

Different elevational environments dictate contrasting patterns of niche evolution in Neotropical *Pithecopus* treefrog species

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Abstract

Understanding how species' ecological niches evolve can shed light on observed large-scale biogeographic patterns, temporal range shifts, and the potential ability for species to cope with climate changes. Here, we investigated climatic niche evolution in the Neotropical treefrog genus *Pithecopus* by testing for phylogenetic niche conservatism (PNC). We first evaluated niche overlap patterns based on pairwise niche comparisons of sister species pairs inferred from two alternative topologies for the genus, where higher niche overlap for those pairs compared to random species pairs would represent evidence of PNC. Second, we evaluated phylogenetic conservatism of climatic niches by fitting evolutionary models for niche position and niche breadth across the two alternative phylogenetic trees for the genus. Sister species pairs did not show higher mean niche overlap when compared to random pairs. Comparisons considering species' elevational habitats, on the other hand, showed that lowland sister species had greater niche overlap and montane species lower overlap than expected given the prevailing environmental conditions in each habitat, suggesting different evolutionary histories of niche differentiation for species with different elevational ranges. The best fit of niche position and breadth to both stasis and drift models supported the existence of PNC. We conclude that evolution of climatic niches in *Pithecopus* suggests overall PNC and that the contrasting patterns found for lowland and mountainous species reinforce the importance of considering the effects of habitat type in understanding climatic niches dynamics.

Abstract in Portuguese is available with online material.

KEYWORDS

anurans, evolutionary models, niche overlap, phylogenetic niche conservatism, South America

1 | INTRODUCTION

The ecological niche is a complex trait defined by requirements and tolerances regarding the external environment that allow persistence of a species (Chase & Leibold, 2003; Peterson et al., 2011). Soberón (2007) defined Grinnellian and Eltonian niches in reference to two early definitions of niche-related concepts (Elton, 1927; Grinnell, 1917). The Grinnellian niche refers to non-interactive variables describing the physical environment determining a species' potential geographic distributions, whereas the Eltonian niche refers to the resource–consumer dynamics and biotic interactions that determine species' populations and distributions at more local scales. Given the coarse spatial structure of variables defining Grinnellian niches, compared with the local and complex dynamics of those defining Eltonian niches, the former is more tractable and has been studied more widely (Olalla-Tárraga et al., 2017). Several studies addressing niche evolution have demonstrated that climatic requirements are often conserved over short-to-medium evolutionary time frames, with closely related species having more similar climatic niches than distantly related species or species chosen at random (Anciães & Peterson, 2009; Peterson et al., 1999; Petitpierre et al., 2012), a pattern known as phylogenetic niche conservatism.

Phylogenetic niche conservatism (hereafter PNC) can be defined as the tendency of species or lineages to retain their ancestral niches over time. This term has been the subject of controversy regarding its validity as either a pattern or a process (Münkemüller et al., 2015; Pyron et al., 2014). For instance, under a “PNC as a pattern” perspective, one would expect to find higher niche similarity between closely related species than between distantly related ones as a result of neutral drift, evolutionary constraints, or stabilizing selection (Cooper et al., 2010; Pyron et al., 2014). On the other hand, under a “PNC as a process” perspective, given the limited ability in generating niche novelties and thus the impossibility of adaptation, niche conservatism would lead to range disjunctions and could function as an adaptive evolutionary process (Gomulkiewicz & Houle, 2009; Holt, 1996). Some authors have suggested that close phylogenetic relationships and the resulting niche similarity between related species are sufficient to drive PNC (Wiens, 2008; Cooper et al., 2010; Wiens et al., 2010), whereas others have postulated that PNC requires additional constraints such as environmental filtering and pervasive stabilizing selection (Desdevises et al., 2003; Harvey & Pagel, 1991; Losos, 2008) or limits to adaptive niche evolution (Gomulkiewicz & Houle, 2009; Holt, 1996). Here, we focus on the “PNC as a pattern” perspective and follow the view that the existence of PNC requires, at least, that closely related species show higher niche similarity when compared to distantly related species (Losos, 2008; Wiens et al., 2010). In addition, we searched for further evidence of PNC by evaluating whether niche similarity is higher than expected under neutral drift and thus corresponds to constrained evolution (Cooper et al., 2010; Münkemüller et al., 2015).

