Acta Oecologica 58 (2014) 12–21

Contents lists available at ScienceDirect

Acta Oecologica

journal homepage: www.elsevier.com/locate/actoec

Original article

Habitat, food, and climate affecting leaf litter anuran assemblages in an Atlantic Forest remnant

Camila Rabelo Rievers [a], Maria Rita Silvério Pires [a], Paula Cabral Eterovick [b,*]

[a] Programa de Pós Graduação em Ecologia de Biomas Tropicais, Universidade Federal de Ouro Preto, 35400-000 Belo Horizonte, MG, Brazil
[b] Programa de Pós Graduação em Zoologia de Vertebrados, Pontifícia Universidade Católica de Minas Gerais, 30535-610 Belo Horizonte, MG, Brazil

ARTICLE INFO

Article history:
Received 1 July 2013
Accepted 7 April 2014
Available online 6 May 2014

Keywords:
Anura
Leaf litter structure
Invertebrate availability
Microclimate
Spatial distribution
Temporal distribution

ABSTRACT

Leaf litter anuran assemblages include both species that have terrestrial development and species that, during the breeding season, aggregate around bodies of water where their tadpoles develop. The resources used by these two groups in the leaf litter are likely to differ, as well as their sampled species richness, abundance and biomass as resource availability changes. We conducted a 12-month survey of leaf litter anuran assemblages at three forest areas in the largest Atlantic Forest remnant in the state of Minas Gerais in southeastern Brazil. Each month we estimated, based on capture rates, anuran species richness, abundance, and biomass as assemblage descriptors. We also measured variables that could potentially affect these descriptors in space and time: invertebrate litter fauna (abundance and richness of taxa), leaf litter biomass, and microclimatic conditions (air humidity, air and soil temperature, soil water content, and rainfall). We tested for differences in these variables among areas. We used general linear models to search for the variables that best explained variation in anuran abundance (based on capture rates) throughout the year. We analyzed species with terrestrial development (TD) and with aquatic larvae (AL) separately. We recorded 326 anurans of 15 species. Sampled anuran abundance (correlated to species richness and biomass) was explained by air humidity and/or invertebrate abundance for species with TD, and by soil water content or air humidity and leaf litter biomass for species with AL. The variability in the results of studies on leaf litter frogs that try to find variables to explain changes in community descriptors may be due to spatial variation of resources among areas and also to the fact that TD and AL species are frequently analyzed together, when in fact they are likely to show different responses to resources present in the leaf litter habitat, reflected on capture rates.

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1. Introduction

Neotropical leaf litter anurans are mostly represented by species that lay eggs on the forest floor and species that aggregate around puddles for breeding (Donnelly and Crump, 1998; Haddad et al., 2008; Walting and Donnelly, 2002). The former depend on the leaf litter habitat for foraging, shelter, and breeding with their eggs being deposited in the leaf litter itself (e.g., Brachycephalidae, Craugastoridae, and Eleutherodactylidae). The latter live on the leaf litter and use it to forage and for shelter, but usually breed and deposit eggs at flooded areas or puddles on the forest floor (e.g., Leiuperidae, Leptodactylidae, Microhylidae, and Bufonidae; Donnelly and Crump, 1998; Haddad et al., 2008). Other species may occasionally move through the leaf litter although they are essentially arboreal (e.g., Hylidae; Rocha et al., 2007). From an ecological standpoint, forest leaf litter is an interesting habitat to study the resources that are important for maintaining resident anuran populations, because resources used for both reproduction and subsistence may be present.

Previous research suggests that the density and diversity of leaf litter frogs is mostly related to three main niche dimensions (sensu Pianka, 1973): food (e.g., productivity, availability of food resources), space (altitude, habitat quality, habitat heterogeneity) and time (seasonality of climatic conditions). Many of these studies on leaf litter anuran assemblages have been conducted in Brazil, Costa Rica, and east Africa (e.g., Gardner et al., 2007; Heinen, 1992; Lieberman, 1986; Rocha et al., 2007). In Brazil, such studies took place in the Amazon (Allmon, 1991; Gascon, 1996; Rojas-Ahumada et al., 2012) and in the Atlantic Forest biomes (Dixo and Verdade, 2006; Rocha et al., 2001; Van Sluys et al., 2007). However, none of these studies assessed variables related

* Corresponding author.
E-mail addresses: pceterovick@gmail.com, eterovick@yahoo.com (P. C. Eterovick).

