






Burrowing habit in *Smilisca* frogs as an adaptive response to ecological niche constraints in seasonally dry environments

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Abstract

As environmental conditions change over time, some species can follow the spatial footprint of their ecological niches or can adapt physiologically to the new conditions; modifying behavior can offer an alternative means of adapting to novel environments. The burrowing habit allows organisms to avoid adverse climatic conditions during part of the year by remaining inside burrows. *Smilisca fodiens* and *S. dentata* are two burrowing hylid frogs that inhabit areas beyond the northernmost distributional limits of the other six arboreal species of their genus, and indeed beyond of most American hylids. In this study, we tested whether burrowing habit allows these species to adapt to drier conditions while conserving the climatic niche of the arboreal species. We compared the annual niches of the arboreal species to those of the burrowing species under two assumptions: true seasonal niches and full annual niches. Through ecological niche similarity tests, we performed 24 comparisons in both geographic and environmental spaces. In geographic space, when considering burrowing annual niches, only five of 24 tests indicated similarity, yet as regards seasonal niche, 18 of 24 tests indicated similarity. In environmental space, all tests failed to reject null hypotheses. The analyses showed clearly that burrowing and arboreal species were closer in environmental space when seasonal niches of the burrowing species were used, rather than annual niches. That is, climatic conditions in seasonal niches of burrowing species resemble the annual niches of arboreal species, supporting the proposition that reduction of activity to certain periods of the year is a strategy in burrowing species to conserve their tropical niches while living in dry regions.

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Highlights

- Most New World hylid frogs have tropical distributions but two burrowing species of the *Smilisca* group, *S. fodiens* and *S. dentata*, extend into higher latitudes and drier conditions in regions of North America, raising the question of how are they able to do so?
- We found that seasonal niches of burrowing species showed reduced environmental distances in relation to the remaining species of the *Smilisca* group, supporting the hypothesis that they evolved a novel behavior while maintaining physiological conservatism.
- Members of this group of frogs appear to have adapted to novel environments at higher latitudes by adopting behaviors that restrict activity to the warm and wet seasons, while conserving their tropical niche characteristics.
- Our findings therefore highlight the importance of considering seasonal niches of burrowing species as facilitating the colonization of regions with adverse seasonal conditions.
- Failure to consider aspects of a species' life history, such as behavior, can lead to misinterpretation of niche evolution and conservatism.

Keywords: behavior, Central America, ecological niche modeling, frogs, hylids, niche conservatism, niche divergence,

Introduction

In amphibians, species' presence in permanent populations at higher latitudes is limited by narrow physiological tolerances with respect to temperature and precipitation since the annual variation of these parameters is more significant within temperate regions than in tropical regions (Janzen 1967, Ghalambor et al. 2006, Hua and Wiens 2009, Sunday et al. 2010, Sunday et al. 2019). These physiological limits might be the factor that prevents large numbers of amphibian groups from expanding further northward into the drier and temperate regions of North America (Wiens et al. 2006). This pattern fits with Janzen's hypothesis, which links two important assumptions: that the degree to which topographic barriers limit dispersal depends on the temperature gradient across that barrier, and that seasonal stability of temperature (as in tropical mountains) would select for species with narrow thermal tolerances (Janzen 1967, Ghalambor et al. 2006, Sunday et al. 2010, Sunday et al. 2019).

In anurans, physiological limitations can be observed within the family Hylidae, and specifically in the Hylinae subfamily. The Hylidae are a group of frogs well-represented worldwide (Duellman 2001, Faivovich et al. 2005), divided into seven subfamilies: Acrisinae, Cophomantinae, Dendropsophinae, Hylinae, Lophohylineae, Pseudinae, and Scinaxinae. The Hylinae are widely distributed in the New World, including ~174 described species. They are known as treefrogs because most species have adhesive discs on their toes: the secretion of mucus glands creates surface tension, allowing them to climb (Vitt and Caldwell 2014, Wells 2010). Almost all species of Hylinae have tropical distributions; the clade apparently encountered a climatic barrier roughly corresponding to the latitude of central Mexico that has prevented them from expanding further northward into temperate regions (Wiens et al. 2006). Explanations for these barriers have focused on the limited thermal adaptation in this group, and interactions with climates available in this region (Wiens et al. 2006, Hua and Wiens 2009).

Nevertheless, as every rule has its exception, a few species of Hylinae extend their distributions further northward in North America. The genus *Smilisca* includes two of these species. As with most Hylinae species, *Smilisca* is distributed across the Neotropics, but *S. fodiens* (Boulenger, 1882) extends north along the Pacific slope of Mexico from Michoacán to south-central Arizona (Sullivan et al. 1996, Duellman 2001). *Smilisca baudinii* (Duméril & Bibron, 1841) and *S. cyanosticta* (Smith, 1953) are distributed in southern Mexico's coastal lowlands and *S. dentata* (Smith, 1957) extends farther north onto the dry Mexican Plateau in Jalisco and Aguascalientes (Duellman 2001). The species *S. puma* (Cope, 1885), *S. sordida* (Peters, 1863), and *S. sila* (Duellman & Trueb, 1966) are distributed further south in Central and South America. Finally, *S. phaeota* (Cope, 1862) reaches Colombia and northern Ecuador (Duellman 2001, Fig. 1). In summary, of the eight species of the group, only *S. fodiens* and *S. dentata* have invaded regions with drier and more seasonal conditions—these same two species are those

in the genus that have the burrowing habit (Duellman 2001, Vitt and Caldwell 2014).