Two approaches have been applied most frequently to evaluate PNC of species' climatic niches: those comparing the climatic representation of species' geographic distributions between closely

related species (i.e., species-pair approach) and those using phylogenetic trees and evolutionary model selection to evaluate evolutionary trajectories of niche features (i.e., whole-tree approach) (Wiens et al., 2010). In the species-pair approach, the existence of PNC is tested at the species level by measuring the degree of niche overlap between closely related pairs of species, with higher niche overlap being expected between sister taxa compared to between non-sister taxa (Warren et al., 2010). Under the whole-tree approach, fit of different models representing distinct evolutionary scenarios to the observed data can be evaluated in explicit phylogenetic frameworks, ranging from niche evolution independent of species' relationships to constrained niche evolution consistent with PNC (Münkemüller et al., 2015). These two approaches are complementary and can and should be applied in tandem (Kozak & Wiens, 2010b; Münkemüller et al., 2015; Peixoto et al., 2017; Rodrigues et al., 2019).

Treefrogs of the genus *Pithecopus* are charismatic Neotropical frogs. Their geographic distributions *in totum* cover much of South America, comprising a diverse sample of the landscapes and environments (Antonelli et al., 2018). Currently, the genus includes 11 recognized species (Frost, 2020) that are grouped in two clades occurring in different elevational ranges (Duellman et al., 2016): one with species with restricted distribution, isolated on peaks and plateaus of mountain ranges (600–1500 m) (montane clade), and the other with broadly distributed species in lowland regions (lowland clade). Among species with the broadest geographic distributions are *P. azureus* (Cope, 1862), restricted to the Brazilian cerrado, Paraguayan and northern Argentine chaco, the two largest biomes in the South America diagonal of open formations (Werneck, 2011); *P. hypochondrialis* (Daudin, 1800) and *P. palliatus* (Peters, 1873), species associated to open formation and forested regions within Amazonia, respectively; *P. nordestinus* (Caramaschi, 2006), distributed in dry caatinga in northeastern of Brazil; and *P. rohdei* (Mertens, 1926), in Atlantic forest along the Brazilian coast. The genus also includes geographically restricted species such as *P. ayeaye* (Lutz, 1966); *P. centralis* (Bokermann, 1965); *P. megacephalus* (Miranda-Ribeiro, 1926); and *P. oreades* (Brandão, 2002), from different isolated mountain ranges scattered throughout Brazil, and *P. araguaui* (Haga et al., 2017) and *P. rusticus* (Bruschi et al., 2014), from the Amazon rainforest / cerrado transition in central Brazil and Araucaria forest in highlands of southern Brazil, respectively.

Because environments associated with different habitats may influence many of species' traits (e.g., body size, Buskirk & Arioli, 2005; home range and abundance, Buskirk, 2005 and Eterovick & Barata, 2006; extinction risk, Cooper et al., 2008 and Sohdi et al., 2008; diversification rate, Kozak & Wiens, 2010a), including the evolution of their climatic niches (e.g., Graham et al., 2004), the distribution of *Pithecopus* across a mosaic of contrasting environments, as well as in different elevational habitats, represent an opportunity to evaluate climatic niche evolution across its lineages.

Here, we aimed to evaluate evolutionary patterns in the climatic niches of *Pithecopus* species by testing the existence of phylogenetic niche conservatism using both species-pair and whole-tree approaches, and investigating effects of two alternative phylogenetic

hypotheses proposed for the genus. We first investigated climatic niche evolution across the whole genus irrespective of species' elevational ranges to provide a general scenario for the group and compared patterns of lowland *versus* montane habitat of species. More specifically, we aimed to (1) evaluate whether PNC occurs across the whole genus and (2) evaluate whether climatic niche evolution differs between montane and lowland species. According to PNC, we expect that (a) sister species pairs would show greater niche overlap than non-sister species pairs, and (b) the evolutionary pattern of climatic niches across the genus' phylogeny would follow a model of constrained evolution. When considering species with different elevational ranges separately, species from montane regions may have experienced less stable systems when compared to lowland species (Rahbek et al., 2019), so we expect higher niche overlap between lowland species than between montane species, hypothesizing that niche evolution will be different between montane and lowland clades. Overall, this suite of analyses painted a picture of complex contrasts of evolutionary change *versus* stasis in ecological niche characteristics in this clade.

2 | METHODS

2.1 | Phylogenetic information

To conduct our niche evolution analyses in a phylogenetic context, we used the most recently published and complete phylogeny for treefrogs, which had significant representation of *Pithecopus* species (9 of the 11 species currently recognized) (Duellman et al., 2016; hereafter called the DPP tree). Phylogenetic relationships in this tree were inferred through maximum likelihood (ML) based on sequences of 19 genes (see "DPP" in Figure 1). Given that this phylogeny does not include all currently recognized species of *Pithecopus* (Frost, 2020), and given that it was inferred from a concatenated matrix with many missing genes (see Appendix 1 of Duellman et al., 2016), basing our analyses exclusively on this topology could bias conclusions about climatic niche evolution. So, to evaluate the robustness of our results, we also ran all analysis under an alternative topology from a novel complete phylogenetic inference that sampled all 11 *Pithecopus* species (Magalhães et al., unpublished data; hereafter

