

Thermal niche breadth and their relationship with *sturnira* bat species diversification

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ABSTRACT

The interaction between climatic conditions and the ability of organisms to maintain homeostasis regulates the distribution of species on the planet. However, its influence on macroevolutionary dynamics is not well understood. It has been suggested that diversification rates will be different in lineages with narrow thermal niches (specialists) to diversification rates in generalist lineages, but the evidence for this is elusive. Here, we tested this hypothesis by using the most diverse (in species richness and geographic range variation) tropical bat genus within the Phyllostomidae family. We estimated the realized thermal niche breadth of *Sturnira* species from their geographic range and categorized them as generalists, cold specialists, or warm specialists. We compared dynamic evolutionary models that differ in 1) niche breadth evolution, 2) parental niche breadth inheritance, and 3) whether niche breadth evolution is associated with shifts in diversification rates. Our best-performing model indicates that most *Sturnira* species arose as specialists in warm climates and that over time, their niche breadth broadens, and just a subset of those species becomes specialists in cold environments. We found that the evolution of realized thermal niche breadth causes fluctuations in per-lineage rates of diversification, where warm specialists boast the highest speciation rates. However, we found no evidence of these changes in niche neither triggering nor being a result of speciation events themselves; this suggests that diversification events in *Sturnira* could instead depend on allopatric speciation processes such as the development of geographic barriers.

1. Introduction

Ecological niche theory postulates that species occupy specific positions within ecosystems, and the boundaries of their positions are set by abiotic and biotic factors (Hutchinson 1957, 1959). How species have sorted out in this niche space results from ecological and evolutionary drivers. Ecological niche theory has been used to understand species coexistence, trophic position, geographic range, ecological specialization, and species diversification (Colwell and Futuyma, 1971; Devictor et al., 2010; Johnson, 2010; Slatyer et al., 2013). The emergence and popularization of computational models and phylogenetic and environmental data availability have facilitated that niche is being analyzed in an evolutionary phylogenetic context for different taxa (Lancaster and

Humphreys, 2020; Pie et al., 2021; Rice et al., 2003; Varzinczak et al., 2019). In the first instance, reconstructing the ancestral states of the ecological niche of species (Eaton et al., 2008; Rice et al., 2003), but recently modeling the niche breadth evolution (Castro-Insua et al., 2018; Gómez-Rodríguez et al., 2015; Rolland and Salamin, 2016). Niche breadth could have multiple dimensions, one of them being the thermal niche which is crucial to understand how biotic and abiotic factors impact the geographic distribution, survival, and reproduction of organisms (Gvoždík 2018; Saldaña-Vázquez et al., 2020; Sexton et al., 2017). However, how the thermal niche of species influences the chances of speciation/extinction has been scarcely explored (García-Porta et al., 2019; Lancaster and Humphreys, 2020; Rohde, 1992; Rolland and Salamin, 2016), especially in species of the same genera,

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but with great thermal niche diversity.

How does the position of species within the niche space inform us about underlying macroevolutionary dynamics? For example, a group of closely related species occupying a specific region of ecological niche space may indicate: 1) they may have escaped the density-dependent dynamics of the entire clade and/or 2) they may have evolved into a zone of adaptation. The position of a given species in the niche space can change over time or occupy more than one position. Previous studies have documented a variation in niche volume at the onset of species divergence, which suggests a link between the niche breadth of species and speciation events (Castro-Insua et al., 2018; Gómez-Rodríguez et al., 2015; Pie et al., 2021; Rolland and Salamin, 2016). In the case of thermal niche, changes in its breadth could impact the ability to maintain a constant temperature, which is a fundamental physiological challenge: the tolerance to high or low temperatures is a good predictor of geographic range size or the ability to colonize various habitats (Young et al., 1989; Zhaozhi et al., 2017). The current variability in the thermal niche can result from rapid evolution during speciation events or changes in the thermal niche occurring over the species' evolutionary time (Ortega-García et al., 2017). At the same time, differences in the frequency of warm/cold specialists and generalists can directly be linked to differences in diversification rates (i.e., the frequency of

diversification events per time unit; Pie et al., 2021; Rolland and Salamin, 2016). Changes in thermal niche breadth leading to specialization could significantly shape diversification patterns (Castro-Insua et al., 2018; Rolland and Salamin, 2016; see also studies reviewed in Sexton et al., 2017), and literature suggests two routes for this. On the one hand, niche specialization promotes population subdivision, increasing the chances for allopatric speciation (e.g., Salisbury et al., 2012). On the other hand, sympatric speciation could also result from niche specialization when niche partitioning allows the coexistence of a greater number of species (Futuyma and Moreno, 1988).