A molecular phylogenetic study placed *S. fodiens* and *S. dentata* within *Smilisca* (Faivovich et al. 2005); however, they share morphological characteristics and were previously placed in a separate genus *Pternohyla* (Duellman, 2001). They have morphological features typical of digging anurans: integumentary-cranial co-ossification of the skull, short limbs, reduced terminal discs on the digits, and a specialized inner metatarsal tubercle (Duellman 2001). Burrowing anurans are adapted to digging, so they share morphological characteristics designed for this purpose. Some frogs burrow only occasionally; others spend long periods underground, surfacing periodically for feeding and breeding; and still others are entirely subterranean, feeding and reproducing under the substrate (Emerson 1976, Nomura et al. 2009, Wells 2010, Sunday et al. 2014, Beever et al. 2017, Moore et al. 2018, Székely 2018).

Both *S. fodiens* and *S. dentata* are known to spend long periods underground, avoiding dry and cold surface conditions at certain times of the year: indeed, they can form cocoons and go through a dormancy period inside burrows. As adverse conditions pass through the year, the activity that makes individuals detectable on the surface is triggered (Ruibal and Hillman 1981, Sullivan et al. 1996, Stebbins 2003, Quintero-Díaz and Vázquez-Díaz 2009). On a large scale, in *S. fodiens*, a latitudinal gradient of seasonal climate variation on the surface is linked to favorability of conditions during the year (Encarnación-Luévano et al. 2013). The burrowing habit in *Smilisca* may have evolved in response to increased aridity during the Pleistocene (Duellman and Trueb 1966). Studies of the population biology of *Smilisca* species have been developed (Sullivan et al. 1996, Stebbins 2003, Quintero-Díaz and Vázquez-Díaz 2009, Cox et al. 2012). However, despite its ecological, biogeographic, and evolutionary importance, the relationship between these behavioral traits and adaptation to dry climates has not been analyzed in detail (Encarnación-Luévano et al. 2013). This discussion leads us to consider that burrowing habit in *Smilisca* species constitutes a behavioral adaptation that permits populations to inhabit drier regions while retaining the same physiological constraints for climatic conditions as the tropical species.

Although direct evaluation of physiological constraints would be ideal for testing this assumption, specific data are unavailable for many species in the group. However, correlative ecological niche modeling can be used as a proxy. Actual tolerance limits, reflecting the fundamental ecological niche of a species, are physiological characteristics that can be assessed fully only via physiological measurements. Those characteristics can also be studied via coarse-resolution associations with environments manifested across their geographic distributions (Grinnell 1917, Soberón and Peterson 2005, Soberón 2007, Barve et al. 2014). Under certain assumptions and limitations, correlational ecological niche modeling approaches

