climatic gradient would strongly influence the composition of the assemblages (Ben Hassine and

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Nouira, 2012) i.e., that the sites within the arid belt would host species-poor assemblages. I also expected that the presence of competition, if it is relevant to the assemblage structure, would be apparent as non-random patterns of spatial exclusion (Gotelli, 2000).

2. Material and methods

2.1. Study area and surveys

The study region was the country of Tunisia, with a surface area of 163,610 km^2. The climate in the northern part of the region is Mediterranean (*Csa* type, Köppen classification; Peel et al., 2007). Aridity rapidly increases along a latitudinal axis, giving rise to subtropical desert conditions (*BWh* type) throughout most of the country (Peel et al., 2007). A total of seven species of amphibians appear in the region, one Caudata, *Pleurodeles nebulosus* (Guichenot, 1850), and six Anura, *Bufo spinosus* Daudin, 1803, *Bufotes boulengeri* (Lataste, 1879), *Discoglossus pictus* Otth, 1837, *Hyla meridionalis* Boettger, 1874, *Pelophylax saharicus* (Boulenger, 1913) and *Sclerophrys mauritanica* (Schlegel, 1841).

Data were collected by Ben Hassine and Nouira (2012) and in several field surveys conducted in 2012–2015 at a total of 328 sites and seven species (Fig. 1 and Fig. 2). The sites were visited three times, on average, during the breeding period (October–June). Species occurrence was determined with dip-netting and visual and acoustic detection (aquatic habitats) and by lifting stones and stumps (terrestrial habitats; Wilkinson, 2015). The species were considered to occur in a single assemblage when they were found together within a radius of 1 km. This distance represents the typical dispersal range of several species of amphibians (Sinsch, 1988; Trenham et al., 2001; McDonough and Paton, 2007; Schmidt et al., 2007); therefore it can be assumed that in this range of distances the species interact (e.g., Porej et al., 2004; Gibbs and Shriver, 2005; Stevens et al., 2006). On the other hand most of the study region is under arid conditions. In this type of xeric environments amphibians complete their life cycle in the vicinity of the aquatic habitats, to reduce the risk of dehydration during reproductive migrations or because adults require some level of environmental moisture to develop surface activity (Salvador, 1996; Ben Hassine, 2013). For this reason in xeric habitats dispersal distances of amphibians and species' home ranges are small (e.g., below 142 m^2 in two bufonid species from Moroccan semi-deserts; Gallix, 2002).

2.2. Environmental data

The relationship between species presence and the environment was assessed from a set of variables that were considered potentially influential in temperate and subtropical regions (Rodríguez et al., 2005; Escoriza and Ruhí, 2014). Amphibian occurrence in north-western Africa is influenced to a large extent by aridity and temperature (Escoriza and Ben Hassine, 2017). Vegetation cover and topography are also important factors influencing amphibian occurrence, because they generate buffered microclimates (Herbeck and Larsen, 1999; Gifford and Kozak, 2012).

Elevation was determined in situ with a global positioning system (Garmin Etrex 10; Garmin Ltd., Olathe, KS, USA). The climate was characterized with an aridity index and the mean annual temperature (Hijmans et al., 2005; Trabucco and Zomer, 2009). Vegetation cover was characterized with a vegetation index (enhanced vegetation index, EVI) and five categories: forest, cultivated vegetation, bush, grassland, and barren landscape (Tuanmu and Jetz, 2014). EVI estimates the vegetation biomass, and is particularly useful in regions with scarce vegetation (Jiang et al., 2008). The EVI data were obtained from Landsat8 (32–day composite) for a period of 12 months. The data from GIS databases were obtained at 1000 m $pixel^{-1}$ resolution using the package QuantumGIS vs 2.18 (QGIS Development Team, 2017).

2.3. Data analysis

I estimated the extent to which the species inventory represented the regional amphibian diversity. To do this, I constructed sample-

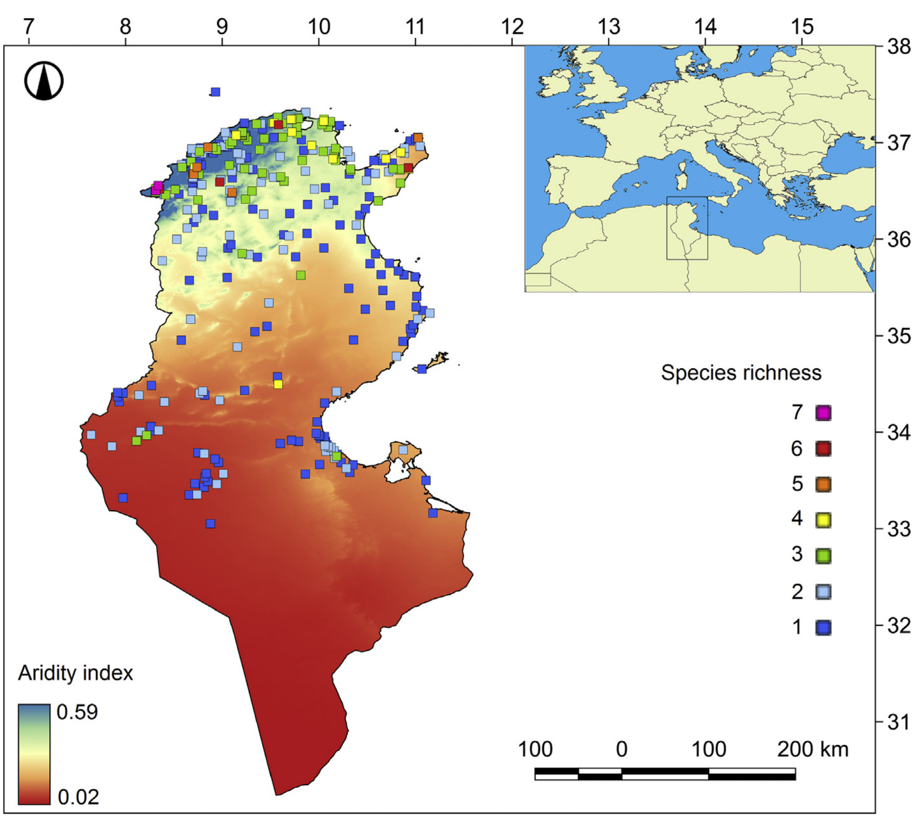

Fig. 1. Map of Tunisia, showing sampling localities and the species richness per locality. The aridity gradient, based on an aridity index, is included. Warm colors indicate higher aridity (0.02; hyperarid) than cold colors (0.59; subhumid). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)