Evidence of thermal niche shifts taking place is largely missing (but see Hill et al., 2013; Burjan et al., 2021). Hence, we must use phylogenetic reconstructions and modeling to infer the frequency and timing of the events, across a macroevolutionary scale. Branch lengths in a phylogenetic reconstruction depict the time elapsed between species divergences so that changes in diversification rate regimes (clade wide) can be inferred from the distribution of nodes in a phylogenetic tree. The detection of these changes, when linked to thermal niche or any other relevant trait, calls for approaches that can handle the evolutionary processes taking place along the tree branches and at the nodes (Goldberg and Igić, 2012) while being statistically robust (Beaulieu and O'Meara, 2016; Herrera-Alsina et al., 2019).

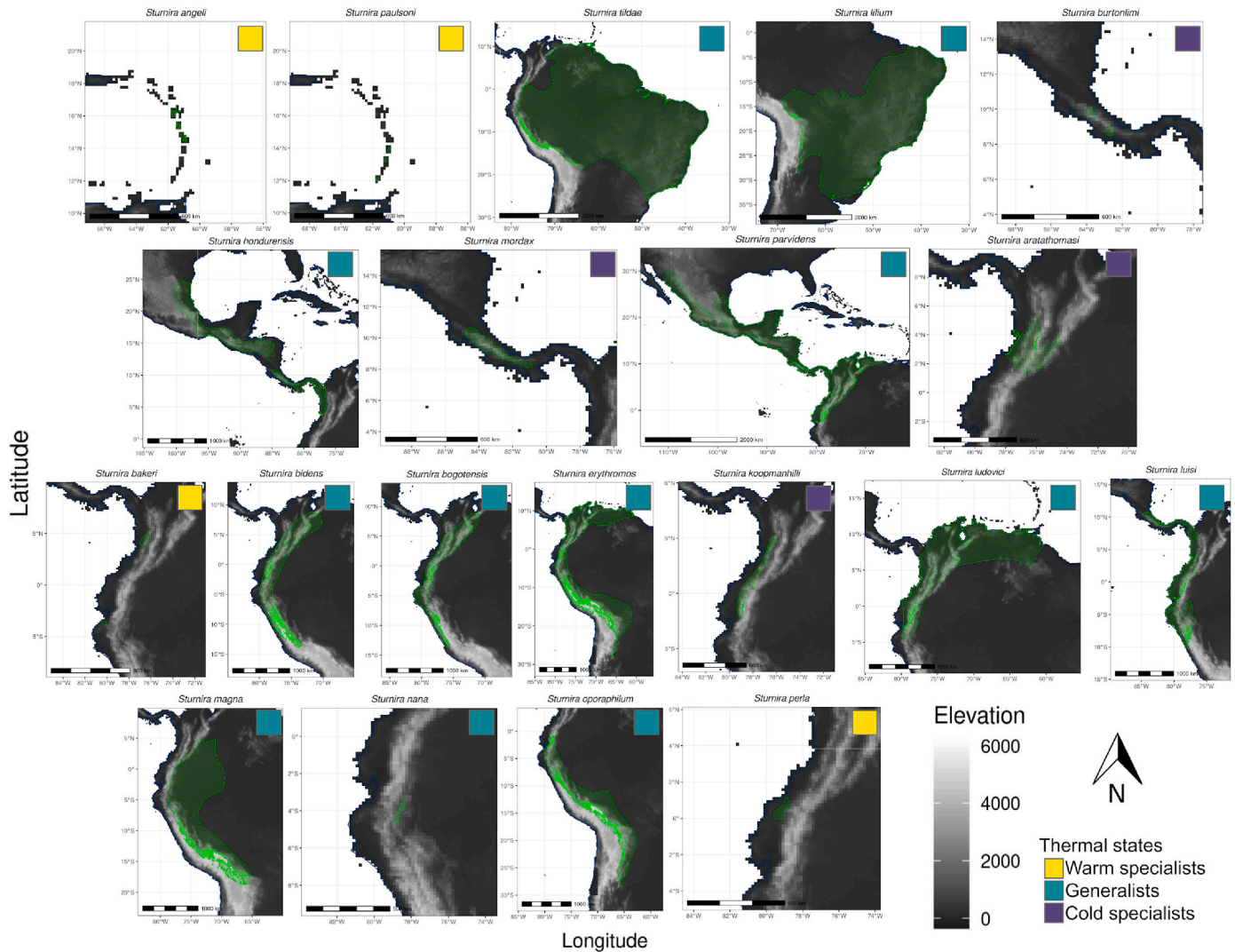


Fig. 1. Geographic distribution maps of *Sturnira* species (shaded and green-edged polygons) overlapped with an elevation layer. The square in the upper right corner of each map indicates the thermal state of the species. All distribution layers were taken from Rojas et al., (2018), and the elevation layer from WorldClim (Fick and Hijmans, 2017). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

The genus *Sturnira* is the result of fast radiation (24 species) occupying 12 biomes, which makes this genus the most diverse and geographically widespread in the Neotropical family Phyllostomidae (Mosquera-Izquierdo et al., 2022; Velasco and Patterson, 2013). The wide distribution of *Sturnira* is reflected in its large altitudinal variation, which ranges from 0 to 3000 m. a.s.l. (Mantilla-Meluk et al., 2017; Velasco and Patterson, 2013) and is associated with a wide range of temperature conditions (Fig. 1). Because *Sturnira* species' presence is more influenced by temperature than food resource availability (Mello et al., 2008), *Sturnira* is an excellent biological model to study the evolution of the thermal niche and its role in its diversification. Do *Sturnira* species change their thermal niche over evolutionary time? Alternatively, could thermal diversity be the outcome of species formation if speciation events are coupled with thermal niche divergence? Previous studies have shown that widespread lineages with exposure to high climatic variation could have diversification processes related to their thermal niche breadth (Gómez-Rodríguez et al., 2015; Sexton et al., 2017), but how this contributes to clade-wide patterns is unknown.