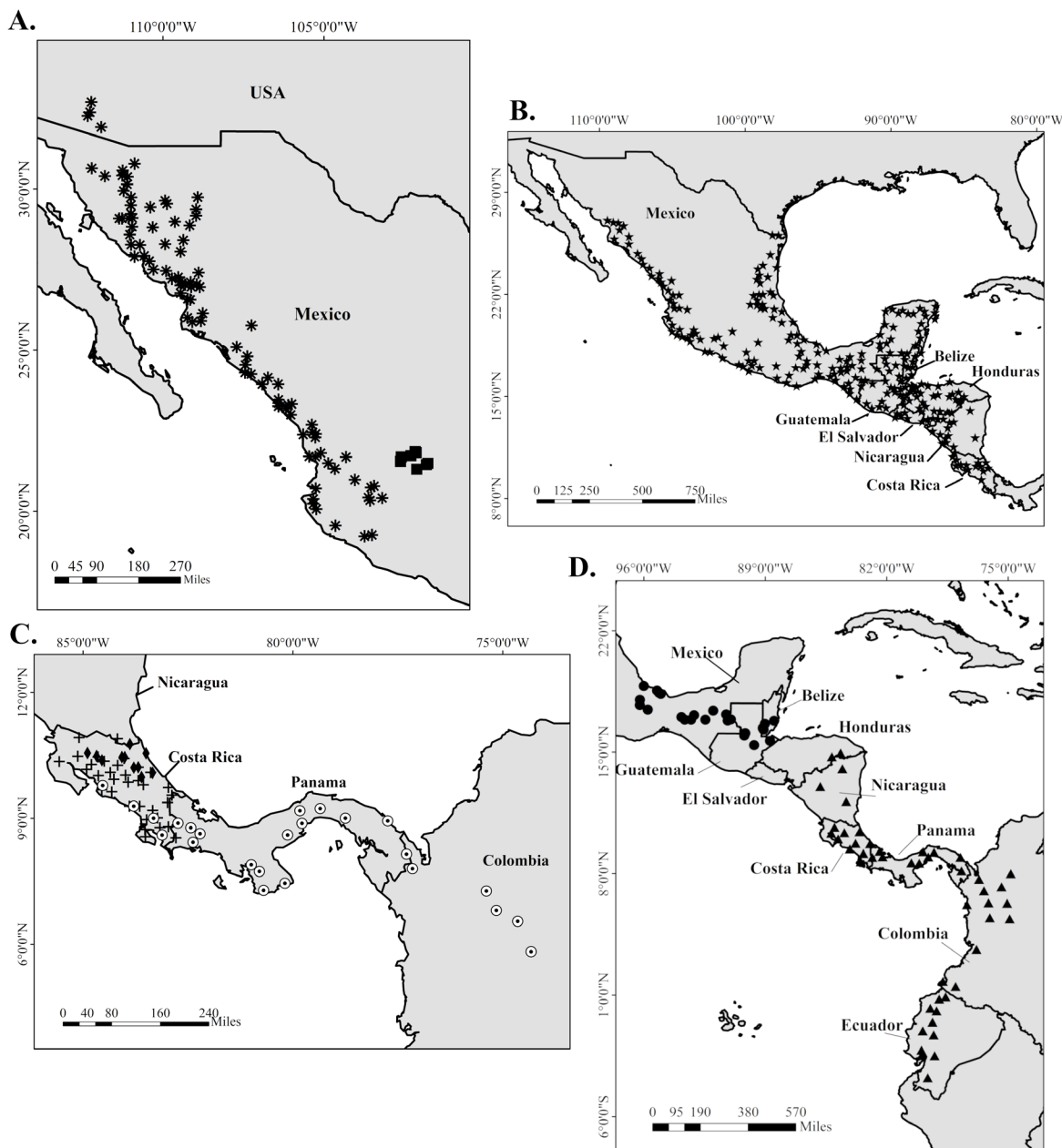


Figure 1. Distribution of *Smilisca* frogs across North and South America. *Smilisca fodiens* (asterisks) ranges along the Pacific slope of Mexico north to Arizona, *S. dentata* (squares) is found on the Mexican Plateau (a). In lowlands, further south are *S. baudinii* (stars) (b), *S. puma* (rhombs), *S. sordida* (cross), *S. sila* (gray circles) (c). *S. cyanosticta* (black circles) is distributed from southern Mexico to Central America and, finally, the group reaches its southern boundary with *S. phaeota* (triangles) in Colombia and northeastern Ecuador (d).

can estimate limits that approach the fundamental niche (Peterson et al. 2011).

Within the fundamental niche, the realized (existing) niche is that which corresponds to environments actually represented within the species' distributional area (Jackson and Overpeck 2000, Soberón and Peterson 2005). This realized niche can be estimated using correlative modeling approaches (Peterson et al. 2011). In this sense, it has been shown that niches constitute a long-term stable constraint on the geographic potential of species (e.g. Araújo

and Pearson 2005, Soberón 2007). However, as the environmental conditions available within the historically accessible area change over time, the species can follow the spatial footprint of its ecological niche through dispersal and colonization, or it adapt its ecological niche via evolutionary responses at the physiological level (Holt 1990), or it can become extinct. However, evolved behavioral changes can offer an alternative, thus avoiding the need for dispersal (Duckworth 2009), even if optimal physiological ranges do not change (Angilletta et al. 2002, Navas et al. 2008,

Wells 2010, Weatherhead et al. 2012, Beever et al. 2017), and such changes can affect the direction and rate at which morphological or physiological traits evolve (Huey et al. 2003, Muñoz et al. 2016, McEntire and Maerz 2019).

Ideas regarding the evolution of ecological niches have caught the interest of many authors (e.g., Wiens and Graham 2005, Warren et al. 2008, Peterson 2011, Broennimann et al. 2012). For example, several studies matched evolutionary information with adaptation to climate and other aspects of the environment to improve the understanding of species' niche evolution (e.g., Peterson et al. 1999, Martínez-Meyer et al. 2004a, Jakob et al. 2007, Pearman et al. 2008, Pearman et al. 2010, Brown and Carnaval 2019). However, few studies have explored relationships between behavioral innovation and ecological niche conservatism (Martínez-Meyer et al. 2004a, Martínez-Meyer et al. 2004b, Nakazawa et al. 2004). Using ecological niches as a proxy of physiological constraints, we tested whether burrowing *Smilisca* species have retained ecological niche characteristics similar to those of the arboreal species distributed under tropical conditions by relaxing climatic constraints in a seasonal niche behaviorally. We made niche comparisons between the annual niches of the arboreal species and niches of the burrowing species under two assumptions: seasonal niches corresponding to the periods that the species spend active on the surface, and full annual niches. It is important to emphasize that niches were measured via climatic conditions corresponding to environments outside burrows. We then employed ecological niche similarity tests in geographic and environmental spaces to assess niche similarity and difference patterns.

Materials and Methods

In ecological niche modeling (ENM), three major factors are considered to explain distributions of species: biotic (**B**), abiotic (**A**), and mobility (**M**) constraints (BAM; Soberón and Peterson 2005). Biotic factors are denoted by **B**; however, at coarse resolutions, the biotic component is frequently diffuse and non-limiting, in contrast to how it is manifested at finer spatial resolutions (Peterson and Soberón 2012). On the other hand, the remaining two components have broad-scale effects. The abiotic factors, called **A**, represent the geographic region presenting favorable conditions, and, finally, **M** is the area that has historically been accessible to the species via dispersal over relevant periods (Peterson et al. 2011). Although this approach is simplified based on static approximations to the three classes of factors (Barve et al. 2011), it has proven to be a useful heuristic test. Since our hypothesis was tested on geographic extents, a coarse resolution, the component **B** was not considered. Evaluations of niche similarity were made in terms of whether two niches are more similar than expected given the set of environments

accessible to each species across its **M** (Warren et al. 2008, Peterson 2011).

