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Anuran species distribution along an elevational gradient and seasonal comparisons of leaf litter frogs in an Atlantic Rainforest area of southeastern Brazil

Pablo Goyannes-Araújo, Carla Costa Siqueira, Rafael Camilo Laia, Marlon Almeida-Santos, Diego Medeiros Guedes & Carlos Frederico Duarte Rocha

Departamento de Ecologia, Instituto de Biologia, Universidade do Estado do Rio de Janeiro, Rua São Francisco Xavier 524, 20550-011 Rio de Janeiro, RJ, Brasil

Documenting elevational gradients in species richness is important to understand the determinants of spatial distributions. We studied anuran richness along an elevational gradient in an Atlantic Rainforest area to evaluate i) how anuran richness and elevation are related; ii) if the data support the hypothesis of the mid-domain effect or the Rapoport effect and iii) if there is seasonal variation in species richness and abundance of leaf litter anurans in the studied site. Sampling was carried out using time-constrained visual encounter surveys and plot (quadrat) methods at six elevational levels. We found 406 individuals belonging to 19 anuran species. The most abundant frog species were *Ischnocnema parva* (6.2 individuals per 100 m²) and *Adenomera marmorata* (2.0 individuals per 100 m²). The overall leaf litter frog abundance was 11.2 ind/100 m², with highest values at 150 m (26.6 ind/100 m²) and 300 m (25.6 ind/100 m²) elevations. We found high species turnover across altitudes. Our data neither supported the mid-domain effect nor the elevational Rapoport effect. There was no significant difference in frog abundance among seasons, although most of the leaf litter frogs species were found in the wet season (235 individuals or 69.3%). Our study demonstrates a high local frog species richness and abundance in combination with an abundance decreasing with elevation.

Key words: altitude, Amphibia, mid-domain effect, montane rainforest, range size, Rapoport effect

INTRODUCTION

Biogeographical variation in species richness and composition is critical to our understanding of biological diversity (Grytnes & Vetaas, 2002; Diniz-Filho et al., 2004). Latitudinal and altitudinal gradients in species richness are one of the most studied spatial diversity patterns (Huey, 1978; Lomolino, 2001). Previous studies on species richness variation along altitudinal gradients have revealed maximum richness at an intermediate point of the gradient, a plateau of high species richness at lower altitudes, or a linear decrease in species richness with increasing elevation (Terborgh, 1977; Rahbek, 1995, 2005; Almeida-Neto et al., 2006). Depending on the study, area (e.g., Rahbek, 1997; Fu et al., 2006), water availability, energy (e.g., McCain, 2007; Fu et al., 2006) and the mid-domain effect (McCain, 2004) explained the highest proportion of variation in species richness. The mid-domain effect is the pattern that results from the random overlap in the distribution of species ranges along a bounded domain, with more ranges overlapping in the middle of the domain (i.e. mid-elevations) than at the edges (i.e. higher and lower elevations, Colwell & Lees, 2000; Colwell et al., 2004). A positive relationship

between the elevational range and the midpoint of the species' distribution along the gradient is known as the Rapoport effect (Stevens, 1992; Blackburn & Gaston, 1996). This hypothesis, an extension of Rapoport's latitudinal rule, postulates that species from high altitudes tend to have higher tolerance to environmental changes than species from low elevation (Stevens, 1992). Systems in which Rapoport effects are found are characterised by negative correlations between species richness and elevation, and between species richness and the mean elevational range of species present at a given elevation (Fleishman et al., 1998).

There have been relatively few attempts to understand the general patterns of frog species richness variation along altitudinal gradients (Fu et al., 2006; Naniwadekar & Vasudevan, 2007), and most existing studies focused on specific clades (e.g., Shoo & Williams, 2004; Hu et al., 2011). Beside variation along the elevational gradient, the species composition and abundance of frog assemblages may also change seasonally, although few studies have tested this (e.g., Scott, 1976; Giaretta et al., 1999; Watanabe et al., 2005; Santos-Pereira et al., 2011).

Only two studies so far investigated the altitudinal distribution of leaf-litter frogs in the Atlantic Forest biome of Brazil, and were conducted across a limited

Correspondence: Carla C. Siqueira (carlacsiqueira@yahoo.com.br)

altitudinal range (<350 m; Giaretta et al., 1997, 1999). In the present study we aim to investigate the patterns of anuran richness along an elevational gradient of the Pico do Papagaio Mountain, Ilha Grande. We address the following questions: (i) Is there a relationship between anuran richness and elevation? (ii) Do the data for this area support the hypothesis of the mid-domain effect and/or the Rapoport effect? (iii) Is there seasonal variation in species richness and abundance of leaf litter anurans?