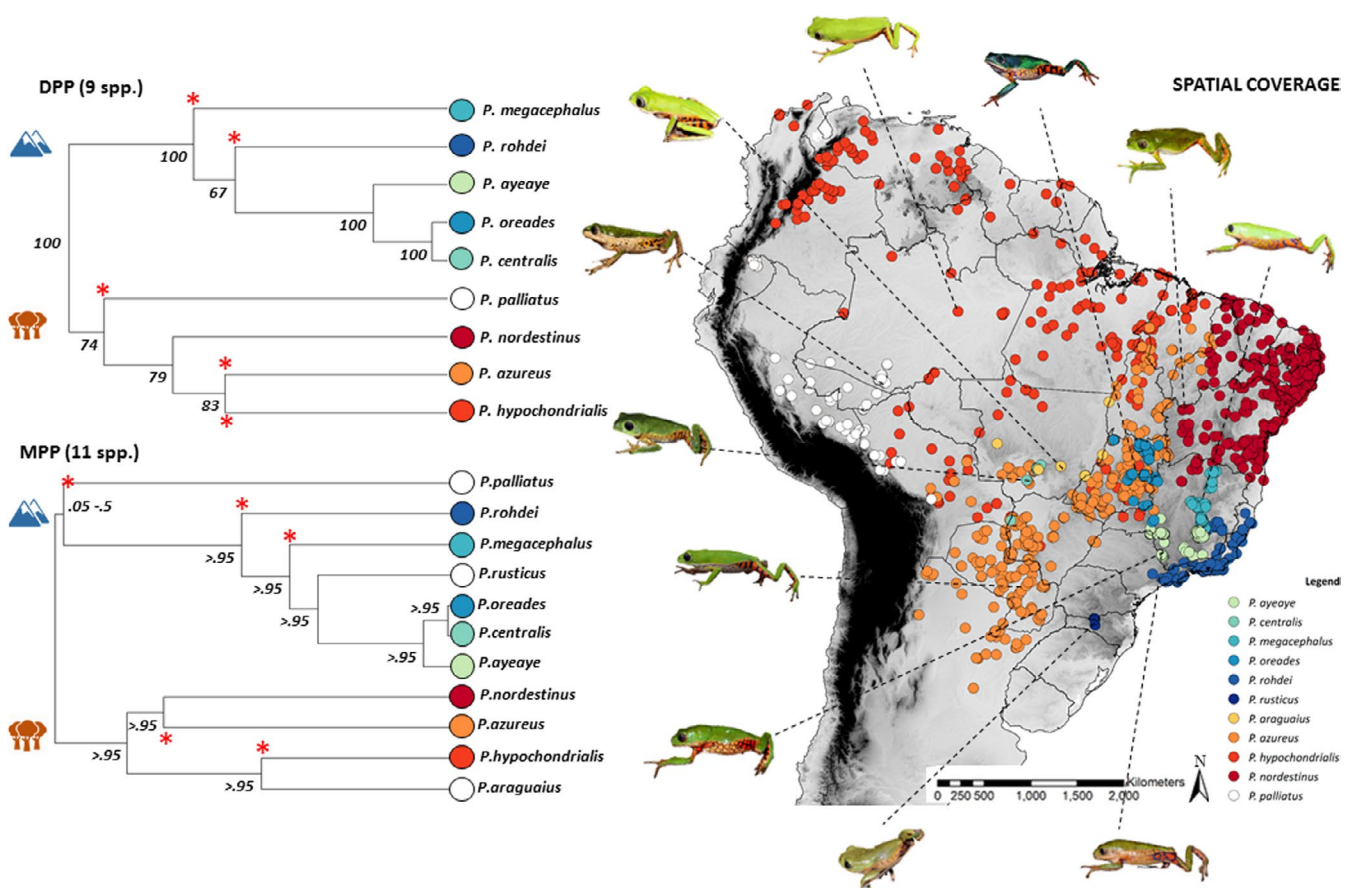


FIGURE 1 "DPP": Representation of maximum likelihood (ML) phylogeny of nine *Pithecopus* treefrogs based on DNA sequence data from 19 genes (modified from Duellman et al., 2016). "MPP": Representation of phylogeny of 11 *Pithecopus* species estimated under Bayesian inference based on four genes (two mitochondrial and two nuclear) (modified from Magalhães et al., unpublished data). Numbers at the nodes in DPP correspond to bootstrap support values and at the nodes in MPP correspond to posterior probability values. "*": indicate changes in the position of the taxon to which they are linked between the phylogenies. "mountain icon (draw) designates the montane clade, and the tree icon (draw) designates the lowland clade. "Spatial coverage": distributional summary of 1456 geographic records compiled for 11 species in the genus *Pithecopus*

called the MPP tree). For this phylogeny, relationships were estimated under Bayesian inference based on four genes (two mitochondrial and two nuclear) (see “MPP” in Figure 1) (R. Magalhães, pers. comm.; see Appendix S1, Supplementary Information SI-1 for details).

