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# Composition of Terrestrial Anurans in Areas with Different Degrees of Alteration in San Rafael National Park (Paraguay)

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**Abstract.** We examined the effects of landscape changes in an environmental gradient of forest, a *Vernicia fordii* plantation, and crops on the distribution patterns of amphibians in San Rafael National Park. We conducted eight periods of fieldwork between June 2012–April 2013 and used pit fall traps with drift fences to capture amphibians. We recorded eight species of the families Bufonidae, Leptodactylidae, and Odontophrynidae. The environmental variables correlated with the abundance of amphibians were relative humidity, litter depth, herbaceous cover, and air temperature, and significant differences were found in species composition. Generalist species like *Leptodactylus mystacinus* and *Physalaemus cuvieri* were found in the most altered areas such as crops and the plantation. *Rhinella ornata* and *Proceratophrys avelinoi* were primarily restricted to primary forests, and their abundance was sensitive to forest loss and degradation. Our results support the idea that modified habitats influence distribution patterns of amphibians, and the protection of the remnants of pristine Atlantic Forest is a critical step in the conservation of anuran biodiversity in Paraguay.

**Keywords.** Amphibians; Atlantic Forest; Frog abundance.

**Resumen.** Se estudió el efecto de un gradiente ambiental de bosque, plantación de *Vernicia fordii* y cultivos, y sus respectivos ecotonos, en los patrones de distribución de anfibios en el Parque Nacional San Rafael. Se realizaron ocho viajes entre junio de 2012–abril de 2013 y se utilizaron trampas pozo con cercas de conducción. Se registraron ocho especies pertenecientes a las familias Bufonidae, Leptodactylidae y Odontophrynidae. Las variables ambientales correlacionadas con la abundancia de anfibios fueron la humedad relativa, la profundidad del mantillo, la cobertura herbácea y la temperatura del aire; y se encontraron diferencias significativas en la composición de las especies. Especies generalistas como *Leptodactylus mystacinus* y *Physalaemus cuvieri* fueron abundantes en zonas alteradas, como cultivo y plantación de tung. *Rhinella ornata* y *Proceratophrys avelinoi* se encontraron restringidos a los bosques primarios, y se consideran sensibles a la degradación de los bosques. Nuestros resultados apoyan la idea de que los hábitats modificados influyen en los patrones de distribución de los anfibios, y la protección de los remanentes de Bosque Atlántico es un paso crítico en la conservación de la biodiversidad de anuros en Paraguay.

## INTRODUCTION

San Rafael National Park covers an area of approximately 73,000 ha and is part of the Atlantic Forest ecoregion, specifically the Upper Paraná Atlantic Forest (Dinerstein et al., 1995). This ecoregion extends from southeastern Brazil to northeastern Argentina and eastern Paraguay (Dinerstein et al., 1995; Fragano and Clay, 2003), and is considered a global biodiversity hotspot (Olson and Dinerstein, 2002). In Paraguay, just 10% of the original Atlantic Forest cover remains and deforestation rates remain high, despite the “Zero Deforestation Law” 2524/04, which aims to promote the protection, recovery, and improvement of the native forest in the Eastern Region of the country (Da Ponte et al., 2017).

The greatest modification of the forest landscape occurred between 1960–2002, primarily due to the expan-

sion of agriculture and cattle ranching and an increase in poorly planned human settlements (Cartes, 2005; World Wildlife Fund, 2016). These anthropogenic activities affect protected areas by turning them into isolated ecological islands, especially in eastern Paraguay (Huang et al., 2009). San Rafael National Park is one of the four key areas for the conservation of the Upper Paraná Atlantic Forest in Paraguay; in 1992 it was declared as an “Area reserved for a National Park” and in 2002 its category was changed to “Managed Resources Reserve”, which was then reversed in the 2005 (Esquivel et al., 2007). Despite its conservation status, the massive forest loss in surrounding areas of the SRNP has impacted the buffer zone of the park, modifying the core zones in some cases (Huang et al., 2007).

Changes in forest cover can cause the decline or loss of many species that are endemic to these systems, since

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the altered areas have vegetation in different degrees of succession and are surrounded by crop fields and rangelands with poor vegetation richness and low biomass (Saunders et al., 1991; Osorno, 1999; Guariguata and Ostertag, 2002; Urbina-Cardona et al., 2008). Organisms that remain in fragmented areas are exposed to edge-effect conditions and environmental gradients through which certain abiotic factors fluctuate (Ries et al., 2004; Suárez et al., 2016). Abiotic changes include decreased moisture availability, increased temperature and solar radiation in the most exposed sites, and increased canopy gaps due to wind disturbance (Murcia, 1995; Schlaepfer and Gavin, 2001; Harper et al., 2005). All these changes can generate cascade effects that promote the establishment of opportunist and generalist species and the loss of specialist ones, leading to new interactions in the systems (Ries et al., 2004). These changes can also result in high biodiversity values due to the richness and abundance of generalist species (De la Sancha, 2014).