METHODS

Sampled areas are located at Pico do Papagaio mountain (23°09'16.0"S, 44°11'46.0"W) on the Parque Estadual da Ilha Grande conservation unit, Ilha Grande island, municipality of Angra dos Reis, state of Rio de Janeiro, southeastern Brazil. Ilha Grande is a continental island

with a total area of ca. 19,000 ha covered by Atlantic Rainforest. The Atlantic Forest in the region can be subdivided into Lowland Forest (up to 50 m), Submontane Forest (50 to 500 m), and Montane Forest (above 500 m, Veloso et al., 1991). Pico do Papagaio mainly comprises primary rainforest (Oliveira, 2002). Altitudes vary from sea level up to 959 m in the Pico do Papagaio and 1031 m in the Serra do Retiro (Araújo & Oliveira, 1988). The climate is wet and warm, with mean annual temperature of 22.5°C and annual rainfall of 2200 mm (NUCLEN, 1996); there is a warm-wet season from October to April, and a cooler and drier season from May to September.

Sampling was carried out using time-constrained visual encounter surveys (Crump & Scott, 1994) employed monthly from January to December 2008, and a plot (quadrat) method (Jaeger & Inger, 1994), between July and August 2008 (dry season) and February and March 2009 (wet season). We sampled six elevational levels:

Table 1. Abundances of frog species and estimated overall densities (ind/100 m²) of leaf litter frogs found along an elevational gradient in Pico do Papagaio mountain, in the Brazilian Atlantic Rainforest of Ilha Grande. * Species endemic to Ilha Grande.

Species	Elevation (m)						Total
	150	300	450	600	750	900	
BRACHYCEPHALIDAE							
<i>Brachycephalus didactylus</i>		3				1	4
<i>Ischnocnema guentheri</i>	1	1			1	4	7
<i>Ischnocnema parva</i>	73	73	22	6	2	17	193
BUFONIDAE							
<i>Dendrophryniscus brevipollicatus</i>						2	2
<i>Rhinella ornata</i>	5	4					9
HEMIPHRACTIDAE							
<i>Flectonotus</i> sp.						1	1
CRAUGASTORIDAE							
<i>Haddadus binotatus</i>	17	15	14	10		6	62
CYCLORAMPHIDAE							
<i>Proceratophrys tupinamba</i> *				2			2
<i>Thoropa miliaris</i>	3	7	1				11
<i>Zachaenus parvulus</i>	8	19	1				28
HYLIDAE							
<i>Aplastodiscus eugenioi</i>		2					2
<i>Bokermannohyla circumdata</i>						3	3
<i>Phasmahyla</i> cf. <i>guttata</i>		2					2
<i>Scinax trapicheiroi</i>		3					3
HYLODIDAE							
<i>Hylodes fredj</i> *	1						1
LEPTODACTYLIDAE							
<i>Adenomera marmorata</i>	43	21	4			1	68
<i>Physalaemus signifer</i>	3					1	4
MICROHYLIDAE							
<i>Chiasmocleis</i> sp. *	1						1
<i>Myersiella microps</i>		2					2
TOTAL ABUNDANCE	155	152	42	18	3	36	406
DENSITY (ind/100 m ²)	26.6	25.6	7.4	3.2	0.4	3.8	11.2

