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Predicting geographic distributions of *Phacellodomus* species (Aves: Furnariidae) in South America based on ecological niche modeling

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ABSTRACT. *Phacellodomus* Reichenbach, 1853, comprises nine species of Furnariids that occur in South America in open and generally dry areas. This study estimated the geographic distributions of *Phacellodomus* species in South America by ecological niche modeling. Applying maximum entropy method, models were produced for eight species based on six climatic variables and 949 occurrence records. Since highest climatic suitability for *Phacellodomus* species has been estimated in open and dry areas, the Amazon rainforest areas are not very suitable for these species. Annual precipitation and minimum temperature of the coldest month are the variables that most influence the models. *Phacellodomus* species occurred in 35 ecoregions of South America. Chaco and Uruguayan savannas were the ecoregions with the highest number of species. Despite the overall connection of *Phacellodomus* species with dry areas, species such as *P. ruber*, *P. rufifrons*, *P. ferrugineigula* and *P. erythrophthalmus* occurred in wet forests and wetland ecoregions.

Keywords: Synallaxinae, climatic variables, ecoregions, maxent.

Predição das distribuições geográficas das espécies de *Phacellodomus* (Aves: Furnariidae) na América do Sul utilizando modelagem de nicho ecológico

RESUMO. *Phacellodomus* Reichenbach, 1853 é composto por nove espécies de furnarídeos que ocorrem na América do Sul em áreas abertas e geralmente secas. Este estudo objetivou estimar as distribuições geográficas das espécies de *Phacellodomus* utilizando modelagem de nicho ecológico. Os modelos foram desenvolvidos com base em seis variáveis climáticas e 949 registros de ocorrência de oito espécies, utilizando o algoritmo Maxent. Maior adequabilidade climática para as espécies de *Phacellodomus* foi estimada em áreas abertas e secas. Áreas úmidas na Amazônia não foram muito favoráveis para a ocorrência dessas espécies. A precipitação anual e a temperatura mínima do mês mais frio foram as variáveis que mais influenciaram os modelos. As espécies de *Phacellodomus* ocorreram em 35 ecorregiões da América do Sul. O Chaco e as savanas do Uruguai foram as ecorregiões com o maior número de espécies. Apesar da ampla ocorrência das espécies *Phacellodomus* em áreas secas, espécies como *P. ruber*, *P. rufifrons*, *P. ferrugineigula* e *P. erythrophthalmus* ocorreram em florestas úmidas e ecorregiões alagadas.

Palavras-chave: Synallaxinae, variáveis climáticas, ecorregiões, maxent.

Introduction

Distribution and abundance of bird species depend on climatic characteristics and variability within temporal and spatial dimensions (WATKINSON et al., 2004). The influence of climatic variables on the distribution of organisms may be investigated by ecological niche modeling (ENM). Several ENM methods have been used to estimate the potential distributions of species based on occurrence points and on the analysis of environmental variables (TSOAR et al., 2007). Although EMN has been widely used to predict the distribution of bird species (ANCIÃES; PETERSON, 2009; CORREA et al., 2010; ECHARRI et al., 2009; FERIA; PETERSON, 2002; GRAHAM et al., 2010; LEE et al., 2010; MARINI et al., 2009; MARINI et al., 2010a, b; SCHIDELKO, et al., 2011; STRUBBE; MATTHYSEN, 2009), no studies examining ecological niches of *Phacellodomus* spp. (Aves, Furnariidae, Synallaxinae) have yet been developed. Such information and knowledge may be a great help in planning bird conservation strategies and may also be applied in health sciences since *Phacellodomus* nests are the habitats for some triatomine species which are vectors of Chagas´ disease (DI IORIO; TURIENZO, 2009; GURGEL-GONÇALVES et al., 2012).

The genus *Phacellodomus* was described by Reichenbach in 1853. Later, Vaurie (1980) reviewed ecological, behavioral and geographical variation of 10 species. Some of these species were later included in the genera *Thripophaga* Gray, 1849, and *Clibanornis* (Pelzeln, 1859) (RIDGELY; TUDOR, 1994). Since two subspecies were later elevated to species (NORES; YZURIETA, 1981; SIMON et al., 2008), the genus *Phacellodomus* is actually comprised by nine species.