Amphibians are a good group to study these effects because they are sensitive to different environmental variables (Pearman, 1997; Tewksbury et al., 2008; Suárez et al., 2016; Nowakowski et al., 2017a) and have moderate mobility (Schlaepfer and Gavin, 2001). Amphibians are thermal-conformers with a moist, well-vascularized skin that allows cutaneous respiration that brings them into intimate contact with their environment and makes them sensitive to changes in air humidity and temperature (Tewksbury et al., 2008; Wake and Vredenburg, 2008; Nowakowski et al., 2017a).

Significant changes in composition and richness of amphibians have been reported in the tropics due to changes in environmental variables, microhabitat structure and vegetation types (Crump, 1971; Fauth et al., 1989; Heinen, 1992; Pearman, 1997; Rodrigues et al., 2016; Suárez et al., 2016; Nowakowski et al., 2017a, b). Furthermore, amphibians are among the most endangered vertebrates in the world (Wake and Vredenburg, 2008; Barnosky et al., 2011; Alroy, 2015) due to a combination of anthropogenic causes such as habitat modification, climate change, invasive predators, and outbreaks of infectious diseases (Pounds et al., 1999, 2006; Becker et al., 2007; Whitfield et al., 2007; Wake and Vredenburg, 2008; Almeida-Gomes and Rocha, 2015; Carvalho et al., 2017; Nowakowski et al., 2017b). Understanding the response of amphibians to changes in their habitats provides baseline information to implement effective conservation strategies (Santos-Barrera and Urbina-Cardona, 2011; Suárez et al., 2016). In this context, the effects of landscape changes on amphibian populations in one of the last large remnants of Upper Paraná Atlantic Forest in Paraguay were evaluated, with two main objectives: (1) to study the effects of different land uses on amphibian community composition, and (2) to analyze the response of individual amphibian species to environmental variables.