To test hypotheses of niche similarity, we considered those climatic conditions that a species experiences when it is active outside burrows. In the case of arboreal species, the niche is annual since these species experience the environment outside burrows throughout the year (Duellman, 2001). In the case of burrowing species, however, the niche is seasonal since they are active outside burrows during specific periods of the year. However, a comparison was also made considering the burrowing species as having activity throughout the year, which is not the case (Sullivan et al. 1996, Stebbins 2003, Quintero-Díaz and Vázquez-Díaz 2009). Our analyses of niche similarity were therefore performed by (1) comparing niches of the two burrowing species as if they were active all year outside their burrows (i.e. annual niches) with annual niches of the non-burrowing species, and (2) comparing seasonal niches of burrowing species (June – October) with the annual niches of the non-burrowing (i.e. arboreal) species (see *Niche similarity tests* section for details). These comparisons were achieved using the background similarity test, as manifested in geographic (Warren et al. 2008) and environmental (Broennimann et al. 2012) spaces.

Biological and environmental data

Occurrence data were obtained from online portals providing access to primary biodiversity data, including GBIF, VertNet, and UNIBIO¹, as well as from specialized literature (Sullivan et al. 1996, Duellman 2001). All records were assessed and verified in both geographic and environmental spaces in ArcGIS (v10.1, ESRI, Redlands, CA), in search of inconsistencies in either or both of the spaces. For records lacking geographic coordinates but including textual information about location, coordinates were assigned using digital gazetteers: BioGeomancer (www.biogeomancer.org) and Georeferencing Calculator (www.manisnet.org, Wieczorek and Wieczorek 2015). Numbers of occurrence points available for each species after these checks were 121 for *S. fodiens*, 8 for *S. dentata*, 311 for *S. baudinii*, 30 for *S. cyanosticta*, 30 for *S. sila*, 11 for *S. puma*, 43 for *S. sordida*, and 58 for *S. phaeota*.

Environmental data were obtained from WorldClim Version 1.4 (Hijmans et al. 2005; <http://www.worldclim.org/>), at a spatial resolution of 2.5' (~4.7 km). Of the 19 climatic variables, we selected 11: annual mean temperature, mean diurnal range, isothermality, temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, temperature annual range, annual precipitation, precipitation of wettest month, precipitation of driest month, and precipitation seasonality. For the seasonal period of the burrowing species, these variables were constructed using monthly climatic information of minimum temperature, maximum temperature, mean temperature, and total precipitation, considering the period June-October and following the calculation

¹ <https://www.gbif.org/>, <http://vertnet.org/>, <http://unibio.unam.mx/>, last accessed 04/02/2020

of the bioclimatic predictors proposed in O'Donnell and Ignizio (2012) and Nakazawa et al. (2004). We established this period as the seasonal niche since the occurrence data for *S. fodiens* and *S. dentata* came from those months only. To assure comparability of models, we used the same reduced set of climatic variables for the annual niches (the 11 previously selected climatic variables along the whole year).

Ecological Niche Modeling

For niche model calibration, we applied the maximum entropy algorithm implemented in Maxent (v3.3.3.e; Phillips et al. 2006), which fits a distribution of probabilities across the study area subject to the constraints of the environmental characteristics of known occurrences. Evaluation data were separated *a priori*, so no data were assigned for evaluation within Maxent. Other settings included: regularization value = 1, maximum number of points for the background = 10,000, maximum iterations = 500, and convergence threshold = 0.00001. We turned off the clamping and extrapolation options, following Owens et al. (2013), to avoid extrapolation to extreme values of environmental variables. To convert outputs into binary maps, we used an adjusted least presence training approach (Pearson et al. 2007), with a maximum omission tolerance threshold of $E = 10\%$ (Peterson et al. 2011).

Species for which >25 occurrences were available were divided into random subsets of 80% for model calibration and 20% for model evaluation. Models for *S. dentata* and *S. puma*, for which fewer occurrence points were available, were calibrated with all available data. Models were calibrated across regions posited as historically accessible to each species (**M**, see Fig. S1), which were delimited considering aspects of the distribution and life history of each species (Barve et al. 2011), using the limits of the surrounding ecoregions (Olson et al. 2001) as a guide, selecting those ecoregions that coincided with at least one locality of the species to represent the accessible area (see Fig. S1). Once models were calibrated, they were transferred to a broader region, which covered the union of the **M** hypotheses across all of the species: these geographic views of suitability were used in Warren's geography-based niche similarity tests.

For species with ≥ 25 occurrences available, model evaluation was accomplished using a modification of the area under the curve of the receiver operating characteristic (partial ROC AUC ratios; Peterson et al. 2008), as implemented in Barve (2008). This test only evaluates models over the spectrum of the prediction and allows for differential weighting of the two error components (omission and commission; Peterson et al. 2008). Thus, AUCs were limited to the proportional areas over which the models actually made predictions, and we only considered models that presented omission errors < 5% (Peterson et al. 2008). For two species with fewer occurrences (*S. dentata*, *S. puma*), model evaluation was accomplished via the jackknife strategy developed for small sample-size situations by Pearson et al. (2007): significance was evaluated over

n models, each excluding one locality from among the n available and evaluating the success of the model in terms of anticipating the excluded locality. The probability of these observed levels of success and failure was calculated using scripts provided by Pearson et al. (2007). This test was applied to binary models created by applying minimum training presence (MTP) approaches (Pearson et al. 2007).