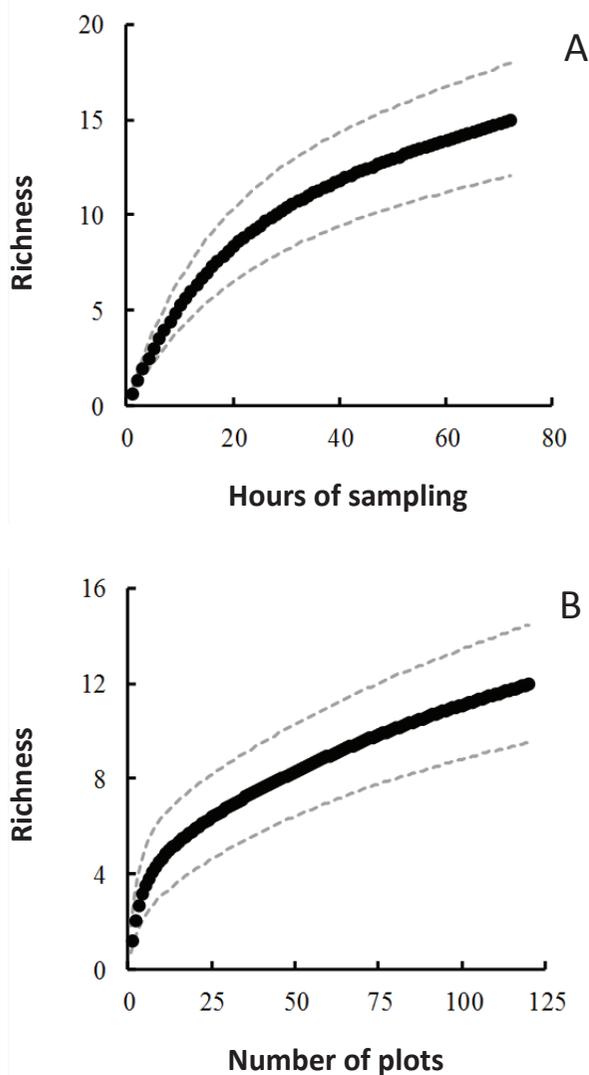


Fig. 1. Rarefaction curves, with the respective standard deviation (dashed lines), of anuran species richness recorded in the Atlantic Rainforest area in Pico do Papagaio mountain, in the Brazilian Atlantic Rainforest of Ilha Grande. Richness estimated by A) sampling hours (visual encounter survey method) and B) number of plots.

150, 300, 450, 600, 750, and 900 metres above sea level with equal effort of sampling at each of these sites.

For the visual encounter surveys, we sampled each altitude for 12 hours (1 h/month/elevation) at night, totaling a 72-hour sampling effort. We also established 20 quadrats of 5x5 m at each altitude (10 per season at each altitude), totalling 120 quadrats corresponding to 3,000 m² of sampled forest floor. During the day, we marked the corners of each plot with wooden stakes and the plot was completely enclosed by a 60 cm high plastic fence. The bottom of the plastic fence was buried or attached to the ground with strings and sticks to prevent frogs from escaping. At night (between 1830 and 0000 hours), each plot was carefully searched for frogs by four persons wearing head lamps. Each plot was searched for about half an hour.

All frogs found by the two sampling methods were captured, identified and most were released after fieldwork. Voucher specimens of all frog species collected

during the study were deposited in the amphibian collection of the Museu Nacional, Rio de Janeiro (MNRJ).

To estimate species composition and richness we merged the data from both methods (visual encounter survey and plots). Estimates of leaf litter frog density (individuals/100 m²) were obtained based on the plot sampling. We considered a species as present at a particular elevation if it was recorded both at a higher and at a lower altitude adjacent to it (following Almeida-Neto et al., 2006; Naniwadekar & Vasudevan, 2007). Sampling saturation was assessed with a rarefaction curve and by the richness estimator Chao 1 using abundance data, performing 1,000 randomisations without replacement, with the program EstimateS v.8.2.0 (Colwell, 2005). For seasonal comparisons, we used only data from plots. We evaluated differences between seasons in terms of leaf litter species richness and abundance per plot using One-Way Analysis of Variance (ANOVA) (Zar, 1999).

The empirical richness and elevational range size of species were compared with null predictions computed through Monte Carlo simulation procedures using the software Mid-Domain Null (McCain, 2004). The mid-domain null models are generated by randomly placing ranges or range midpoints between two hard boundaries (Colwell & Hurtt, 1994). Mid-domain null allows sampling without replacement and therefore restricts the sampling to observed species (McCain, 2004). The 95% confidence intervals generated by this procedure are narrower than those created by sampling with replacement (McCain, 2004). Simulations (150 m elevational belts) were carried out using the empirical range sizes with 50,000 resampling events without replacement (McCain, 2004, 2007). To examine how empirical richness and species richness predicted by the mid-domain effect (simulated richness) along elevations are related, we used linear regressions (Zar, 1999). The relationships between empirical richness and abundance of frogs versus elevation were also evaluated by linear regressions.

The relationship between elevational range and elevation (Rapoport effect) of frog species was evaluated by the midpoint method (Rohde et al., 1993), using species as sample units (e.g., Fleishman et al., 1998; Almeida-Neto et al., 2006) in linear regressions (Zar, 1999). The midpoint of each species was calculated as the equidistant elevation between the extremes at which a species was recorded.