## MATERIALS AND METHODS

### Study site

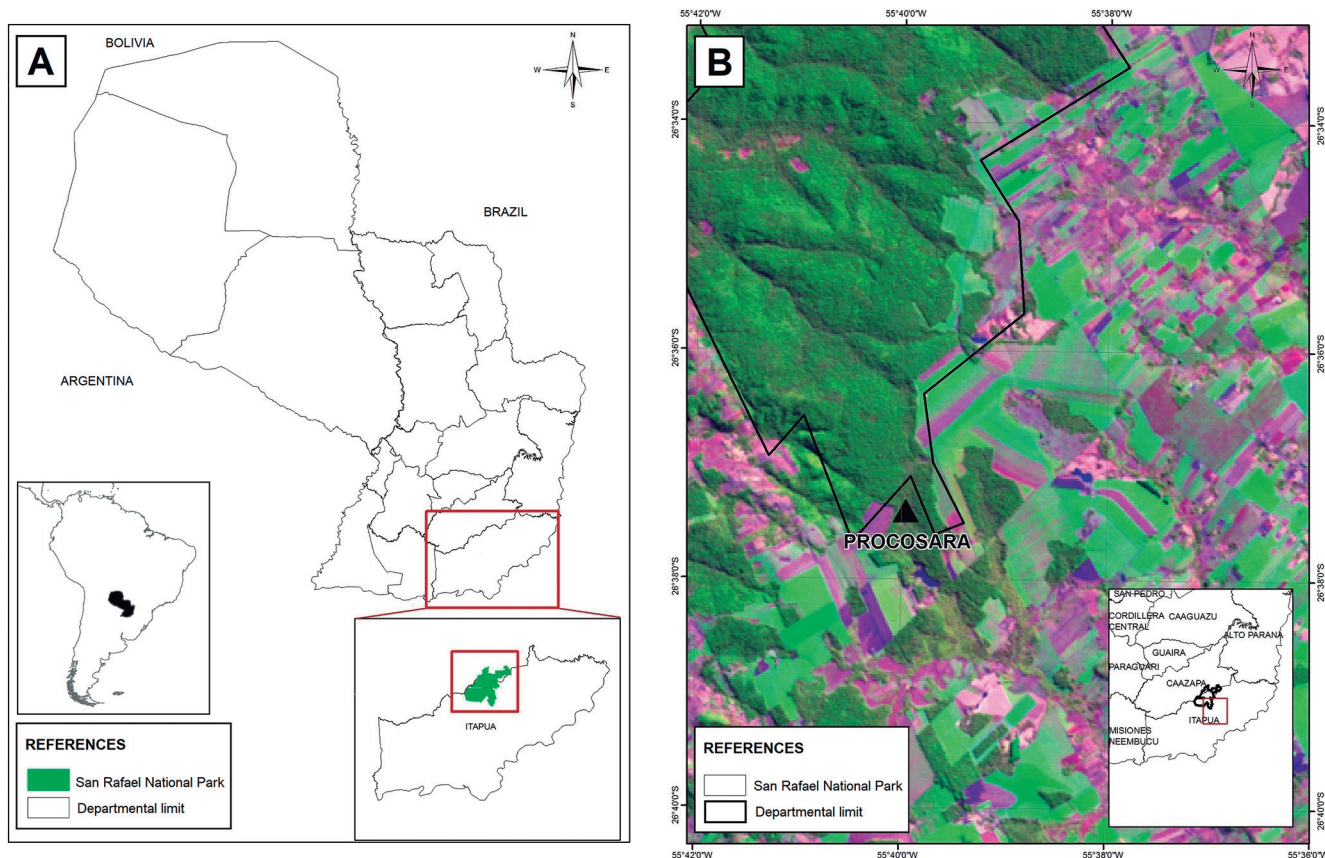
We carried out field research in PROCOSARA (Asociación Pro Cordillera San Rafael; 26°37'S, 55°40'W), a private property at the southern tip of San Rafael National Park (SRNP), situated in Itapúa Department, eastern Paraguay (Fig. 1). The property covers 440 ha within the San Rafael mountain range (Cartes, 2005). Rainfall averages 2,100 mm per year and the mean temperature is 17°C in the coldest periods and 23.8°C in the hottest months (Esquivel et al., 2007).

The basaltic soils of eastern Paraguay sustain environments comprised of streams, waterfalls, ponds, dense forests, riparian forests, and grasslands, which are associated with a great diversity of flora and fauna (Galindo-Leal and Gusmão-Câmara, 2005; Clay et al., 2008). The dominant vegetation type in SRNP is a semi-deciduous sub-tropical forest (Esquivel et al., 2007), but forest edges, ecotones, and plantations have been increasing in the last decades (Huang et al., 2009).

### Sampling methods

To assess richness, abundance and composition of the anuran community in the study site we delimited four main habitats from pristine forest to altered areas based on vegetation composition and structure. (1) Primary forests (26°37'10.9"S, 55°40'27.36"W): complex stratification, with a main canopy up to 18 m high with isolated emergent trees up to 30 m, dominated by *Apuleia leiocarpa* (Vogel) J.F. Macbr., *Holocalyx balansae* Micheli, *Inga uraguensis* Hook. and Arn., and *Jacaratia spinosa* (Aubl.) A. DC.; (2) ecotonal secondary forest (26°37'22.64"S, 55°40'20.48"W): two poorly differentiated strata dominated by light-demanding tree species, such as *Balfourodendron riedelianum* (Engl.), *Bastardiopsis densiflora* (Hook. and Arn.) Hassl., and *Cecropia pachystachya* Trécul in the highest stratum (12–20 m), and a low stratum invaded by the shade-tolerant *Chusquea ramosissima* Lindm.; (3) Tung plantations of *Vernicia fordii* (Hemsl.) Airy Shaw (26°37'32.24"S, 55°40'8.39"W): introduced and cultivated for oil production, with a canopy of 10 m and no stratification; and (4) crops (26°37'28.80"S, 55°40'14.79"W): areas with two harvests per year in rotational cultivation of *Triticum* spp. L. (wheat) and *Glycine max* (L.) (soy).