Phacellodomus species occur in South America in open and generally dry areas (VAURIE, 1980). Some species, such as *P. ruber* (Vieillot, 1817), are associated with more humid environments. *Phacellodomus striaticeps* (Orbigny & Lafresnaye, 1838) and *P. maculipectus* Cabanis, 1883, occur in mountain areas at 2500-4200 m altitude. *Phacellodomus rufifrons* (Wied, 1821) has a discontinuous distribution (RIDGELY; TUDOR, 1994). These variations in the geographic distribution of *Phacellodomus* may be explored by using spatial analysis methods that consider ecological preferences of each species to better understand the distribution patterns. Current study aims at predicting the geographic distributions of *Phacellodomus* species in South America.

Material and methods

Distributional data

Distributional data for *Phacellodomus* species in South America was obtained from Naumburg (1930), Short (1975), Barnett et al. (1998), Robbins et al. (1999), Braz and Cavalcanti (2001), Accordi (2003), Belton (2003), Willis (2003), Farias (2002), Gussoni and Campos (2004), Ribon (2004), Ridgely et al. (2005), Maia-Gouvêa (2005), Gagliardi and Pacheco (2011), Gurgel-Gonçalves and Silva (2009), Gurgel-Gonçalves and Cuba (2011), and Gurgel-Gonçalves et al. (2012). The distributional data for *Phacellodomus* species available in museums were also analyzed, among which may be mentioned Royal Ontario Museum, Natural History Museum of Los Angeles County, Museum of Comparative Zoology of Harvard University, Delaware Museum of Natural History, Kansas University Natural History Museum, University of Michigan Museum of Zoology, National Museum of Natural History, US. The above data were obtained from the Global Biodiversity Information Facility - GBIF (http://data.gbif.org) and complementary summaries of geographic distributions of *Phacellodomus* species were obtained from Vaurie (1980) and Ridgely and Tudor (1994).

Records of nine *Phacellodomus* species that could be referenced to geographic coordinates with a reasonable degree of confidence (i.e., with an uncertainty of < 5 km, to a precision of 0.01°) were compiled. Records were georeferenced based on http://www.fallingrain.com/world. An occurrence data sample size criterion of 20 unique latitude-longitude points per species were set as a minimum to permit robust ENM development, based on previous analyses (STOCKWELL; PETERSON, 2002).

Ecological niche modeling

ENM uses associations between environmental variables and known occurrences of species to identify environmental conditions where populations may be maintained (TSOAR et al., 2007). Environmental datasets consisted of ‘bioclimatic’ variables characterizing climates during the 1950-2000 period, drawn from the WorldClim data archive (HIJMANS et al., 2005). The environmental database used in current analyses covers all South America at a spatial resolution of 2.5’ (5 km). To avoid confounding effects of calibrating models in an overly dimensional environmental space (PETERSON; NAKAZAWA, 2008), only a subset of the 19 ‘bioclimatic’ variables in the climatic data file was chosen: annual mean temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, annual precipitation, precipitation of the wettest month, and precipitation of the driest month. According to Schidelko et al. (2011), these parameters mainly affect thermophile passerines in tropical and subtropical environments and represent dimensions in which potential physiological limits may be manifested.

Occurrence data were separated into two sets, one for model calibration (75% of points) and the other for model evaluation (25% of points). ENM-based distribution maps were produced using the maximum entropy method (PHILLIPS et al., 2006) as implemented in Maxent v. 3.3.3 selecting default parameters which are considered appropriate for most situations (PHILLIPS; DUDÍK, 2008). Maxent software for species habitat modeling has been shown to perform well, in particular when sample size is low (HERNANDEZ et al., 2006). To emphasize the fact that omission error takes considerable precedence over commission error in niche modeling applications, a modified version of the least training presence thresholding approach was used (PEARSON et al., 2007). Specifically, models were thresholded at the suitability level that included 90% of the occurrence records of each species used in model calibration (PETERSON et al., 2008). All maps were edited using ArcView version 3.3 (ESRI, 2002).

