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Original article

Amphibian assemblages in dry forests: Multi-scale variables explain variations in species richness

Julián N. Lescano [a, *], Laura M. Bellis [b], Laura E. Hoyos [c], Gerardo C. Leynaud [a]

[a] Instituto de Diversidad y Ecología Animal (CONICET-UNC) and Centro de Zoología Aplicada, Facultad de Ciencias Exactas Físicas y Naturales, Universidad Nacional de Córdoba, Rondeau 798, Córdoba 5000, Argentina
[b] Instituto de Diversidad y Ecología Animal (CONICET-UNC), Velez Sarfield 299, Córdoba 5000, Argentina
[c] Instituto Multidisciplinario de Biología Vegetal (CONICET-UNC), Vélez Sarsfield 1611, Córdoba 5000, Argentina

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ABSTRACT

Pond-breeding amphibians depend on several habitats and scales throughout their complex life cycle. For pond-breeding amphibians inhabiting seasonal dry forests, landscape is composed of a set of scarce and ephemeral isolated ponds surrounded by a contrasting matrix. The Chaco ecoregion is one of the most extensive dry seasonal forests in South America. In the last four decades, agricultural expansion and transformation from subsistence livestock farming to commercial livestock production have triggered dramatic deforestation processes all across the region, changing landscape composition and configuration. We postulate that richness of pond-breeding amphibians in the Chaco dry forest is negatively associated with pond hydroperiod and isolation, and terrestrial matrix degradation. Pond attributes and landscape configuration and composition were used to fit a statistical model to predict amphibian species abundance and richness in Arid Chaco ponds. Our results show that amphibian abundance and species richness in Chaco ponds is related to local and landscape predictors. Isolated and ephemeral ponds located in degraded shrublands showed low species richness values in Chaco dry forests. These results suggest that present-day land-use changes in the Chaco will have important effects on amphibians assemblages from the region, because such changes imply not only the loss of native vegetation but also a reduction of rural people devoted to extensive livestock production, where the artificial ponds used for watering livestock are also used as breeding sites by Chaco amphibians.

1. Introduction

Amphibians are undergoing a global conservation crisis (Houlahan et al., 2000; Stuart et al., 2004), with anthropogenic alterations to natural environments being the most important drivers of their global decline (Becker et al., 2007; Cushman, 2006; Gardner et al., 2007; Young et al., 2004). The sensitivity of Amphibians to habitat alterations is strongly related to their complex life cycle, since most species present an aquatic larval stage that metamorphoses into a terrestrial adult (Duellman and Trueb, 1994). Therefore, amphibian populations and assemblages usually respond to modifications in both aquatic and terrestrial habitats (Herrmann et al., 2005; Prevedello and Vieira, 2010; Rittenhouse and Semlitsch, 2007; Skelly, 2001).

Pond-breeding amphibians are dependent on availability of lentic aquatic habitats. From the landscape perspective, for pond-breeding amphibians, ponds can be considered habitat patches, embedded within a terrestrial matrix (Hamer and Parris, 2011; Marsh and Trenham, 2001; Mazerolle and Desrochers, 2005; Ribeiro et al., 2011). Therefore, amphibian assemblage attributes (e.g. species composition and richness) depend not only on pond characteristics (i.e. local patch characteristics) but also on terrestrial matrix attributes and pond connectivity in the landscape (Funk et al., 2005; Hanski, 1994; Prevedello and Vieira, 2010; Ribeiro et al., 2011).

Taking into account the different scales of influence and the multiple habitats used by amphibians throughout their complex life cycle, in the last decade researchers on amphibians ecology and conservation have turned their attention to the response of anuran assemblages to habitat variables that operate at the local and landscape scales. At the local scale, occurrence and abundance of many pond-breeding amphibians are strongly related to variations

* Corresponding author.
E-mail address: lescanojul@gmail.com (J.N. Lescano).

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in characteristics of water bodies, such as hydroperiod, surface, water chemistry, predators, and vegetation cover (Blaustein, 1999; Heyer et al., 1975; Rodrigues da Silva et al., 2012; Skelly, 2001; Skelly et al., 1999). At the landscape scale, spatial arrangement of ponds has a strong influence on amphibian populations and assemblages (Funk et al., 2005; Guerry and Hunter, 2002; Rothermel, 2004). Frog populations in isolated ponds have less probabilities of being rescued from local extinctions (which are frequent in pond-breeding amphibians) by the arrival of individuals from nearby ponds (Funk et al., 2005; Sjögren Gulve, 1994; Skelly et al., 1999). Moreover, vegetation around ponds is crucial for the migration (periodic intra-populations movements) of amphibians (Pope et al., 2000; Semlitsch, 2008; Semlitsch and Bodie, 2003; Sinsch, 1990; Smith and Green, 2005). Since amphibians are very sensitive to desiccation and high temperatures, individuals avoid movements across surfaces without vegetation cover (Rothermel and Semlitsch, 2002). Matrix quality also affects assemblage diversity and composition of pond-breeding amphibians because altered vegetation offers more resistance to migratory events and to other terrestrial activities (Guerry and Hunter, 2002; Hecnar and M'Closkey, 1998; Hermann et al., 2005; Lehtinen et al., 1999; Mazerolle and Desrochers, 2005; Prevedello and Vieira, 2010; Rothermel and Semlitsch, 2002).