We used pitfall traps with drift fences (Corn, 1994; Dixo and Martins, 2008) to collect amphibians: five in primary forests, four in ecotonal secondary forest, two in tung plantations and two in crops (differences in sample size were due to differences in the extent of the habitats studied). The distance between trap arrays was at least 50 m to ensure independence, and they were located far



**Figure 1.** Location of San Rafael National Park (SRNP). **(A)** Position of Paraguay in South America and map of Paraguay highlighting Itapúa department and SRNP shaded green, **(B)** Satellite image of SRNP showing land use (dark green: forest; pale green: pastures; purple: crops).

from breeding sites to avoid biases (Willson and Gibbons, 2010). We placed the pitfall traps in a Y format (Ribeiro-Júnior et al., 2011), with buckets of 20 L, 390 mm deep, connected with plastic fences 5 m long and 60 cm high. Forest sampling was performed more than 100 m inside the forest border to avoid edge effects (Corlett and Primack, 2011).

We conducted eight periods of fieldwork from June 2012–April 2013 (all months except July and August), including the rainy and dry seasons. Every trap array was opened for five consecutive nights and checked once a day, every morning, with a total sampling effort of 520 pitfall-trap array nights. Climbing amphibians were not included in this study since they can use the buckets as shelter and escape (Saccol et al., 2017). All captured amphibians were collected according to national regulations and deposited in the Colección Zoológica de la Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Asunción, San Lorenzo (FACEN). Next to each pitfall array, we established five plots of  $1 \times 1 \text{ m}^2$ , with plots located every 10 m along a 50 m transect to register the percentage of herbaceous and soil cover (Villarreal et al., 2006). Additionally, litter depth was measured to the nearest millimeter in five random points per plot and averaged. Air temperature (AT) and relative humidity (RH) were

measured during each five-day period with an Easylog data logger (Lascar Electronics) and averaged per pitfall array. We also measured the distance of each pitfall array to the nearest forest edge.

Climatic data (monthly precipitation and monthly mean temperature) were obtained from the CRU TS v. 4.01 gridded time-series dataset (Harris et al. 2014) using the KNMI Climate Explorer tool (KNMI, 2016).

### Data analysis

We performed a principal component analysis (PCA) to characterize the relationship between the environmental variables (centered and standardized) and each sampling station. To estimate amphibian richness, we used the non-parametric approach of Chao 1 (Chao 1987; Colwell and Coddington 1994). To measure the difference in species composition we used non-metric multidimensional scaling (NMDS) with two dimensions and the Bray-Curtis distance as a measure of dissimilarity (Quinn and Keough, 2002; Kindt and Coe, 2005; Oksanen, 2015). Additionally, we performed an analysis of similarities (ANOSIM) to test differences in the composition of amphibians between the four different habitats (Clarke, 1993). We also tested if

**Table 1.** Eigenvalues for each axis generated in the PCA analysis of the measured environmental variables.

	PC1	PC2	PC3	PC4	PC5	PC6	PC7
Eigenvalue	3.71	1.3455	0.8324	0.51225	0.42899	0.11921	0.05189
Proportion explained	0.53	0.1922	0.1189	0.07318	0.06128	0.01703	0.00741
% proportion explained	0.53	0.7222	0.8411	0.91427	0.97556	0.99259	1

composition dissimilarity measured with the Bray-Curtis distance was correlated with the distance between pitfall arrays using the Mantel test with the Pearson's product moment correlation, with 1,000 permutations.

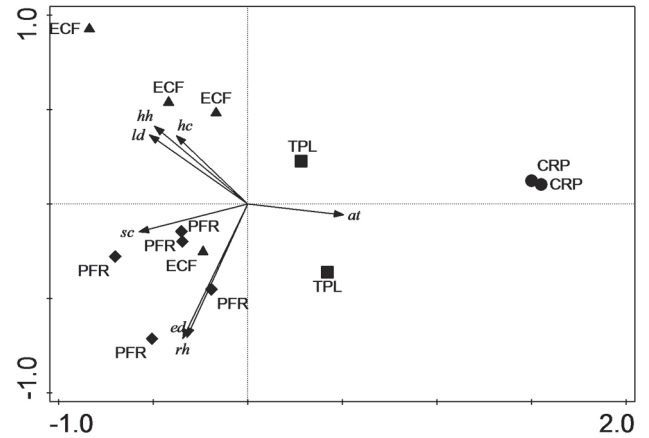
We analyzed the relationship between the abundance of amphibian species and environmental variables using generalized linear models (GLMs). Only species with at least five records were used in the binomial negative model (Kindt and Coe, 2005). We analyzed the correlation between all environmental variables using the Pearson coefficient, and environmental variables with correlations higher than 0.6 were eliminated except one, which resulted in variance inflation factors (VIF) being always less than 2 units and no collinearity in our models. The environmental variables we selected were average RH, average AT, litter depth, and herbaceous cover. The best model for each species was chosen through backward selection. First, full models with all the variables were performed and then checked with a type-II analysis of variance (ANOVA) to see if the deletion of each variable resulted in a lower value of Akaike's Information Criterion (AIC; Kindt and Coe, 2005). We followed the rule that an increase of at least 2 AIC units after the elimination of any given predictor variable from the full model indicates a significant effect of this predictor on the dependent variable (Burnham and Anderson, 1998).