Niche similarity tests

We used two complementary testing approaches to assess the null hypothesis that two species were not less similar than expected by chance, given the environments available to each of them across its accessible area. The first method was carried out in geographic space with the background similarity test proposed by Warren et al. (2008), in which Schoener (D) and Hellinger (I) indices were used to quantify similarity between niches of each pair of species. Index values were compared against a null distribution of similarity values from comparisons to models based on random points from sites across the transfer area and comparisons in both directions (i.e. species A vs. random points for species B and *vice versa*). With this test, the environmental heterogeneity across the **M** regions was incorporated explicitly in our testing. Probabilities were calculated based on direct counts of numbers of null model replicates (out of a total of 100): if the observed similarity value fell in the lower 5% of the null distribution, the null hypothesis was rejected and the niches were considered to be more different than expected by chance. Niche-overlap values were calculated through the niche-overlap function of the PHYLOCLIM package (Heibl and Calenge 2013) R (v3.4.1, R Foundation for Statistical Computing, Vienna, AT). It is important to note that this method demands that models for the two species be transferred to a common geographic area, which generally involves some degree of model extrapolation (Owens et al. 2013).

The second method of assessing niche similarity was performed in environmental space (following Broennimann et al. 2012). This method uses the Schoener's D metric (Schoener, 1970) as a measure of environmental overlap, and includes a statistical framework to test for niche similarity parallel to that of Warren et al. (2008). We used the same criteria for conclusions of statistical significance. With this method, a multivariate environmental grid is created using the first two axes of a PCA (PCA-env) that summarizes the environmental variables previously selected. A Gaussian kernel density is applied to estimate the occupancy of each cell (z_{ij}), and the D metric is calculated based on the different z_{ij} values obtained (Broennimann et al. 2012). This analysis was performed using the Ecospat package (Di Cola et al. 2017) in R. We used the "lower" option to focus our tests on cases of niche differentiation; we developed these tests for annual and seasonal comparisons. Thus, for both testing approaches, we present 24 comparisons: six arboreal species versus two burrowing species, and considering two periods of activity (annual and seasonal).

Results

The occurrence data for *Smilisca* overall reflect a distribution centered in tropical lowland regions (Fig. 1). With the exception of the broad distribution of *S. baudinii*, three biogeographic features interrupt the geographic continuity of the group: Transverse Volcanic Belt, Balsas Depression, and Sierra Madre del Sur, all located in central and southern Mexico. Apart from *S. baudinii*, these features separate the dry-zone burrowing species, *S. fodiens* and *S. dentata*, from the arboreal species in the tropical environments to the south. Of the six arboreal species, only *S. baudinii* occurs in xeric environments, overlapping with the southernmost parts of the range of *S. fodiens*.

The ecological niche models for *S. fodiens*, *S. baudinii*, *S. cyanosticta*, *S. phaeota*, *S. sila*, and *S. sordida* performed better than expected by chance ($P < 0.001$). Mean AUC ratios ranged from 1.21 (*S. phaeota*) to 1.88 (*S. sordida*), with no AUC ratios < 1 in any replicate, indicating a performance that was uniformly better than random (Table S1). The niche models generated for the two species with < 25 localities, *S. dentata* and *S. puma*, also performed better than would be expected by chance, although this finding was based on a different statistical test (Pearson et al. 2007) ($P < 0.001$; Table S1).

In geographic space, with the background similarity test, the comparisons were made in both directions (i.e. species A vs. species B and *vice versa*). When annual niches were used for burrowing species and compared with annual niches of arboreal species, 18 of the 24 tests rejected the null hypothesis of niche similarity ($P < 0.05$; Fig. 2a). In contrast, when seasonal niches

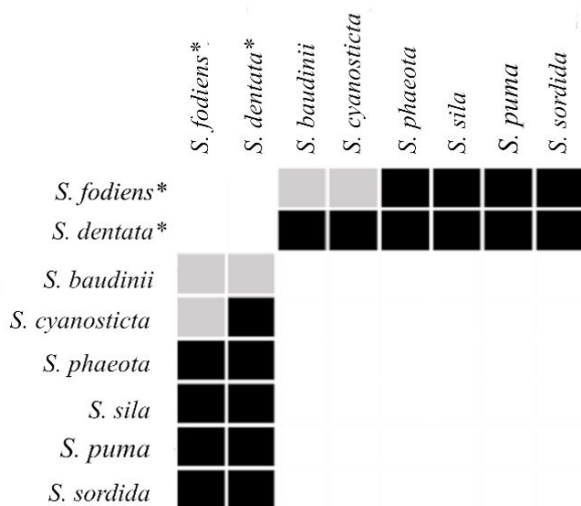
for burrowing species were compared to annual niches of the remaining species, the null hypothesis of niche similarity could be rejected in only 5 of the 24 tests (i.e., most of the comparisons with $P > 0.05$; Fig. 2b).