Data analysis

The quality of the models generated was evaluated using the Receiver Operating Characteristic (ROC) curve, which relates two characteristics of model performance, namely, sensitivity and specificity (PHILLIPS et al., 2006). Sensitivity is defined as the proportion of true presences in relation to the total number of presences predicted by the model. It is also a measure of the absence of omission error; good quality models should show greater sensitivity. Specificity is the proportion of true absences in relation to the total number of absences predicted by the model; 1 - specificity is a measure of the degree to which predicted areas exceed observed occurrence. The area under this curve (AUC) provides a measure of model performance, ranging between zero and one: AUCs close to 1 indicate high performance, while readings around 0.5 indicate poor performance (ELITH et al., 2006).

The predictive power of the models was also compared with a random null hypothesis. The developed model was checked to see whether test points fell into areas predicted to be present more often than expected at random, given the overall proportion of pixels showing predicted presence vs. predicted absence for that species. In addition to the model significance (departure from random predictions), model accuracy was assessed by examining the proportion of test points falling into regions of predicted presence (ANDERSON et al., 2002).

Using the Jackknife test and adopting procedures described by Pearson et al. (2007), variables that most influenced the distribution of the species of *Phacellodomus* were identified. Additionally, an analysis was made by reporting the presence of *Phacellodomus* species within the terrestrial ecoregions of Latin America (WWF, 2012). An intersection between the distribution range of *Phacellodomus* species and the terrestrial ecoregions shapefile was designed with ArcView v 3.3.

Results

In all, 949 records of *Phacellodomus* species were analyzed: *P. dorsalis* Salvin, 1895 (n = 7); *P. erythrophthalmus* (Wied 1821) (n = 117); *P. ferrugineigula* (Pelzeln, 1858) (n = 77); *P. maculipectus* (n = 27); *P. ruber* (n = 227); *P. rufifrons* (n = 256); *P. sibilatrix* Sclater, 1879 (n = 77); *P. striaticeps* (n = 79), and *P. striaticollis* (Orbigny & Lafresnaye, 1838) (n = 82). *Phacellodomus rufifrons* and *P. ruber* were widely distributed in South America, whereas *P. dorsalis* was limited to a few localities in Peru. *Phacellodomus sibilatrix* and *P. striaticollis* were distributed in southern South America; *P. erythrophthalmus* and *P. ferrugineigula* inhabited the Brazilian Atlantic coast and southern Brazil; and *P. striaticeps* and *P. maculipectus* occurred in the Andean cordillera (Figure 1). All models derived from the analysis performed well (AUC > 0.94) and showed sensitivity higher than 95%. The binomial probabilities were statistically significant for *Phacellodomus* species ($p < 0.01$).

The models indicated higher climatic suitability for the occurrence of *Phacellodomus* species in open-dry areas when compared to rain forest areas. Jackknife tests showed that annual precipitation and minimum temperature of the coldest month were the variables that most contributed to the models.

Although *Phacellodomus* species occurred in 35 ecoregions and seven macrohabitats of South America, the Chaco and Uruguayan savannas were the ecoregions with the highest number of species (Table 1). In fact, grasslands and savannas were the main macrohabitats of *Phacellodomus* species, even though at least 14 (40%) of the 35 ecoregions where *Phacellodomus* species occurred were wet forests and wetlands.

Discussion

The geographic distributions of *P. dorsalis*, *P. rufifrons*, *P. striaticeps*, *P. maculipectus*, *P. ferrugineigula*, and *P. erythrophthalmus* in current study were similar to those described in previous studies (VAURIE 1980, RIDGELY; TUDOR, 1994; SIMON et al., 2008). However, a broader distributional range was attributed to *P. sibilatrix* (in Argentina, Paraguay and southern Bolivia); *P. striaticollis* (in Argentina, particularly in Corrientes and Cordoba); and *P. ruber*, with new occurrence records in several Brazilian states (Piauí, Tocantins, Mato Grosso, Goiás, Distrito Federal, Mato Grosso do Sul and Minas Gerais).