Data analyses were performed with the package *vegan* (Oksanen, 2015) using the BiodiversityR graphical user interface (Kindt and Coe, 2005) in the R environment (R Development Core Team, 2011). The Chao 1 estimator was calculated using EstimateS 9.1.0 (Colwell, 2013).

## RESULTS

### Environmental variables

In the PCA, the first and second axis explained 53.0% and 19.2% of the total variance, respectively (Fig. 2, Table 1). The first axis appeared strongly correlated with AT, with the more anthropogenic sites (crops and tung plantations) being warmer than primary and ecotonal forest. Distance edge and RH were correlated with the second axis and separated the more humid primary forests from the ecotonal forests in the left side of the PCA (Fig. 2). Herbaceous vegetation height and cover and litter depth scored higher for ecotonal forest and lower for crops and tung plantations (Fig. 2).



**Figure 2.** PCA ordination biplot of the study sites based on the measured environmental variables. Habitat types: Primary Forest (PFR, diamonds), Ecotonal Forest (ECF, triangles), Tung Plantations (TPL, squares), and Crops (CRP, circles). Environmental variables: air temperature (*at*), distance to the edge (*ed*), herbaceous cover (*hc*), herbaceous cover height (*hh*), litter depth (*ld*), relative humidity (*rh*), and soil cover (*sc*).

A total of 64 individuals of 8 species were captured, corresponding to the families Bufonidae Gray, 1825, Leptodactylidae Werner, 1896 and Odontophrynidae Lynch, 1969 (Table 2). The most abundant species were *Rhinella ornata* (Spix, 1824), which accounted for 46.9% ( $n = 30$ ) of the captures, followed by *Physalaemus cuvieri* Fitzinger, 1826 (15.7%,  $n = 10$ ) and *R. diptycha* (Cope, 1862) (11%,  $n = 7$ ). *Leptodactylus elenae* Heyer, 1978 and *Melanophryniscus devincenzii* Klappenbach, 1968 were represented only by one individual captured each.

The largest number of individuals and species were recorded in October, which coincides with the period of greatest rainfall registered in the area (Fig. 3). The species found in that period were *Rhinella ornata*, *Odontophrynus americanus* (Duméril and Bibron, 1841), *Proceratophrys avelinoi* Mercadal de Barrio and Barrio, 1993, *Physalaemus cuvieri*, *Leptodactylus mystacinus* (Burmeister, 1861), and *L. elenae*.

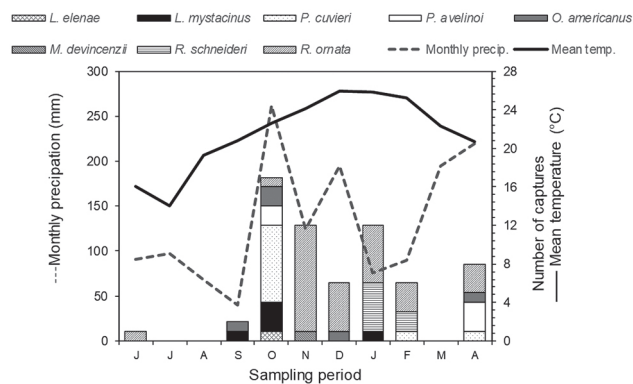
The Chao 1 estimator shows that all species expected in forest and ecotone were found (Table 3). Regarding

**Table 3.** Number of species observed per habitat (S obs.) and Chao 1 richness estimators for terrestrial anurans in SRNP.

Habitat	S obs.	Chao 1
Forest	6	6
Ecotone	6	6
Plantation	4	7
Crop	4	5

**Table 2.** Species of amphibians registered in SRNP (Paraguay). Conservation Status of each species is shown accordingly to the IUCN Red List. EN: Endangered; LC: Least Concern; VU: Vulnerable (\* Critically Endangered according to 525/06 SEAM legal resolution).