In environmental space, we performed 24 comparisons of the species' ecological niches. The D values of these tests ranged from 0 to 0.13, and P values from 0.287 to 0.98, such that all of the observed similarity values between annual or seasonal niches of burrowing species and annual niches of arboreal species did not differ from random expectations (Table 1). However, environmental distances (PCA-env) between burrowing and arboreal species were much shorter when seasonal niches of the burrowing species were used, rather than annual niches (Fig. S2). As examples, comparisons between the burrowing species *S. fodiens* and the arboreal species *S. phaeota* and *S. sila* show clearly the proximity between occurrences in environmental space when seasonality is taken into account (Fig. 3). For the burrowing species *S. dentata*, seasonal-niche proximity is not as clear as in *S. fodiens*. However, the reduction in distance between environmental densities of occurrence and environments of the area of accessibility can be observed in comparisons with *S. baudinii* and *S. cyanosticta* (Fig. 3).

Discussion

Our results suggest that the success of the *Smilisca* group in adapting to novel environments at high latitudes was achieved by adopting behaviors that restrict activity to the warm and wet seasons and thereby involve the conservation of a niche of tropical

a) Annual niche comparisons



b) Seasonal niche comparisons

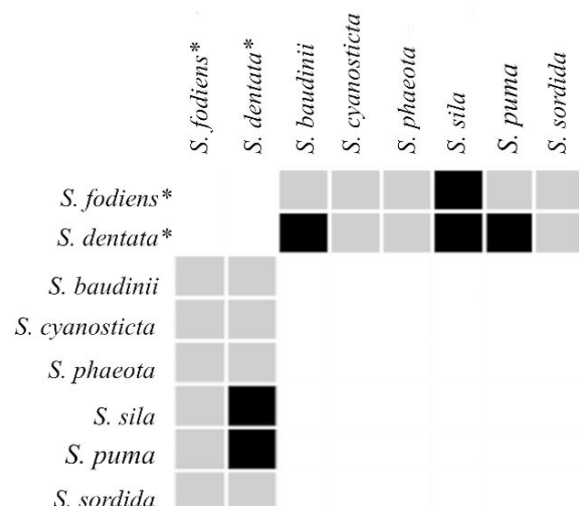


Figure 2. Matrices showing results of the geographic background similarity test approach of Warren et al. (2008) applied to *Smilisca* species. Niche comparisons are shown under two scenarios: when burrowing species (*) are considered in terms of their annual niches (a) and when they are considered in terms of their seasonal niches (b). In the matrices, we present comparisons in both directions (i.e. species A vs. species B and *vice versa*). Cells in gray indicate that the niche comparisons cannot be distinguished from what is expected under the null model ($P > 0.05$); cells in black correspond to comparisons in which the null hypothesis was rejected ($P < 0.05$).

Table 1. Comparisons in environmental space of seasonal niches of burrowing species of *Smilisca* versus annual niches of arboreal species, and of annual niches of burrowing species versus annual niches of arboreal species. We present the Schoener's index (*D* values) and the significance of the similarity tests. Tests were performed choosing alternative = "lower" for divergence.

Burrowing species	Arboreal species	Seasonal tests		Annual tests	
		<i>D</i> value	<i>p</i> value	<i>D</i> value	<i>p</i> value
<i>Smilisca fodiens</i> vs.	<i>S. baudinii</i>	0.095	0.851	0.1310	0.9207
	<i>S. cyanosticta</i>	0.153	0.950	0.1116	0.9802
	<i>S. phaeota</i>	0.132	0.901	0	–
	<i>S. puma</i>	0.019	0.673	0	–
	<i>S. sila</i>	0.035	0.851	0	–
	<i>S. sordida</i>	0.157	0.911	0	–
	<i>S. baudinii</i>	0.005	0.851	0	–
<i>S. dentata</i> vs.	<i>S. cyanosticta</i>	0	0.842	0	–
	<i>S. phaeota</i>	0	0.634	0	–
	<i>S. puma</i>	0	0.871	0	–
	<i>S. sila</i>	0	0.881	0	–
	<i>S. sordida</i>	0	0.901	0	–

origin. There is evidence that populations of *S. dentata* and *S. fodiens* exhibit no surface activity during parts of the year, in contrast to other species of the group. For *S. baudinii*, formation of a cocoon was described for a single individual found in a roadbed at Estación Experimental Enrique Jiménez Núñez in Guanacaste, Costa Rica (McDiarmid and Foster, 1987), yet surface records exist throughout the species' geographic distribution during all months of the year, which we interpret as annual activity outside burrows. It has also been described that *S. baudinii* finds refuge in bromeliads, elephant-ear plants, tree holes, or tree bark under unfavorable conditions (Duellman 2001). *Smilisca cyanosticta*, *S. phaeota*, and *S. puma* are active throughout the year, and *S. sila* and *S. sordida* are active for most of the year, although their reproduction is concentrated in dry seasons to exploit the low levels and transparency of the water in streams at that time (Duellman 2001). We believe that it is of the utmost importance to expand field information to better understand the natural history of these species, especially in the form of population studies across their distributional areas. Such a set of studies would enrich hypotheses like the one explored here, perhaps managing to integrate mechanistic (fine-scale) and correlative models (coarse scale).