2.2 | Geographic and climatic data

We used occurrence records for *Pithecopus* species compiled from 9 herpetological collections (see Table S1). After obtaining, verifying, and validating each occurrence record through direct specimen examination during collection visits, our final data set included 19 records for *P. araguaeus*, 73 for *P. ayeaye*, 388 for *P. azureus*, 10 for *P. centralis*, 273 for *P. hypochondrialis*, 65 for *P. megacephalus*, 345 for *P. nordestinus*, 45 for *P. oreades*, 72 for *P. palliatus*, 161 for *P. rohdei*, and 5 for *P. rusticus*, with satisfactory geographic coverage of each species' distribution (see “Spatial coverage” in Figure 1).

To characterize climatic niches of *Pithecopus* species, we used a multivariate representation based on 22 climatic variables closely related to ecological and physiological tolerances of anurans (Duellman & Trueb, 1994; Wells, 2007). Nineteen bioclimatic variables were obtained from WorldClim, version 1.4, at the 30" resolution (about 1 km²), representing monthly climate data for minimum, mean, and maximum temperature and total precipitation for 1960–1990 (bio1-bio19; Hijmans et al., 2005). Three additional variables (annual evapotranspiration, AET; global aridity index, AI; and global potential evapotranspiration, PET) were obtained from the consortium for spatial information IAR-CSI (Trabucco & Zomer, 2009), also at the 30" resolution. These latter three variables summarize physical processes (e.g., ability of the atmosphere to remove water through evapotranspiration) that may influence the biology of anurans (Duellman & Trueb, 1994; Wells, 2007).

2.3 | Climatic niche evolution

We evaluated PNC across *Pithecopus* species by applying both species-pair and whole-tree approaches. Given the complementarity of these two approaches, comparing their results is a more robust way to evaluate niche evolution and thus a more appropriate way to address PNC across clades (Peixoto et al., 2017; Rodrigues et al., 2019). As an exploratory test to evaluate the potential association among climatic niches and phylogenetic relationships and a trend that would indicate PNC, we also performed *a priori* a Mantel test to investigate for the presence of phylogenetic signal (Cooper et al., 2010; Münkemüller et al., 2015; Wiens et al., 2010).

2.3.1 | Species-pair approach

We compared mean niche overlap among pairs of sister species with mean niche overlap among random species pairs drawn from the

genus' phylogeny. To this end, we first calculated climatic niche overlap among all species pairs, both sister and non-sister species, using Schoener's D values (see Appendix S1-Supplementary Information SI-2 for details). Then, we compared average niche overlap for the sister species pairs in each phylogeny (i.e., two in DPP, three in MPP) against the mean niche overlap of a null distribution of overlap values from non-species pairs chosen at random. We built this null distribution by drawing the same numbers of non-sister pairs as we had sister species pairs, and calculating their mean niche overlap, repeating this process 1000 times (Rodrigues et al., 2019). We assessed statistical significance by comparing the observed mean overlap value against the null distribution, where observed values higher than the 95% percentile of the null distribution were considered significant ($\alpha = .05$, one-tailed test); higher overlap among observed sister species would suggest PNC (Cooper et al., 2010).

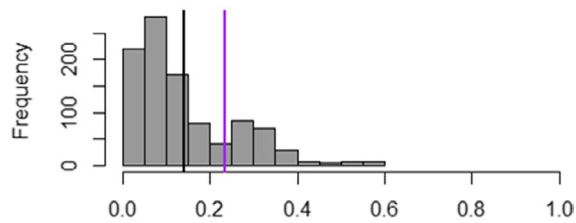
To evaluate whether mean niche overlap between species pairs from the montane clade differed from that from the lowland clade, we compared mean niche overlap between species pairs belonging to each elevational range with the mean niche overlap between random species pairs drawn from the entire corresponding phylogeny as described above for the procedure considering genus as a whole. Different patterns would suggest that related species occurring in each clade have different evolutionary regimes, whereas similar patterns would suggest similar evolutionary regimes regarding their niches (Rodrigues et al., 2019). We compared mean niche overlap using ANOVAs.