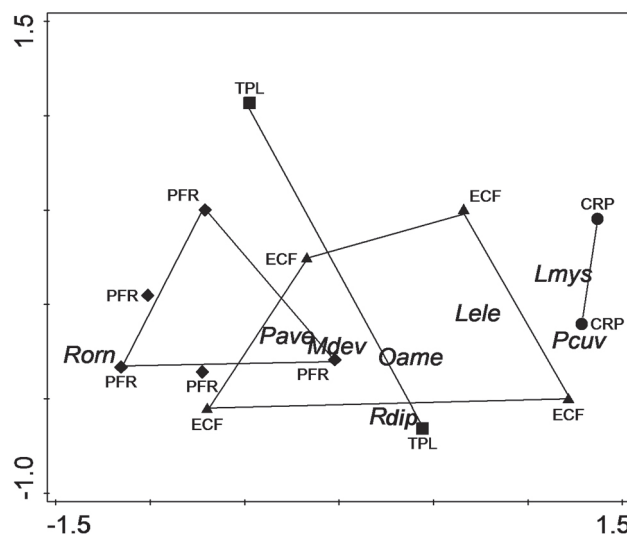
Taxa	Common names (Spanish, Guaraní, English)	IUCN status	Motte et al., 2009	Number of individuals			
				Forest	Ecotone	Plantation	Crop
<b>Leptodactylidae</b>							
1. <i>Leptodactylus elenae</i>	Rana marmolada, Ju'i, Marbled White-lipped frog	LC	LC				1
2. <i>Leptodactylus mystacinus</i>	Rana de bigotes, Ju'i, Moustached frog	LC	LC		3		2
3. <i>Physalaemus cuvieri</i>	Rana ladradora, Ju'i, Barker frog	LC	LC	2	4	1	3
<b>Odontophrynidae</b>							
4. <i>Odontophrynus americanus</i>	Escuercito chico, Kururú chini, Common lesser escuerzo	LC	LC	2	1	1	1
5. <i>Proceratophrys avelinoi</i>	Escuercito, Ju'i, Avelino's smooth horned frog	LC	VU*	3	2		
<b>Bufoidea</b>							
6. <i>Melanophryniscus devincenzii</i>	Sapito de panza roja, Toky tosyry, Rivera redbelly toad	EN	-		1		
7. <i>Rhinella ornata</i>	Sapo franjeado, Kururú, Stripped toad	LC	LC	21	8	1	
8. <i>Rhinella diptycha</i>	Sapo común, Kururú, Cururu toad	LC	LC	1	3	3	



**Figure 3.** Monthly variation of the richness and abundance of terrestrial anuran species compared to the monthly average temperature and the accumulated monthly precipitation in the PNSR.

plantations and crops, fewer species than expected were found (Table 3). According to Chao 1, tung plantations should be richest and crops the poorest.

The dissimilarities between sites were shown through the NMDS graph, which presented a low stress value of 0.085 (Fig. 4). Low dissimilarities were found among primary forest sites, which were mainly represented by *Proceratophrys avelinoi* and *Rhinella ornata*. The ecotonal forest sites were scattered in the multidimensional space, sharing species with primary forests, tung plantations, and crops. Tung plantations did not show a consistent pattern, sharing most of their species with the ecotonal forests. The crop areas were represented by *Leptodactylus mystacinus* and *Physalaemus cuvieri*, which were also common in ecotonal forests. The ANOSIM test showed significant differences in anuran composition between the four evaluated habitats ( $P = 0.019$ ,  $R = 0.3861$ ), confirming the results obtained with the NMDS. The Mantel test did not show that dissimilarities in the com-



**Figure 4.** Non-metric multidimensional scaling (NMDS) graph grouping the habitats sampled in SRNP (Itapúa, Paraguay) according to the abundance of terrestrial anurans, Stress value: 0.085. Habitat types: Primary Forest (PRE, diamonds), Ecotonal Forest (EST, triangles), Tung Plantations (TPL, squares) and Crops (CRP, circles). Anuran species: *Rhinella ornata* (Rorn), *R. diptycha* (Rdip), *Proceratophrys avelinoi* (Pave), *Melanophryniscus devincenzii* (Mdev), *Odontophrynus americanus* (Oame), *Leptodactylus mystacinus* (Lmys), *L. elenae* (Lele), *Physalaemus cuvieri* (Pcuv).

position were correlated with distances between sites ( $P = 0.15601$ ,  $r = -0.18$ ).

### Abundance and environmental variables

*Rhinella ornata* and *Proceratophrys avelinoi* abundances were positively related to RH and litter depth, with an additional and positive effect of herbaceous cover for the

**Table 4.** Summary of the results obtained in binomial negative models using abundance of amphibians in SRNP as a response.  $\Delta$ AIC is shown in relation to the full model. Environmental variables: Air Temperature (AT), Relative Humidity (RH), Litter Depth (LD), Herbaceous Cover (HC).