Species turnover between pairs of adjacent sampling sites was estimated as $1-X$, where X is the Sorensen's index [$S=2c/(a+b)$], and a and b are the number of species at each altitude and c is the number of species common to both localities (Wolda, 1981). To analyse which altitudes were more similar in terms of species composition we performed a Cluster Analysis using unweighted pair-group average with abundance data for each species in the six altitudinal sites sampled. Variables were log-transformed whenever the criteria for normality and homocedasticity were not met. Descriptive statistics are represented in the text as arithmetic mean \pm 1 standard deviation (SD).

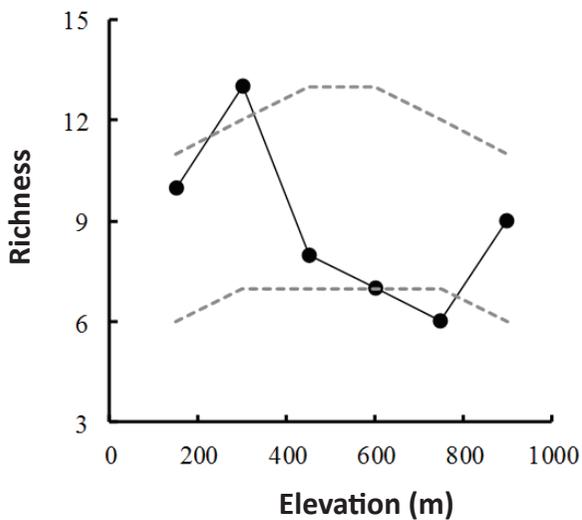


Fig. 2. Relationship between simulated richness of anurans and elevation (in metres) along an altitudinal gradient in Pico do Papagaio mountain, in the Brazilian Atlantic Rainforest of Ilha Grande. Dotted lines enclose 95% prediction curves sampled without replacement from empirical range sizes.

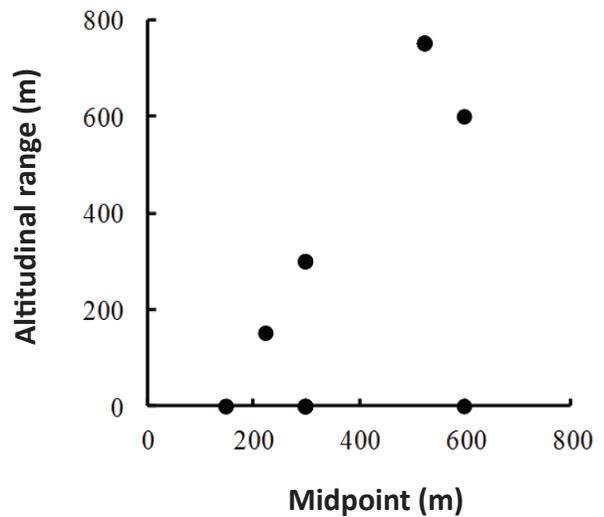


Fig. 3. Relationship between altitudinal range and elevation midpoint (both in metres) of anuran species along an altitudinal gradient in Pico do Papagaio mountain, in the Brazilian Atlantic Rainforest of Ilha Grande.

RESULTS

We found 406 individuals belonging to 19 species at Ilha Grande (Table 1). The rarefaction curves showed an asymptotic shape, with a tendency to reach stability (Fig. 1). Our estimate of frog richness using visual encounter surveys (Chao 1=16.0±1.8) was relatively close to the observed richness values obtained (18 spp.), whereas for large plots, the estimated richness (Chao 1=17.0±6.0) was larger than that obtained (12 spp.). The local frog

Table 2. Densities (ind/100 m²) of each leaf litter frog species found at dry and wet seasons in Pico do Papagaio mountain, in the Brazilian Atlantic Rainforest, of Ilha Grande, using 5x5 m plots.