To illustrate patterns of climatic niche similarities and differences, we constructed density plots for each species with the frequency values for all 22 environmental variables using the *sm* package in R (Bowman & Azzalini, 2014). The use of density estimates is an effective way of summarizing the climatic profile of each species; by comparing frequencies, it can highlight contrasts between species.

2.3.2 | Whole-tree approach

To evaluate PNC within *Pithecopus* considering phylogenetic relationships among all species in the genus, we fit different evolutionary models to the distribution of two niche characteristic—niche position (NP) and niche breadth (NB)—across the phylogeny. These characteristics were derived from the climatic niches estimated for each species, for which we used the outlying mean index (OMI) analysis (Dodélec et al., 2000) (see Appendix S1, Supplementary Information SI-3 for details). We then compared the fit of three alternative evolutionary models following Peixoto et al. (2017) and Rodrigues et al. (2019): (1) a Brownian motion (BM) model, in which niche differences accumulate over time under a single evolutionary rate (i.e., divergence is proportional to time) (Felsenstein, 1985), indicating trait evolution through drift and thus consistent with phylogenetic signal in niche evolution as a minimum requirement for PNC (Cooper et al., 2010; Münkemüller et al., 2015); (2) an Ornstein-Uhlenbeck (OU) model with a single optimum that describes constrained evolution, in which traits are pulled toward an optimal value

DPP



MPP

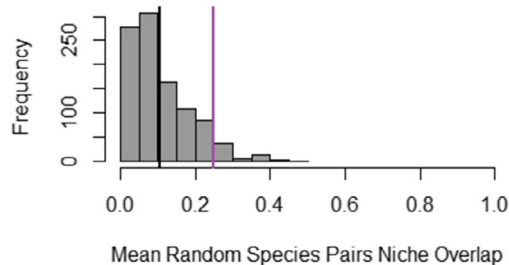


FIGURE 2 Distribution of mean niche overlap values and the comparison between the mean pairwise climatic niche overlaps among the sister species pairs (purple line) and the mean pairwise niche climatic overlap of pairs selected 1000 times at random (black line). DPP = Duellman's *Pithecopus* phylogeny; MPP = Magalhães *Pithecopus* phylogeny. Differences were not statistically significant ($p > .05$), in both phylogenies

and are thus evolving more slowly than expected under BM (i.e., from their divergence time) (Butler & King, 2004; Hansen, 1997), considered as strong evidence of PNC (Losos, 2008; Münkemüller et al., 2015); and (3) an early burst (EB) model, in which evolutionary rates decrease over time (Harmon et al., 2010), providing evidence that rates of niche evolution vary through time, considered evidence against PNC. These models were compared using the Akaike information criterion corrected for small sample sizes (AICc) to determine the best-fit model. Models with ΔAICc (delta AICc) larger than two were considered as effectively different from alternative models (Burnham & Anderson, 2002). All models were fitted using the *Geiger* package in R (Harmon et al., 2008).

3 | RESULTS

Our exploratory Mantel test evaluating the relationship between climatic niche overlap and divergence times (i.e., phylogenetic distances) was significant for both topologies (DPP: $r = .3669$, $p = .04$; MPP: $r = .3584$, $p = .02$), indicating phylogenetic signal.

On the DPP tree, mean niche overlap for sister species pairs was not significantly different from that of random species pairs (mean sister = 0.23, mean random = 0.14, $p > .05$, Figure 2), contrary to our first prediction. However, as regards our second prediction, comparisons for each clade (montane and lowland) separately showed that lowland sister species had significantly higher mean niche overlap values in comparison with random species (mean lowland = 0.46, mean random = 0.135, $p < .05$, Figure 3), whereas this value was

lower for comparisons between montane and random species pairs (mean montane = 0.00, mean random = 0.134, $p > .05$, Figure 3), although this latter comparison was not statistically significant. Niche overlap values were significantly different between the montane clade (mean = 0.087, min = 0, max = 0.346) and the lowland clade (mean = 0.325, min = 0.117, max = 0.580) (ANOVA: $F_{1, 30} = 21.09$, $p < .05$).

Results for the species-pair approach based on the MPP tree were similar to those obtained for the DPP tree. Mean niche overlap among sister species pairs (three in this tree) was not significantly different from that of random non-sister species pairs (mean sister = 0.24, mean random = 0.10, $p > .05$, Figure 2). Results for comparisons between the two were also similar between the two phylogenies, with lowland sister species having significantly higher mean niche overlap values in comparison with random species (mean lowland = 0.37, mean random = 0.10, $p < .05$, Figure 3), and this value being markedly lower in comparisons between montane and random species pairs (mean montane = 1.10^{-8} , mean random = 0.10, $p > .05$, Figure 3). Again, the comparison of mean values of niche overlap of sister species pairs was significantly different between clades (ANOVA: $F_{1, 25} = 32.45$, $p < .05$).