Ecological niche models indicated distant and discontinuous areas when compared to the species´ actual distribution as, for instance, *P. erythrophthalmus*, *P. ferrugineigula*, and *P. striaticollis* (along the Andes in Bolivia and Peru); *P. maculipectus* and *P. sibilatrix* (in the Caatinga of northeastern Brazil). These areas should have been predicted by the models because they had the climatic characteristics of the areas where the species actually occurred. The above overprediction error in ENM approaches derives from potentially habitable regions correctly predicted as presence, but probably outside the species´ dispersal area and, consequently, not inhabited. The examination of congruence or discordance between predicted and actual distributions evaluates the roles of ecological and historical factors in determining the species' eographic distribution (ANDERSON et al., 2002).

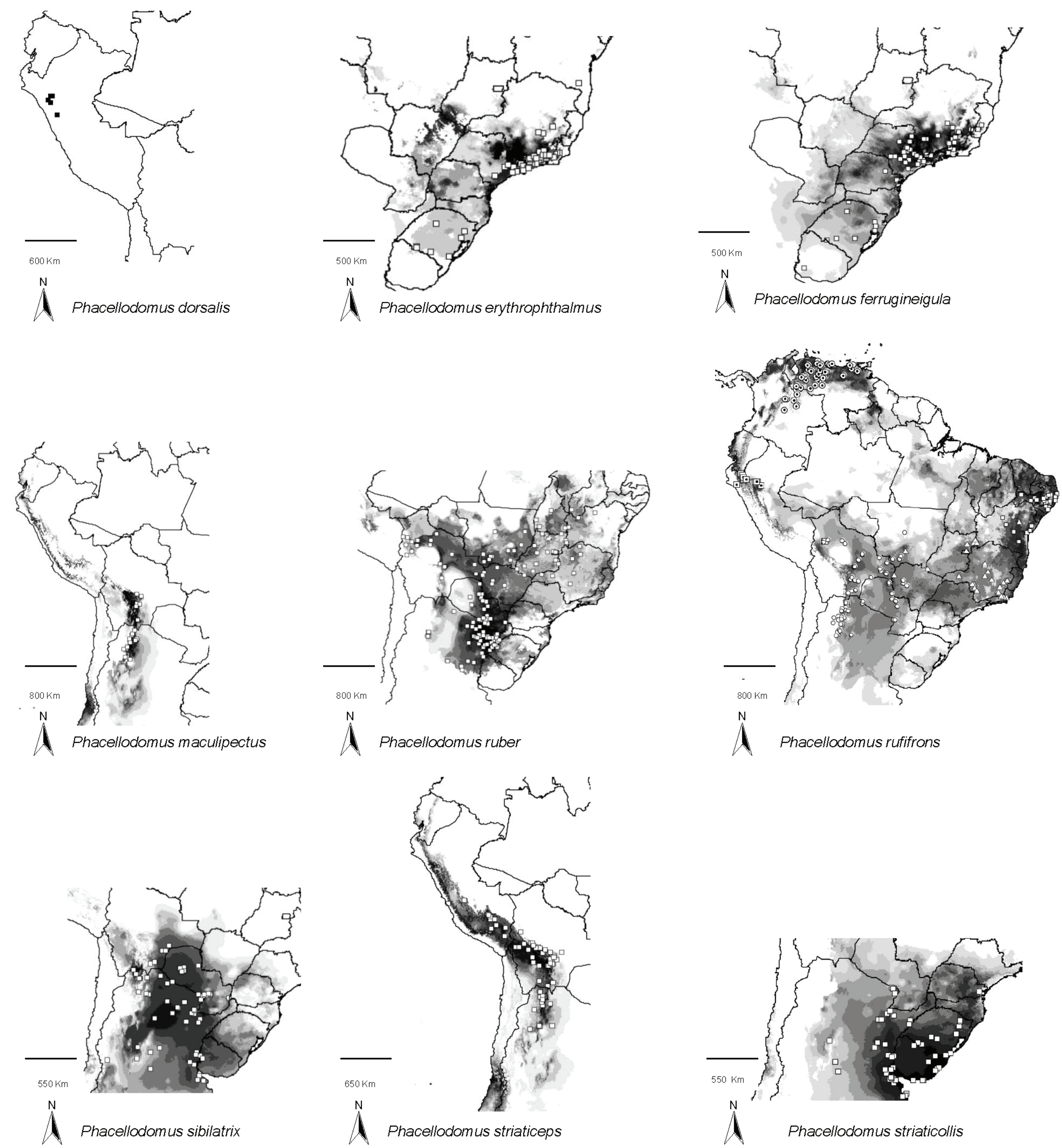

Figure 1. Geographic distributions of *Phacellodomus* species in South America predicted by ecological niche modeling (Maxent). The areas in gray tones show the distribution predicted according to climate suitability: light gray (low), dark gray (high). The white areas represent the absence predicted by the models and the squares represent the occurrence records used in modeling. In the case of *P. rufifrons*, different subspecies are indicated by different symbols: *P. r. specularis* (square), *P. r. sincipitalis* (circle), *P. r. rufifrons* (triangle), *P. r. inoratus* and *P. r. castilloi* (dotted circle), *P. rufifrons peruvianus* (dotted square). In the case of *P. dorsalis*, only occurrence points were presented since it was not possible to predict the distribution due to the sample size criterion of 20 unique latitude-longitude points.

Table 1. Occurrence of *Phacellodomus* species in 35 ecoregions and seven macrohabitats in South America. Dark cells indicate the known presence of the species in the ecoregion. The last line indicates the number of ecoregions where the species occurs. dor: *P. dorsalis*, ery: *P. erythrophthalmus*, fer: *P. ferrugineigula*, mac: *P. maculipectus*, rub: *P. ruber*, ruf: *P. rufifrons*, stc: *P. striaticeps*, stl: *P. striaticollis*, sib: *P. sibilatrix*.