http://dx.doi.org/10.1016/j.actao.2014.04.003
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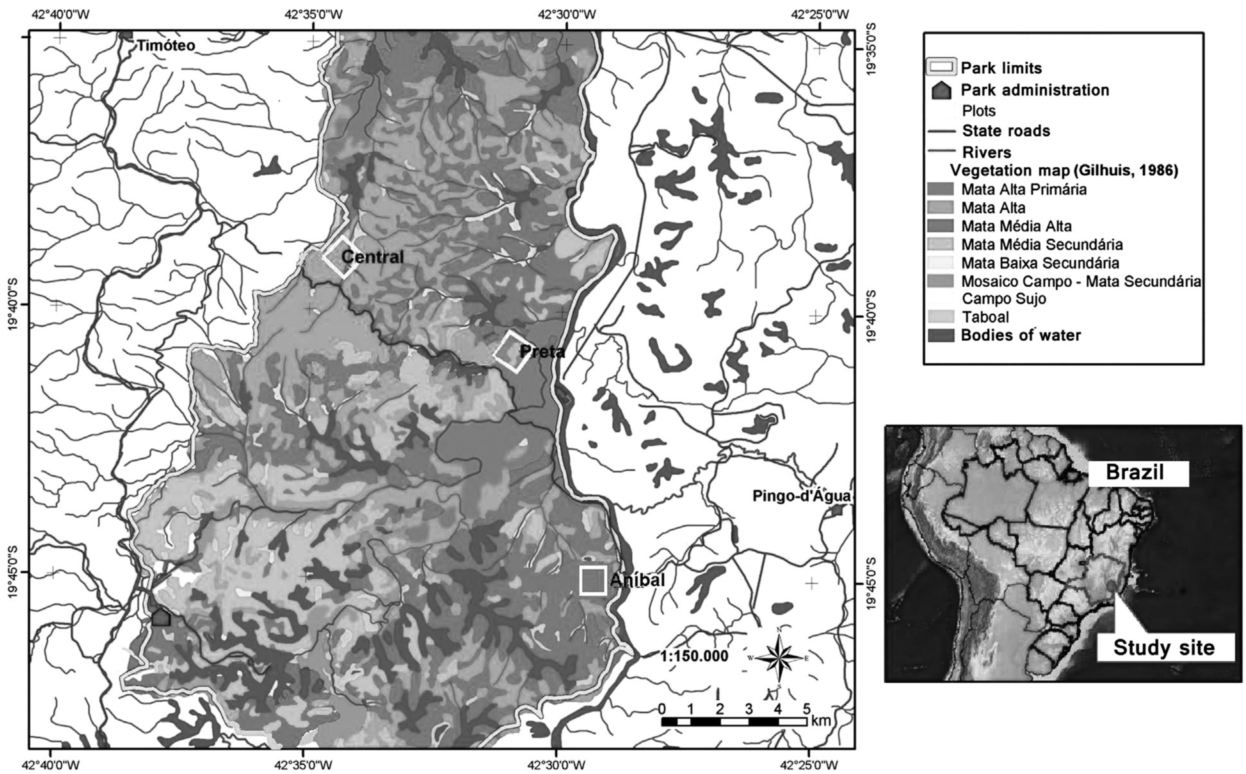

Fig. 1. Map showing the location of the Parque Estadual do Rio Doce (PERD) in the state of Minas Gerais in southeastern Brazil, and the three areas sampled within the park.

to food, habitat, and temporal (seasonal) effects simultaneously. Such factors may be related and present synergetic effects, so a model selection approach is important to detect which factors or combination of factors best explain variation in leaf litter community attributes such as species richness, abundance and biomass, also reflected on capture rates. Additionally, responses to these factors are likely to differ between species with terrestrial development and those with aquatic larvae (see Becker et al., 2007, 2010). Species with aquatic larvae must migrate to breeding sites to reproduce, and the existence of suitable migration routes, as well as specific frog traits (e.g., tolerance to available habitat conditions, migration abilities), are important determinants of their success (see Becker et al., 2007; Dixo and Metzger, 2010). On the other hand, for species with terrestrial development the leaf litter may assume a greater importance for reproduction rather than movement. Regardless of reproductive mode, all species may benefit from food availability in leaf litter habitats. The importance of taking differences in life-history traits, such as reproductive modes, of species into account for planning efficient conservation strategies has already been recognized (Becker et al., 2010).

We aimed to study factors related to the three main niche dimensions of food, space, and time concomitantly and identify which of these has the greatest influence on species richness, abundance and biomass (considered as community descriptors) for species with terrestrial development (TD) and species with aquatic larvae (AL) separately. Since we sampled anurans with pitfall traps, community descriptors are based on capture rates. Our main questions were: (1) Do TD frogs respond to available resources in a different way than AL species? That is, would different variables explain community descriptors of species with TD and AL? (2) Is temporal variation in community descriptors affected by the same variables at forest sites within the same forest remnant?

2. Materials and methods

2.1. Study site

The study was conducted at the Parque Estadual do Rio Doce (PERD), in the southwestern portion of the state of Minas Gerais, Brazil (19°48′18″–19°29′24″S, 42°28′18″–48°38′30″W, Datum WGS 84; Fig. 1). PERD is the largest and best-preserved continuous remnant of Atlantic Forest in Minas Gerais, and encompasses 35,976 ha of forest in various successional stages (Seeliger et al., 2002). The vegetation is tropical, semideciduous and seasonal, with lianas and epiphytes. The park shelters more than 56 independent lakes, being the largest lake complex in Latin America (IEF, 2008). The terrain is hilly, with altitudes that vary from 200 to 500 m above sea level (IEF, 2008) and the soils are acidic with low natural fertility (Metzker, 2007; Teixeira et al., 1989). Mean annual temperatures are 20–22 °C, and annual rainfall averages 1250–1500 mm, with rains concentrated in the warm season (October to March). The dry, cold season extends from April to September (IEF, 2008). A preliminary inventory of anurans found 38 species in PERD, most of which have broad geographic distributions (Feio et al., 1998).

We sampled leaf litter anurans in three forest areas (Preta, Central, and Aníbal) considered as replicates within the park (Fig. 1), and chosen to represent the heterogeneity of the forest in PERD. Preta is covered by primary forest on a flat terrain (mean declivity = −2.6°). Trees reach about 30 m and show a high abundance of epiphytes. The low declivity and proximity to the Doce River and several lakes promote high humidity in this area (Metzker, 2007). In Preta, traps (described ahead) were positioned 370 m from the closest body of water. Central is located on a hilly terrain (declivity can reach −22°, with a mean of −19.6°). The forest is in earlier successional stages than at Preta and with shorter trees reaching up to only 25 m. The lower vegetation strata are denser

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