The relative importance of pond characteristics, matrix quality and pond isolation varies according to intrinsic environmental attributes of natural systems. For animals that inhabit landscapes with discrete and ephemeral patches inserted within a hostile matrix, patch isolation is an important factor influencing population permanence (Fahrig, 2007). For pond-breeding amphibians inhabiting drylands, landscape is composed of a set of scarce and ephemeral ponds surrounded by a contrasting matrix (i.e. a matrix dominated by drylands with low relative humidity and low vegetation cover). In addition, due to the low temporal and spatial availability of water bodies that characterize drylands, pond occurrence and hydroperiod result in a limiting factor for amphibian species abundance, composition and diversity (Beja and Alcazar, 2003; Dayton and Fitzgerald, 2001; Heyer et al., 1975; Welborn et al., 1996). Therefore, drylands subjected to human activities altering landscape features are an interesting model to test associations between populations and assemblages of pond breeding amphibians and environmental variables that operate at different scales, since amphibians have to deal with matrix degradation, pond availability and water permanence.

South America is the continent with the largest number of amphibian species (Stuart et al., 2004) and a large continental portion is occupied by dry forests. One of the most extensive dry seasonal forests of the continent is the Chaco ecoregion, which covers 1,200,000 km^2 in Argentina, Paraguay, Bolivia and Brazil (Bucher, 1982; Prado, 1993). In the arid portions of the ecoregion, most lentic water bodies are small summer rain ponds and temporary farm ponds created for watering livestock (Macchi and Grau, 2012; Morello and Saravia Toledo, 1959). Traditional land use in the Chaco is mostly limited to extensive cattle ranching, charcoal extraction and selective logging. However, in the last four decades, agricultural expansion and transformation from subsistence livestock farming to commercial livestock production have triggered dramatic deforestation processes all across the region (Hoyos, 2012; Zak et al., 2008). In the south of the Chaco ecoregion, current deforestation rate ranges from 2.75 to 3.13% year^{-1}, exceeding the rates of other dry seasonal forests (Trejo and Dirzo, 2010), tropical forests (Archard et al., 2002; Zak et al., 2008) and the global level of gross forest cover loss (Hansen et al., 2010). Therefore, areas that were originally undisturbed forests and halophytic shrublands are now occupied by degraded shrublands, crops and implanted pastures (Boletta et al., 2006; Gasparri and Grau, 2009; Hoyos, 2012; Zak et al., 2004).

The degradation of Chaco dry forests implies an increase in soil temperature and a decrease in relative humidity (Abril and Bucher, 1999). Although some Chaco amphibians presents strategies to avoid desiccation (e.g. *Lepidobatrachus* spp.; *Chacophrys pierottii; Ceratophrys cranwelli; Phyllomedusa sauvagii*; *Leptodactylus bufonius*) (Cei, 1980; Faivovich et al., 2014; McClanahan et al., 1976, 1983), tadpoles of Chaco amphibians are highly susceptible to increases in normal temperatures of the area, since they live near their thermal tolerance thresholds (Duarte et al., 2012). For this reason it is plausible that tadpoles and post-metamorphic of some Chaco amphibians would be susceptible to degradation of Chaco dry forests. Moreover, due to the natural environmental conditions of the Chaco ecoregion (high temperatures and scarce and seasonal rains), pond availability and hydroperiod should be of major importance for the maintenance of pond-breeding amphibian populations and for local species richness.

Here we analyze the associations between amphibian richness patterns, species abundance and pond and landscape characteristics in the southernmost portion of Chaco dry forests. We postulate that species richness and abundance of pond-breeding Chaco amphibians is negatively associated with pond isolation and terrestrial matrix degradation. In addition, we propose that hydroperiod affects species differentially according to their larval development and, therefore, influences composition and richness of Chaco amphibian assemblages.

2. Materials and methods

2.1. Study area

The study area comprises a region of 13,400 km^2 located in the southernmost and driest portion of the Chaco ecoregion: the Arid Chaco sub-region (Hoyos et al., 2013; Morello et al., 1985) (Fig. 1). The original vegetation consists of a mosaic of xerophytic forest with a variable tree canopy cover (40–100%) and three well differentiated strata. The arboreal stratum is 7–8 m in height, with trees up to 15 m high, and is dominated by *Aspidosperma quebracho-blanco*. Forests alternate with halophytic shrublands in salt flats. Saline vegetation together with forests represents the original vegetation of the study area; however, forests have been drastically reduced and modified and currently the dominant matrix is composed of shrublands resulting from forest degradation. Degraded shrublands are characterized by the presence of isolated trees, rarely exceeding 15% of cover. The main stratum is composed of xerophytic shrubs (1.5–3 m high). Herbaceous vegetation is reduced or absent. For a detail of vegetation units in the study area, see Cabido and Zak (1999); Hoyos et al. (2013); Sayago (1969); Zak et al. (2004, 2008).

The climate is subtropical, with a mean annual temperature of 19.9 °C and maximum absolute temperatures that reach 47 °C. Rainfall is mainly concentrated in the warm season (October–April) and is approximately 450 mm yr^{-1} (Morello et al., 1985; Zak and Cabido, 2002).

2.2. Ponds characteristics

Natural ponds are very scarce and ephemeral in the Arid Chaco region. Hence, local small-scale producers that raise cattle construct temporary farm ponds (locally known as “represas”, “aguadas” or “tajamares”) (Morello and Saravia Toledo, 1959). Farm ponds are important water reservoirs all across the Chaco, since water is a limiting resource in the ecoregion (Cavanna et al., 2009; Macchi and Grau, 2012; Morello and Saravia-Toledo, 1959; Morello et al., 1985). Artificial ponds are easily distinguishable from natural ponds, mainly by the contour shape (irregular in natural ponds and