Since most New World hylids have tropical distributions, the more extensive latitudinal range of *Smilisca* represents an evolutionary success story: by overcoming significant biogeographic barriers, two species in this genus have succeeded in adapting to dry regions. The inability of groups to invade novel climatic conditions owing to lack of ecological or physiological adaptations has been cited as evidence of niche conservatism (Hua and Wiens 2009). In ectotherms, low evolutionary potential in thermal traits, and slow rates of evolution at the warm end of the thermal performance curve, have been observed

widely (Snyder and Weathers 1975, Araujo et al. 2013, Grigg and Buckley 2013, Muñoz et al. 2014, Bodensteiner et al. 2020). In general, amphibians have limited dispersal ability (Duellman and Trueb 1986, Smith and Green 2005, Wells 2010). As such, under novel climatic conditions, changes in behavior can offer an alternative for persistence despite environmental pressures (Duckworth 2009, Sunday et al. 2014, Beever et al. 2017), since behavioral traits may be more labile than physiological and morphological traits (West-Eberhard 1989, Pigliucci et al. 2006, Huey et al. 2003, Duckworth 2009). In contrast, Janzen (1967) offered the hypothesis that latitudinal variation in climate and its seasonality shapes the evolution of physiological tolerances, which in turn determines the ability of a species to tolerate novel environments (Janzen 1967, Ghalambor et al. 2006). This hypothesis suggests that, in amphibians, colonization between tropical wet environments and dry environments would be rare (Willig et al. 2003). This is consistent with their narrow thermal limits, as has been shown for many tropical ectotherms (Snyder and Weathers 1975, Addo-Bediako et al. 2000, Sunday et al. 2010, Payne and Smith 2016, Sunday et al. 2019). In fact, the northern distributional limits for most tropical hylids converge around latitude 32°N in the Americas (Wiens et al. 2006).

Our finding can be explained via a new extension of Janzen's hypothesis that refers to subterranean habitat, which asserts that climatic stability is greater in the latter than in surface habitats: thermal seasonality drives subterranean species towards narrow thermal specialization and low dispersal capacity (Mammola et al. 2019), because they would be more likely to encounter temperatures outside their thermal tolerance (Ghalambor et al. 2006). In frogs and lizards, microhabitats (e.g. soil, tree holes, epiphytes, and vegetation) reduce mean temperature by 1–2 °C and