Species	Density (ind/100 m ²)		Total
	Dry season	Wet season	
<i>Adenomera marmorata</i>	1.3	2.6	2.0
<i>Brachycephalus didactylus</i>	0.1	0.2	0.1
<i>Chiasmocleis</i> sp.	0.1		0.03
<i>Dendrophryniscus brevipollicatus</i>		0.1	0.03
<i>Haddadus binotatus</i>	1.0	2.2	1.6
<i>Hylodes fredei</i>	0.1		0.03
<i>Ischnocnema parva</i>	3.5	8.9	6.2
<i>Myersiella microps</i>		0.1	0.1
<i>Physalaemus signifer</i>	0.1		0.03
<i>Proceratophrys tupinamba</i>		0.1	0.03
<i>Rhinella ornata</i>	0.1	0.3	0.2
<i>Zachaenus parvulus</i>	0.5	1.2	0.8
TOTAL	6.7	15.7	11.2

community was dominated by *Ischnocnema parva* (=47.5% of individuals) which together with *Adenomera marmorata* (=16.7%) and *Haddadus binotatus* (=15.3%) comprised about 80% of all individuals recorded (Table 1). The estimated overall frog density of the local leaf litter frog community was 11.2 individuals per 100 m², with highest density values at 150 m (26.6 ind/100 m²) and 300 m.a.s.l (25.6 ind/100 m², Table 1). Species with highest estimated density values were *I. parva* (6.2 ind/100 m²) and *A. marmorata* (2.0 ind/100 m², Table 2).

Fifty percent ($n=6$) of leaf litter frog species (*A. marmorata*, *Brachycephalus didactylus*, *H. binotatus*, *I. parva*, *Rhinella ornata* and *Zachaenus parvulus*) were found in both seasons (Table 2). Leaf litter frog richness per plot did not differ between seasons ($F_{1,118}=2.544$; $p=0.113$), and overall litter frog richness was equal (9 species) in both seasons. We found more leaf litter frogs in the wet ($n=235$ individuals; 69.3%) than in the dry season ($n=100$; 30.7%), but the difference was only marginally significant ($F_{1,118}=3.237$; $p=0.07$).

Frog richness was not related with elevation ($r^2=0.338$; $n=6$; $p=0.226$). There was one peak of species richness at 300 m of elevation (Fig. 2). Empirical species richness did not fit the simulated richness generated by the Mid-Domain Null program ($r^2=0.112$; $n=6$; $p=0.518$). We found a negative relationship between abundance and elevation ($r^2=0.704$; $n=6$; $p=0.037$), with the highest values of frog abundance occurring at 150 m ($n=155$) and 300 m ($n=152$, Table 1).

Five frog species (*Ischnocnema guentheri*, *I. parva*, *H. binotatus*, *Physalaemus signifer* and *A. marmorata*) occurred along the entire altitudinal gradient (Table 1). In disagreement with the Rapoport effect prediction, species with higher elevational midpoints did not have wider altitudinal ranges ($r^2=0.013$; $n=19$; $p=0.638$, Fig. 3). We recorded high values of species turnover for all pairs of consecutive altitudes: 150 vs. 300 m=70%; 300

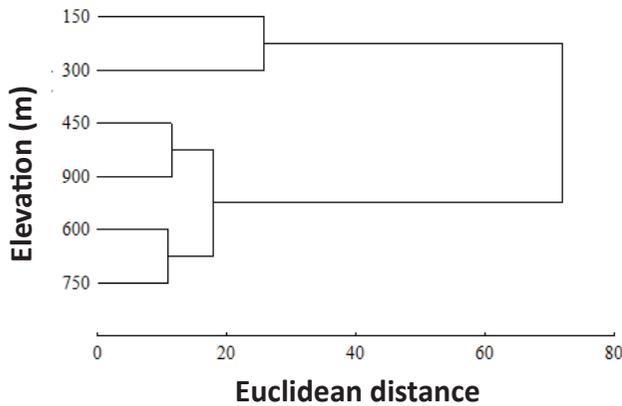


Fig. 4. Similarity estimates (Cluster Analysis) of anuran species composition between elevations (based on abundance data for each frog species) along an altitudinal gradient in Pico do Papagaio mountain, in the Brazilian Atlantic Rainforest of Ilha Grande.

vs. 450 m, 450 vs. 600 m, and 750 vs. 900 m =80%; and 600 vs. 750 m =90%. The cluster analysis detected two main groups: one composed by frog assemblages recorded at 150 and 300 m of elevation and the other with assemblages recorded above 450 m (Fig. 4). Above 450 m, the cluster analysis showed one group at 600 m and 750 m, and another group at 450 m and 900 m (Fig. 4).