Based on the climatic profiles obtained for each of the species, we were able to characterize montane and lowland habitats used by this genus. In general, species belonging to the lowland clade are distributed in regions with high mean temperature and precipitation, whereas those of the montane clade were in areas characterized by lower mean temperatures and precipitation (see Figure S1). Accordingly, when comparing the profiles of two species from the same clade, they were more similar than the climate profiles of species belonging to different clades, which in a way supports the contrasting patterns obtained with the species-pair approach considering different elevational zones.

Niche features estimated for species in *Pithecopus*, as described by outlying mean index (OMI) analysis, showed a strong positive correlation with mean temperature of coldest quarter and a strong negative correlation with temperature seasonality (Table 1). Accordingly, species with high OMI scores had climatic niches characterized by high minimum temperatures and low seasonality.

Evolutionary models, when fit for NP and NB, showed that the dynamics of species' climatic niches over evolutionary time are best explained by different evolutionary models depending on the phylogeny analyzed. For the DPP tree (nine species; Duellman et al., 2016), the evolutionary model with the lowest AICc (best model under this criterion) was the OU model for both niche features (Table 2). In contrast, the MPP tree (11 species) identified the BM model as the evolutionary model with the lowest AICc for both niche features (Table 2).

4 | DISCUSSION

This study represents the first evaluation of phylogenetic niche conservatism across the whole genus *Pithecopus*, while also considering its natural division into clades with mostly contrasting elevational ranges as a way to determine niche evolution patterns. *Pithecopus*

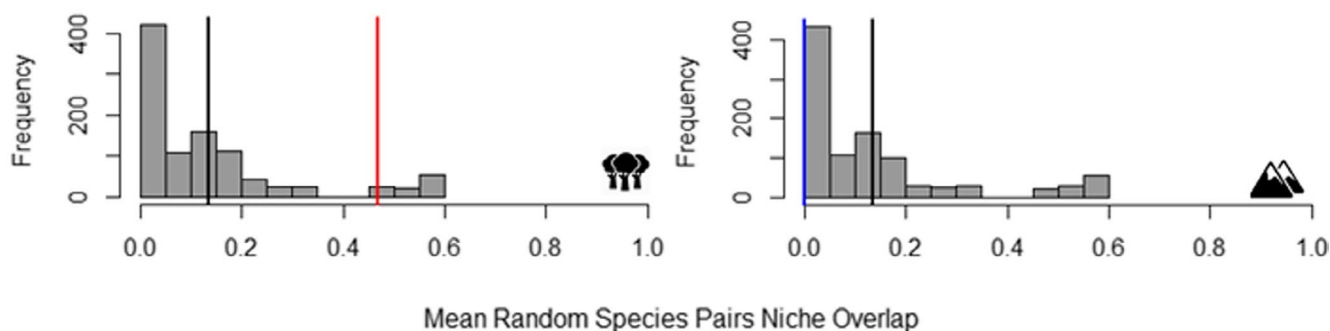
treefrogs showed evidence of phylogenetic niche conservatism (PNC) in their climatic preferences supported by the complementary analytical approaches implemented here, though with substantial differences between montane and lowland species.

Based solely on the results of the species-pair approach, we were unable to confirm or deny the existence of conservatism in *Pithecopus*. Despite the higher value estimated for mean niche overlap for the sister species pairs compared to that for the random pairs, the lack of significance points toward non-conservatism of their climatic niches, at least under the more restrictive definition of PNC (i.e., higher similarity between niches than expected by chance, *sensu* Losos, 2008). Nevertheless, the degree of similarity expected under neutral genetic drift alone, as shown by significant phylogenetic signal, would be evidence for niche conservatism under the less restrictive definition of Harvey and Pagel (1991) (see also Wiens, 2008). Indeed, the exploratory Mantel tests (see section 3. Results) were significant for both topologies indicating phylogenetic signal. As such, at least under the least restrictive definition (i.e., similarity expected under phylogenetic signal), we cannot also discard PNC as a pattern in *Pithecopus*.