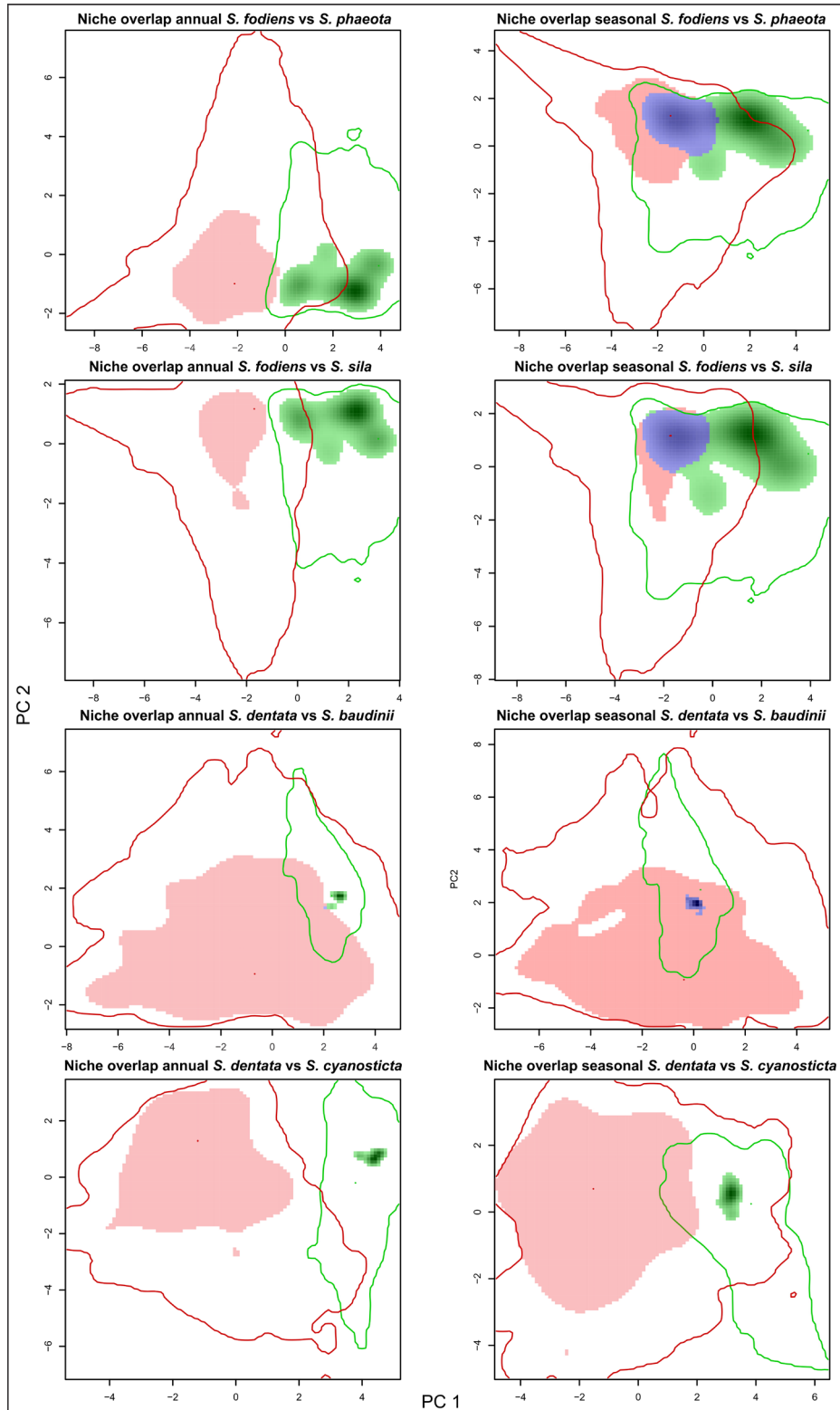


Figure 3. Niche comparisons in environmental space between the burrowing and arboreal species of *Smilisca*. We present comparisons between *S. fodiens* and the arboreal species *S. phaeota* and *S. sila*, and comparisons between *S. dentata* with the arboreal species *S. baudinii* and *S. cyanosticta*. According to the similarity test of Broennimann et al. (2012), we present two principal components plots as a result of PCA-env analysis. The plots on the left are comparisons when burrowing species are considered as annual, and the plots on the right show when the niches of burrowing species are considered as seasonal. In each plot, shading areas show the density of the occurrences of the species by a cell. The solid contour lines illustrate 100% of the available (background) environment. The green color represents the burrowing species and the red color the arboreal species. The blue shaded areas are the niche intersections among kernel densities of occurrences.

reduce the duration of extreme temperature exposure 14- to 31-fold (Scheffers et al. 2014). Moreover, burrows provide an environment buffered against extremes (high temperature, low humidity; Porter et al. 1973, Moore et al. 2018, Szekey et al. 2018). In addition, the temperature ranges that ectotherms tolerate generally represent the same range of equivalent biological rates for both cool and warm adapted species, regardless of latitude (i.e. narrower range of temperatures must be found in both; Payne and Smith 2016). Therefore, subterranean habitat provides optimal range temperatures for high-latitude species where cold and aridity may limit species' ability to persist (Stevenson 1985, Grant and Duhnham 1988, Scheffers et al. 2014, Sunday et al. 2014, Beever et al. 2017, Moore et al. 2018, Bodensteiner et al. 2020).

Our niche comparison results considering seasonal niche activity for burrowing species coincided in highlighting a reduction in the environmental distances that separate these niches from burrowing species to the rest of the species of *Smilisca* group. Thus, we found that apparent differences between niches of burrowing and arboreal *Smilisca* species largely disappeared when tests focused on environments associated with the actual periods of activity of each species. This result may indicate that they evolved a novel behavior that allowed for physiological conservatism, rather than actually changing the physiology *per se*. Our results demonstrate that, at least for some groups, failure to consider aspects of life history, such as behavior, can lead to incorrect results regarding niche conservatism. Numerous studies to date have analyzed the evolution of niches among closely related species in a great diversity of taxa (e.g., plants, invertebrate, vertebrates), and have found that niches generally appear to remain constant over phylogeny, at least in the short-to-medium term (see Peterson 2011). In general, the closer the phylogenetic relationship of the species, the more similar their ecological niches will be (Peterson et al. 1999, Warren et al. 2008, Eaton et al. 2008, Petitpierre et al. 2012). However, these studies make little reference to the life history of the species concerned.

In *Smilisca*, burrowing species have morphological characters that allow them to persist in more arid environments than other members of the group (Duellman 2001), although no evidence clarifies how these adaptations evolved (Nomura et al. 2009). Phylogenetic analysis suggests that burrowing species are derived from southern ancestral populations (Cox et al. 2012). As yet, no physiological studies exist to illuminate similarities in thermal tolerances. However, it has been shown that physiological mechanisms are conserved in these organisms (Angilletta et al. 2002, Navas et al. 2008, Weatherhead et al. 2012, Buckley et al. 2015), leaving behavioral shifts as a means to achieve response to climatic change, buffering mortality and selection, and ultimately reducing local adaptation across geography (Araújo et al. 2013; Scheffers et al. 2014, Sunday et al. 2014, Buckley et al. 2015, Beever et al. 2017, Moore et al. 2018, Székely et al. 2018). In fact, among populations

within the burrowing *S. fodiens*, surface activity across the distribution range is seasonally marked and is predictable from the temporal and geographic variation of suitable climatic conditions (Encarnación-Luévano et al. 2013).

Finally, we would like to emphasize that our niche analyses have illustrated how two species of *Smilisca* managed to invade dry regions through behavioral shifts in the context of niche conservatism. This study illustrates how evolution of behavioral characters can facilitate the invasion or persistence in regions that present otherwise unfavorable environments, as an alternative explanation to Janzen's hypothesis.

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Data Accessibility Statement

The authors confirm that the data supporting the findings of this study are available on request from the corresponding author.

Supplementary Material

The following materials are available as part of the online article from <https://escholarship.org/uc/fb>
Table S1. Performance values for the models evaluated through the partial ROC and n-1 "Jackknife" tests.
Figure S1. Geographic regions posited as historically accessible (**M**) to each species of the *Smilisca* group.
Figure S2. Environmental distances (PCA-env) between burrowing and arboreal species.

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