Here, we analyze whether the evolution of the realized thermal niche (hereafter thermal niche) in *Sturnira* bats is related to macroevolutionary dynamics. Using robust phylogenetic data, and high-resolution climatic and geographic data, we fit phylogenetic-informed models that make explicit and contrasting assumptions on thermal niche change over time and its influence on 1) decrease/increase in speciation rates and 2) events of species divergence.

2. Methods

2.1. Geographic range, thermal data, and phylogenetic tree

We obtained the geographic distribution of 20 *Sturnira* species from the supplementary material of Rojas et al. (2018), which represents an update to the distribution polygons available in IUCN (iucnredlist.org) and considers recent reports of occurrence, as well as spatial and climatic variables. The temperature data used to calculate the thermal niche of each species (see below) was obtained from the WorldClim database (Fick and Hijmans, 2017). We downloaded the monthly geographic layers of minimum and maximum temperature, with a resolution of 5 min (0.083° or ~9 km²). We used the *Sturnira* phylogenetic tree from Velasco and Patterson (2013), which was built using nuclear and mitochondrial DNA sequences. This phylogenetic tree included 21 species. *Sturnira giannae* (see Velasco and Patterson, 2019) is the only one without a geographic range polygon and therefore does not have an estimate of its thermal niche.

2.2. Thermal niche breadth and thermal states of the genus *sturnira*

The geographic range of each species was transformed into a presence and absence matrix (PAM) with a cell resolution of 5 min (i.e., Spatial resolution of the WorldClim original data, equivalent to 0.083° or ~9 km²), using the `lets.presab` function of the `letsR` package (Vilela and Villalobos, 2015). We extracted the monthly temperature variation from the minimum and maximum temperature layers using the PAM and the `lets.addvar` function of the `letsR` package (Vilela and Villalobos, 2015) to a total of 12 minimum and 12 maximum temperature data points for each cell, and repeat this procedure for every *Sturnira* species. We selected the lowest among minimum temperatures and the lowest among maximum temperatures, the rationale behind the latter is that bats use shelters during the day, so they are not exposed to the maximum temperatures (Ortega-García et al., 2017). This aspect has not been taken into account by previous studies on neotropical bats (Castro-Insua et al., 2018; Pie et al., 2021).