Macrohabitat	Ecoregion	Species								
		dor	ery	fer	mac	rub	ruf	stc	stl	sib
Temperate grasslands and savannahs	Semi-arid pampas								■	■
	Humid pampas								■	■
	Argentine Spinal					■			■	■
Tropical grasslands and savannahs	Argentine Monte				■		■		■	■
	Beni savannahs					■	■			
	Cerrado			■		■	■			
	Humid Chaco					■	■		■	■
	Uruguayan savannahs		■	■		■			■	■
	Cordoba montane savannah								■	■
	Llanos						■			
Montane grasslands and shrublands	Central Andean wet puna							■		
	Central Andean dry puna							■		
Deserts and xeric shrublands	Paraguana xeric scrub						■			
	La Costa xeric shrublands						■			
	Caatinga						■			
Tropical and subtropical dry broadleaf forests	Maracaibo						■			
	Apure-Villavicencio						■			
	Chiquitano dry forests					■	■			
	Bolivian montane dry forest				■			■		
	Arid chaco									■
	Chaco					■	■	■	■	■
Tropical and subtropical moist and broadleaf forests	Alto Paraná Atlantic forest			■		■				■
	Peruvian yungas	■					■	■		
	Eastern cordillera montane forests						■			
	Central Andean Yungas					■				
	Southern Andean yungas				■			■		
	Bolivian Yungas				■			■		
	Pernambuco coastal forest						■			
	Bahia coastal forests			■						
	Bahia interior forests		■				■			
	Araucaria moist forests		■						■	
	Serra do Mar coastal forest		■	■			■			
Flooded grasslands and savannahs	Orinoco wetlands						■			
	Southern cone mesopotamian savannahs					■			■	
	Pantanal					■	■			
	Total	1	4	5	4	11	19	7	10	10

Among the species studied, *P. dorsalis* occurred in a single ecoregion (Peruvian yungas), a mountainous area of Peru over 2,500 m. According to Vaurie (1980) and Ridgely and Tudor (1994), ecological data on *P. dorsalis* are scarce. This species is endemic to Peru, apparently restricted to the Marañon Valley, from southern Cajamarca to northern La Liberdad, but probably also in the neighboring Amazonas Department. More information on the occurrence of this species is needed