Species	AIC	$\Delta$ AIC	Best Model	% Explained deviance
<i>Rhinella ornata</i>	47.10	-2.35	$-60.97 + 0.94 \cdot RH + 0.25 \cdot LD$	70.5
<i>Proceratophrys avelinoi</i>	21.07	-3.32	$-25.44 + 3.68 \cdot RH + 2.03 \cdot LD + 0.09 \cdot HC$	74.6
<i>Odontophrynus americanus</i>	26.97	-3.85	$-158.53 + 3.21 \cdot AT + 1.05 \cdot RH$	47.2
<i>Rhinella diptycha</i>	27.70	0	$75.62 - 24.82 \cdot AT - 0.83 \cdot RH - 4.83 \cdot LD - 0.18 \cdot HC$	64.7
<i>Physalaemus cuvieri</i>	36.52	-5.46	$37.36 - 0.59 \cdot RH$	32.0
<i>Leptodactylus mystacinus</i>	22.94	-3.61	$64.36 - 1.02 \cdot RH$	45.6

latter species. In both species, the models explained more than 70% of the null deviances (Table 4). *Odontophrynus americanus* abundance was also positively correlated with RH, but also with AT. However, abundance of *R. diptycha* was negatively correlated with RH and additionally with litter depth and herbaceous cover. Both *Physalaemus cuvieri* and *Leptodactylus mystacinus* showed a significant relationship with RH, showing increasing abundance in drier sites (Table 4).

## DISCUSSION

In the study site, bufonids and leptodactylids were well represented, especially the former. Due to their large body size, parotoid glands, opportunistic oviposition, and generalist diet, bufonids tend to have broad distributions and greater abundance and have been shown to be more active and able to move greater distances compared to sympatric species (Toft, 1981; Strüssmann et al., 1984; Almeida-Gomes et al., 2008; Duré et al. 2009; Van Bocxlaer et al., 2010).

Our study showed that species-specific responses to the environmental variables resulted in characteristic anuran assemblages in each habitat type. The environmental variable that most affected anuran abundance was RH, with all six modeled species showing responses to it. Litter depth, AT, and herbaceous cover were also significant environmental variables (Table 2). Studies in Atlantic Forest regions in Brazil have also found a positive correlation between the abundance of leaf-litter frogs and RH and litter depth (Van Sluys et al., 2007; Oliveira et al., 2013). The high values of these variables indicate the suitability of the microhabitats available for amphibians; since they are a source of food and shelter (Duellman and Trueb, 1994; deMaynadier and Hunter, 1998). Rodrigues et al. (2016) showed that AT is an important factor in the structure of anuran assemblages in the Atlantic Forest, generally with a negative correlation due to the increase in desiccation risk. Surprisingly, the relationship between herbaceous cover and abundance of amphibians has been poorly studied in tropical forests of the region.

Primary forest sites not exposed to edge effects were characterized by low AT and the highest RH values. These sites held the highest abundances of *Rhinella ornata* and

*Proceratophrys avelinoi*, which were also present but less abundant in the drier ecotonal forests. *Rhinella ornata* is a common species in forested habitats (Baldissera et al., 2004; Maia-Carneiro et al., 2013; D'Anunção et al., 2013; Baldi et al., 2015), and its dependence on high RH can be explained by its low resistance to evaporative water loss (Prates and Navas, 2009). Litter depth was also positively correlated with *R. ornata* abundance and is considered a key microhabitat resource, as shown in other tropical forest anurans (Whitfield et al., 2007, 2014). Although its displacement capacity and ecological plasticity enable *R. ornata* to move through open areas (Bertoluci et al., 2009; D'Anunção et al., 2013), its abundance is sensitive to agricultural uses due to exposure to herbicides, high radiation, and low air humidity (D'Anunção et al., 2013), as demonstrated by the absence of this species from the crop and tung plantations. In Paraguay, *R. ornata* populations can be considered potentially threatened by the increase of agricultural expansion and habitat transformation. In the Atlantic Coastal Forest, some populations undergo genetic erosion due to habitat fragmentation and their close relationship with forested habitats (Dixo et al., 2009; Gomes dos Santos et al., 2012).