When the species-pair approach was carried out considering the two clades separately, our results showed substantial differences between clades, with similar results even with the different

hypotheses of phylogenetic relationships of *P. palliatus* that we explored (Figure 1). The lowland sister species pair *P. azureus* + *P. hypochondrialis* found in DPP, as well as the lowland pairs *P. araguaeus* + *P. hypochondrialis* and *P. azureus* + *P. nordestinus* found in the MPP, presented strong evidence of niche conservatism, since the mean niche overlap for those pairs was significantly higher than that for random pairs. Considering that the time of divergence between the species composing these pairs is relatively old (~6.6 million years ago - mya for *P. azureus* + *P. hypochondrialis*, ~3.79 mya for *P. araguaeus* + *P. hypochondrialis* and, >21.73 mya for *P. azureus* and + *P. nordestinus*; Duellman et al., 2016, R. Magalhães pers. comm.), the similarity between their niches perhaps exceeds what would be expected by the phylogenetic signal (i.e., divergence proportional to time, *sensu* Felsenstein, 1985), which would suggest the action of a restrictive selective force in the evolution of this trait and evidence for PNC for this clade. In contrast, the montane sister species pair *P. centralis* + *P. oreades*, recovered with high support in both phylogenetic hypotheses, showed lower niche overlap than expected at random, suggesting niche divergence. For these small-ranged and isolated species, we cannot exclude the possibility that their niches evolved under diversifying selection (Boucher et al., 2014), where divergent natural selection could be responsible for differences in climate tolerances and deviations from the ancestral climatic niche. Therefore,

DPP



MPP

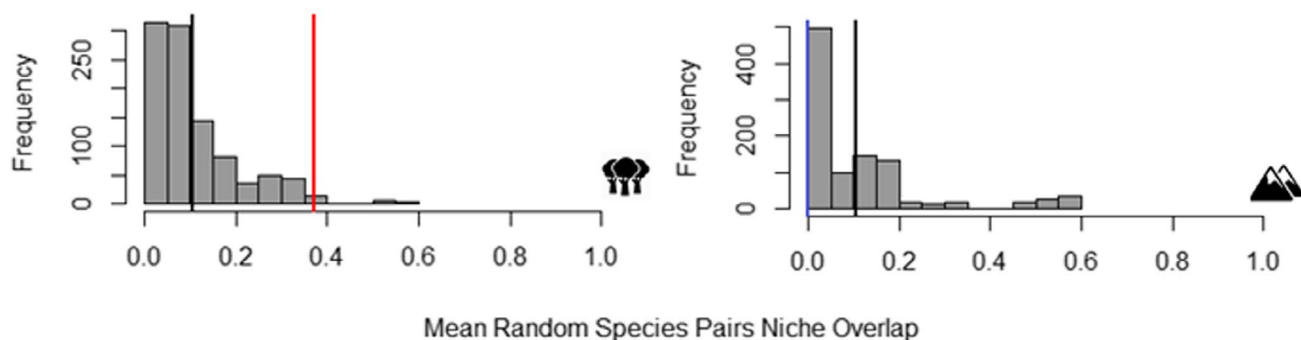


FIGURE 3 Comparison between the observed niche overlap value for the pairs composed of species belonging to the lowland clade (red line, trees icon) and the pair belonging to the montane clade (blue line, mountain icon) against the mean climatic niche overlap between pairs of randomly selected species (black line), for DPP and MPP. The bars represent the distribution of mean random species-pair niche overlap values. In both phylogenies, the difference was statistically significant ($p < .05$) in comparison between lowland and random pairs, and was not statistically significant ($p > .05$) between montane species and random pairs

TABLE 1 Correlations between climatic variables and species' climatic niches (first axis of Outlying Mean Index—OMI)

Environmental variables	Contribution
Mean temperature of coldest quarter	0.3370
Mean temperature of driest quarter	0.3340
Minimum temperature of coldest month	0.3253
Annual mean temperature	0.3206
Isothermality	0.2776
Precipitation of coldest month	0.2622
Mean temperature of warmest quarter	0.2527
Mean temperature of wettest quarter	0.2242
Annual potential evapotranspiration	0.2078
Maximum temperature of warmest month	0.1926
Annual precipitation	0.1639
Precipitation of wettest quarter	0.1116
Annual evapotranspiration	0.1104
Precipitation of driest quarter	0.1101
Precipitation of wettest month	0.1073
Precipitation of driest month	0.0907
Annual aridity index	0.0693
Mean diurnal range	-0.0512
Precipitation seasonality	-0.0768
Precipitation of warmest quarter	-0.1735
Temperature annual range	-0.2154
Temperature seasonality	-0.2289

taken together, these results suggest different evolutionary histories of niche evolution and occupation in *Pithecopus* in distinct habitat types, similar to what has been documented recently for clades of Neotropical lizards from contrasting forested and open ecosystems (Sheu et al., 2020).