DISCUSSION

We found higher values of frog species richness at 150 m, 300 m and 900 m of elevation, with a peak of richness at 300 m. Frog richness at 300 m was higher than predicted by the mid-domain effect, which might be due to the increased presence of water bodies to favour the occurrence of frogs. Moreover, at lower altitudes, the terrain was less steeply inclined. Conversely, at 750 m of altitude simulated richness was lower than that predicted by the mid-domain effect, possibly due to low availability of water bodies and relatively steep terrain. The inclination of slopes can affect negatively the presence of species (Lomolino, 2001), whereas the presence of water bodies tend to favour the occurrence of anurans (Rahbek, 1995; Hofer et al., 1999; Lomolino, 2001; Haddad & Prado, 2005). We found high values of frog species turnover between altitudes, probably explaining a large part of the richness found. Vegetation types in the studied areas change from Submontane (up to 500 m) to Montane Forest (above 500 m, Veloso et al., 1991), which may partly explain the grouping of sites into two main clusters (below 300 m and above 450 m).

Hump-shaped elevational species-richness curves are the most frequently recorded (Rahbek, 1997, 2005). In the Atlantic Rainforest of southeastern Brazil, high richness values at intermediate elevations were found for harvestmen (Almeida-Neto et al., 2006) and mammals (Geise et al., 2004), but not unambiguously for birds (Cavarzere & Silveira, 2012). Other studies on frog

species distribution along elevational gradients in Asia reported a peak of richness at intermediate altitudes (Fu et al., 2006; Hu et al., 2011); an increase in stream frog richness with elevation at the alpha level and three peaks of richness at the gamma level could be explained by soil temperature and moisture (Naniwadekar & Vasudevan, 2007). The spatial distribution of anurans highly depends on the presence of aquatic breeding sites (Hofer et al., 1999; Naniwadekar & Vasudevan, 2007). The poor fit of the relationship between empirical and simulated richness further invalidates the role played by stochastic processes in structuring the leaf litter frog community at Pico do Papagaio. Because the mid-domain effect was an important factor to explain elevational richness patterns in the Hengduan Mountains, China (Fu et al., 2006) but not at Pico do Papagaio (present study) and in the Western Ghats, India (Naniwadekar & Vasudevan, 2007), its influence on frog distribution along altitudinal gradients needs to be better clarified.

Our data did not provide empirical support for an elevational Rapoport effect. Despite species with higher elevational midpoints tending to have broader elevational ranges, species with small altitudinal ranges occurred at both low and high altitudes. The Rapoport effect has been confirmed for Colombian frogs (Navas, 2003), but rejected in other studies on anurans (Stevens, 1992; Bernal & Lynch, 2008; Hu et al., 2011).

Litter frog density at the studied area is high compared to other Atlantic Forest sites (Giaretta et al., 1997, 1999; Rocha et al., 2001, 2007, 2013; Almeida-Gomes et al., 2008, 2010; Santos-Pereira et al., 2011, but see also Siqueira et al., 2009, 2011, 2014). The direct-developing frog *I. parva* dominated the leaf litter community at Ilha Grande, confirming previous studies (Rocha et al., 2000, 2001, 2007). Species with direct development are rather independent of water bodies and thus often numerically dominant in Neotropical leaf litter frog communities (e.g., Scott, 1976; Lieberman, 1986; Fauth et al., 1989; Siqueira et al., 2009; Almeida-Gomes et al., 2008, 2010), whereas species with water-dependent reproduction are limited by the proximity of water bodies (e.g., Heyer & Berven, 1973; Scott, 1976).

The community of frogs living in leaf-litter can vary in their parameters in a temporal scale (e.g., Giaretta et al., 1999; Menin et al., 2008; Watanabe et al., 2005; Santos-Pereira et al., 2011). In our study, we did not find significant differences in richness and abundance of leaf litter frogs between seasons at Pico do Papagaio. However, three species were only observed in one season, at low densities.

At the Pico do Papagaio mountain, we found about 60% of the anuran species recorded for Ilha Grande (Bittencourt-Silva & Silva, 2013), and two of the 19 species found (*Proceratophrys tupinamba* and *Hylodes fredii*) are considered endemic (Frost, 2013) together with a still undescribed species (*Chiasmocleis* sp.). *Aplastodiscus eugenioi* and *Scinax trapicheiroi* are currently categorised as Near Threatened, *Hylodes fredii* as Data Deficient, and *P. tupinamba* (Prado & Pombal, 2008) and *Chiasmocleis* sp. are currently not listed by the IUCN (IUCN, 2013). These records of occurrence can help to protect the amphibians

of the Atlantic Rainforest (Eterovick et al., 2005; Pimenta et al., 2005).

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