*Proceratophrys avelinoi* is restricted to forests with tall, dense vegetation (Kwet and Faivovich, 2001), high RH, abundant leaf litter, and well-developed understory cover. In Paraguay, it is only known from two localities: SRNP (Brusquetti and Lavilla, 2006) and Reserva Limoy in Alto Paraná department (Carosini et al., 2010). According to the International Union for Conservation of Nature (2009), its global conservation status is Least Concern (LC), but at the national level the species is considered Vulnerable (VU) due to threats to its habitat (Motte et al., 2009; Table 2). We agree with the national categorization of the species on the basis of the knowledge that its habitat is restricted to areas with low anthropogenic disturbance. Our data clearly indicate that *Rhinella ornata* and *P. avelinoi* are primarily restricted to primary forests, and that their abundances are highly sensitive to forest lost and degradation.

The anthropic habitats, such as the ecotonal forest, tung plantations, and crops, were dominated by a different assemblage of species (e.g., *Leptodactylus mystacinus*, *Physalaemus cuvieri*, and *Rhinella diptycha*), which showed abundance negatively correlated with RH. A common

trait shared among these three habitats is a lower RH compared to the primary forest, due to degradation or total elimination (in crops) of the canopy cover. *Leptodactylus mystacinus* was previously recorded in plantations of corn, soybeans, and rubber tree (Rodrigues da Silva et al., 2009). It has been proposed that this species is a generalist, tolerant of and rapidly adjusting to non-forest habitat (D’Anuniação et al., 2013; Sanchez et al., 2013; Suárez et al., 2016). *Leptodactylus mystacinus* was more abundant in highly modified agricultural areas in fragmented landscapes, which might indicate that certain levels of agriculture activities provide more resources to this species, such as prey items and sites for reproduction (Suárez et al., 2016).

*Physalaemus cuvieri* is common in flooded savannas and benefits from the creation of open areas, colonizing forest fragments and forest edges (Haddad, 1998; Dixo and Verdade, 2006; Mijares et al., 2010; D’Anuniação et al., 2013; Baldi et al., 2015). *Rhinella diptycha* is considered tolerant to habitat changes and is representative of urban and suburban areas (Aquino et al., 2004; Motte et al., 2009). However, Suárez et al. (2016) consider it a sensitive species, negatively affected by agricultural modification and rural housing density. We found *R. diptycha* associated mainly with ecotonal forest and tung plantations, habitats with lower RH than primary forest, but also lower AT than crop areas, where it was absent. Our data indicate that, although tolerant to forest degradation, it is negatively affected by AT, which could preclude *R. diptycha* survival in open areas, such as agricultural fields.

*Odontophrynus americanus* showed a more complex pattern that was positively associated with RH and AT. It was found in all sampled habitats, as it can colonize modified habitats such as pastures and open areas (Aquino et al., 2010; Sanchez et al., 2013). This fossorial anuran has low detectability, given that it spends much of the year buried and only emerges after heavy rains, undergoing a short period of high breeding activity at most every 2 a or more (Gallardo, 1963; Martori et al., 2005; Suárez et al., 2016). The low abundance of *Leptodactylus elenae* and *Melanophryniscus devincenzii* did not allow a determination of the distribution pattern of these species in SRNP. The former species does not adapt as well as other leptodactylids to anthropogenic disturbance, but it is still found in cattle areas and open formations (Heyer et al., 2004; Piatti and Souza, 2011). In Paraguay, *M. devincenzii* is associated with forest and natural grasslands (Núñez, 2012), but as with *L. elenae*, more studies are needed to evaluate the effect of habitat modification on its abundance.

Lastly, of particular note was the low overall abundance of anurans captured in pitfall traps. Capture efficiency was only 0.12 individuals per pitfall trap-night (primary forest showed the highest level of 0.15 anurans), while other studies in similar tropical forests and compa-

rable sampling protocols have reported capture efficiencies of 0.28–0.30 individuals per pitfall trap-night (Dixo and Martins, 2008; D’Anuniação et al., 2013). Although identifying the cause(s) of this situation is beyond the scope of this work, amphibians are showing alarmingly declines both in modified and well-preserved habitats in many regions of the world (Pounds et al., 1999, 2006; Becker et al., 2007; Whitfield et al., 2007, Wake and Vredenburg, 2008; Almeida-Gomes and Rocha, 2015; Carvalho et al., 2017; Nowakowski et al., 2017b). This study showed that variation in environmental factors linked to landscape use change affect the abundance and composition of anuran assemblages. Other related causes, like pesticide impacts, climate change, or chytrid infections, were not considered in this work but deserve detailed study to elucidate responses.

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