TABLE 2 Comparisons among evolutionary models assessed that describe climatic niche evolution of *Pithecopus* species over their evolutionary history

MODEL	AICc		dAICc	
	NP	NB	NP	NB
BM	57.40	52.75	4.10	9.50
OU	53.30	43.25	0.00 ^a	0.00 ^a
EB	62.20	57.55	8.90	14.30
MODEL	AICc		dAICc	
	NP	NB	NP	NB
BM	68.20	47.49	0.00 ^a	0.00 ^a
OU	71.29	50.89	3.09	3.40
EB	72.13	51.42	3.93	3.93

Notes: Upper table: analysis carried out using the Duellman *Pithecopus* Phylogeny (DPP); bottom table: analysis carried out using the Magalhães *Pithecopus* Phylogeny (MPP). NP =Niche position feature and; NB =Niche breadth feature. BM =Brownian motion; OU =Ornstein-Uhlenbeck; EB =early burst. dAICc =AICc difference between the model and the best model (lowest AICc).

^aBest-fit model.

Results of the whole-tree approach were more conclusive and agreed between phylogenies in indicating PNC for the group. Under the DPP tree, the evolution of niche characteristics followed an OU evolutionary model with a single optimum, providing strong evidence for PNC (Münkemüller et al., 2015). In this model, stabilizing selection would favor individuals with the same niche as their ancestors, because deviations from this condition would generally reduce fitness (e.g., Holt & Barfield, 2008). Accordingly, different species in the clade would present similar climatic niches, as this trait would be actively constrained by selection toward an evolutionary optimum, regardless of how much evolutionary time has elapsed. In turn, this regime could result in greater overlap between climatic niches, concordance between climatic profiles, and similar distributions, patterns that were actually observed here (see Figures 1 and 2; Figure S1).

For the MPP tree, the best-fit evolutionary model for both niche features was the BM. In this model, observed divergences are proportional to time (Felsenstein, 1985), producing a pattern consistent with phylogenetic signal (Harvey & Pagel, 1991). Even though researchers disagree about whether finding phylogenetic signal indicates niche conservatism, here, as in other studies, we consider that the expected pattern under this signal is sufficient to result in PNC (Harvey & Pagel, 1991; Wiens, 2008; Cooper et al., 2010; Wiens et al., 2010) as it expresses the tendency that closely related species have more similar climate niches than less related ones. Therefore, the best fit of niche character evolution to a BM model corroborated with the observed significance of phylogenetic signal in climatic niches (the phylogenetic signal approach, Rodrigues et al., 2019), indicates PNC across *Pithecopus*.

Given that PNC determines which environmental conditions the members of a clade can tolerate and, therefore, constrains the set of regions to which they can disperse and colonize (Wiens & Donoghue, 2004), our results supporting PNC among *Pithecopus* species provide valuable insights on possible origins for the biogeographic patterns

observed for the group. As the climate gradually changed during the Plio-Pleistocene (Lisiecki & Raymo, 2007), species in South America could have been isolated in upland habitats whereas in northwestern and central South America, species underwent range expansions with the increase of climatically suitable areas. However, to confirm this hypothesis, as well as infer its implications for the group's historical biogeography, more data analyses would be necessary (e.g., species tree, ancestral area reconstructions, paleoclimatic models construction, identification of potential migration routes by calculating least-cost corridors based on environmental connectivity, etc.), an endeavor worthy of future studies.

Biological implications of global climate change can also be viewed from a PNC perspective (Peterson et al., 2002; Thomas et al., 2004; Wiens et al., 2010). Unable to develop niche novelties, one alternative for species in the face of global warming is to change their geographic distribution to track optimal climatic regimes. Under this scenario, species unable to move (e.g., due to habitat destruction, geographic barriers or dispersal limitations) are at risk of population loss and even extinction (Anciães & Peterson, 2006; Wiens et al., 2010; Wiens & Graham, 2005). Therefore, our evidence supporting climatic niche conservatism in *Pithecopus* species reinforces the concern that climate change impacts are a future potential problem for anurans (Urban, 2015); assessing these potential impacts is also a topic that deserves to be highlighted in future studies.

In conclusion, the joint consideration of the evidence obtained by the two approaches used here leads us to believe that PNC is a pattern typical in the genus *Pithecopus*. Climatic niches of these treefrogs are overall more similar between sister species pairs than between distantly related species, as expected under neutral drift since their diversification (minimal evidence to consider the presence of conservatism within a clade; Losos, 2008; Pyron et al., 2014). Furthermore, lowland and montane species occupy different climatic niches as highlighted by the contrasting patterns found, possibly indicating different mechanisms (e.g., drift alone versus selection, low versus high dispersal capacity etc.) creating different evolutionary histories within each subclade, and reinforcing the importance of habitat in understanding species' climatic niches and their evolution.

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CONFLICTS OF INTEREST

The authors have nothing to declare.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.r7sqv9sbc> (Bandeira et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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