Phacellodomus erythophthalmus occurred in Uruguayan savannas, Serra do Mar coastal forest, Araucaria forests, and Bahia interior forests. According to Simon et al. (2008), *P. erythophthalmus* has not been observed in Bahia since its description in 1821: our models clearly indicate that the interior forests of Bahia do not seem to have suitable climatic conditions for its occurrence. The potential distribution of *P. ferrugineigula* was very similar to that of *P. erythophthalmus*. Although *P. ferrugineigula* was long considered a subspecies of *P. erythophthalmus*, Simon et al. (2008) presented morphological evidence that it should be acknowledged a valid species. Apparently, the two species occur in sympatry in the Brazilian states of São Paulo, Rio de Janeiro, and Minas Gerais. Our results not only confirm overlapping potential, but even suggest that the area of co-occurrence could be even larger, including the southern Brazilian states of Rio Grande do Sul, Santa Catarina and Paraná.

The distribution of *P. maculipectus* lies in southwestern Bolivia and northwestern Argentina, in forests dominated by *Alnus*, *Podocarpus* and *Miconia*, at altitudes between 1,800 and 3,100 m in Bolivia and between 1,900 and 2,900 m in Argentina (BARNETT et al., 1998).

Phacellodomus ruber is widely distributed across 11 ecoregions. The species is common in the flooded areas of the Brazilian cerrado, associated with *Mauritia flexuosa* palm trees, where it builds its nest (GURGEL-GONÇALVES; CUBA, 2011; GURGEL-GONÇALVES et al., 2012).

Phacellodomus rufifrons, considered a single, polytypic species, is the most widespread species of *Phacellodomus* in South America, covering at least 19 ecoregions, such as La Costa xeric shrublands, Cerrado and Serra do Mar coastal rainforest. Although quantitative data are lacking, the subspecies may be fully detectable by plumage characteristics (RIDGELY; TUDOR, 1994; VAURIE 1980). Records of each subspecies and associated distributional estimates indicated little overlap between their distributions. Future studies applying ecological niche differentiation and phylogeography could provide evidence for the separation of some of these subspecies. *Phacellodomus striaticeps* occurred in seven ecoregions, the only species of *Phacellodomus* with records on the Central Andean wet puna and Central Andean dry puna. *Phacellodomus striaticollis* and *P. sibilatrix* occurred in temperate and tropical savannahs and grasslands with a similar distribution. Our results indicate that the area of co-occurrence of these species may be larger than that described by Vaurie (1980). It may even include northeastern Argentina, southern Brazil and Uruguay. As predicted in our study, *P. sibilatrix* was only recently recorded in Brazil (BELLAGAMBA; DE OLIVEIRA, 2012).

The database spatial resolution in current study could limit the accuracy of niche models. For example, some species occur in habitat patches and only a few meters would separate the limits of their habitat, as the swamp-occurring *P. ferrugineigula*. Coarse raster resolutions may fail to capture sharp environmental gradients that occur at terrestrial habitats, while ecological niche models built from low-resolution data sets tend to overestimate species ranges (SEO et al., 2009). However, the effects of these scale-related uncertainties will differ according to the scale of analysis (WIENS et al., 2009). Some uncertainties may be averaged out if the grain size of predicted distributions is large, as in current study, where the geographic distributions of *Phacellodomus* species were estimated on a continental scale.

Geographic and ecological information on *Phacellodomus* species may allow a deeper understanding on diversity patterns (e.g. SCHIDELKO et al., 2011), species limits (e.g. RAXWORTHY et al., 2007), climate-driven distributional shifts (e.g. MARINI et al., 2009), and conservation (e.g. MARINI et al., 2010a). Indeed, this information may be relevant to health sciences since *Phacellodomus* nests are habitats for various insect species, including triatomine vectors of Chagas' disease.

Conclusion

Current study updated the geographic distributions of *Phacellodomus* species in South America. Despite the overall connection of *Phacellodomus* species with dry areas, the species *P. ruber*, *P. rufifrons*, *P. ferrugineigula* and *P. erythrophthalmus* occurred in humid forests and wetland ecoregions. The resulting ecological niche models showed high specificity and sensitivity, which indicated a high predictive ability and summarized the ecological conditions for the occurrence of *Phacellodomus* species in South America.

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