To measure the thermal niche breadth of a given *Sturnira* species, we used a boxplot of the temperature data of the sites where it is present. The interquartile range (temperature range between the first and third quartile) was taken as its thermal breadth. Next, we needed to classify

the species (see below) into three thermal niche states: thermal generalists, cold specialists, and warm specialists. Using the average of all thermal breadth (10.25 °C) and the median of the thermal data for all species (20.99 °C), we defined generalist species as those with a thermal breadth greater than 10.25 °C. Specialist species are those whose thermal breadth does not exceed 10.25 °C. We further categorized specialists into cold specialists if the median of their thermal breadth (second quartile) is below 20.99 °C or warm specialists if the median of their thermal breadth is greater than 20.99 °C. In Fig. 2, we show boxplots for *Sturnira* species' thermal breadth and their respective thermal niche state: generalists, cold specialists, and warm specialists.

2.3. Models of thermal breadth evolution and its impact on diversification rates

We used *Sturnira* phylogenetic and thermal niche information to fit and compare evolutionary models under a unified likelihood framework (SecSSE; Herrera-Alsina et al., 2019). Although SecSSE requires the transformation of continuous variables into categories (see niche breadth computation above), its usage is recommended because of 1) its statistical performance (i.e., low rates of Type I error) and 2) it enables us to establish a relationship of causality between niche evolution and diversification rates, unlike correlative approaches (e.g., non-parametric methods based on simulations). The latter is accomplished in SecSSE (and similar SSE models) by making rates of speciation and extinction depend entirely on the trait state (i.e., niche width in this case) in a set of equations that are solved to compute the likelihood of the model. We set models that varied in assumptions on processes taking place between speciation events (along the branches of a phylogenetic tree), during the speciation events themselves (nodes in a tree, similar to ClaSSE model; Goldberg and Igić, 2012), and diversification rate fluctuations. Below, we elaborate on these three sources of variations.

We modeled thermal niche evolution as the change in thermal preference that lineages undergo over time. Lineages shifted across the three categories (Warm specialist, Cold specialist, Generalist) under seven different sets of assumptions (Table 1, Fig. 2).

Because changes in the thermal niche could coincide with speciation events (e.g., speciation triggered by a shift in the thermal niche), we considered five modes of how the niche of the parental species (i.e., any internal node in the phylogenetic tree) can be passed onto the daughter species. Under the Thermal Conserved mode, there is no shift in thermal niche during speciation, thus, both daughter species inherit the parental state, i.e., the thermal breadth is phylogenetically conserved. When a subpopulation adapts to different thermal regimes, speciation would occur, causing only one daughter lineage inherits the parental niche (Thermal Divergence mode). In the Thermal Displacement mode, ecological or physiological constraints act upon the parental thermal niche, which is lost during speciation. Therefore, daughter species do not inherit the parental state (i.e., both have the same niche, which is different from the parental one).

Similarly, in Thermal Displacement + Divergence mode, the parental niche is lost, and daughter species drift apart in their thermal niche during speciation: daughter lineages differ in niche from each other and from the parent. Finally, in the Specialization-Triggered mode, both Warm and Cold specialists speciate under Thermal Conserved, while Generalist lineages do so under Thermal Displacement + Divergence, with generalist species producing the two different types of specialists.

We set three different models to explain the branching pattern in the *Sturnira* tree along with thermal niche evolution (hereafter diversification dependence). In the Unique Rate model, we assume that all lineages have the same rate of diversification, which does not fluctuate over time. Compared to the simplistic Unique Rate model, the Variable Rate model assumes variation in diversification regimes across lineages. When comparing across models, the Variable Rate model will be best supported when *Sturnira* species have different rates of diversification due to multiple (unknown) selective pressures. In the Thermal Dependent

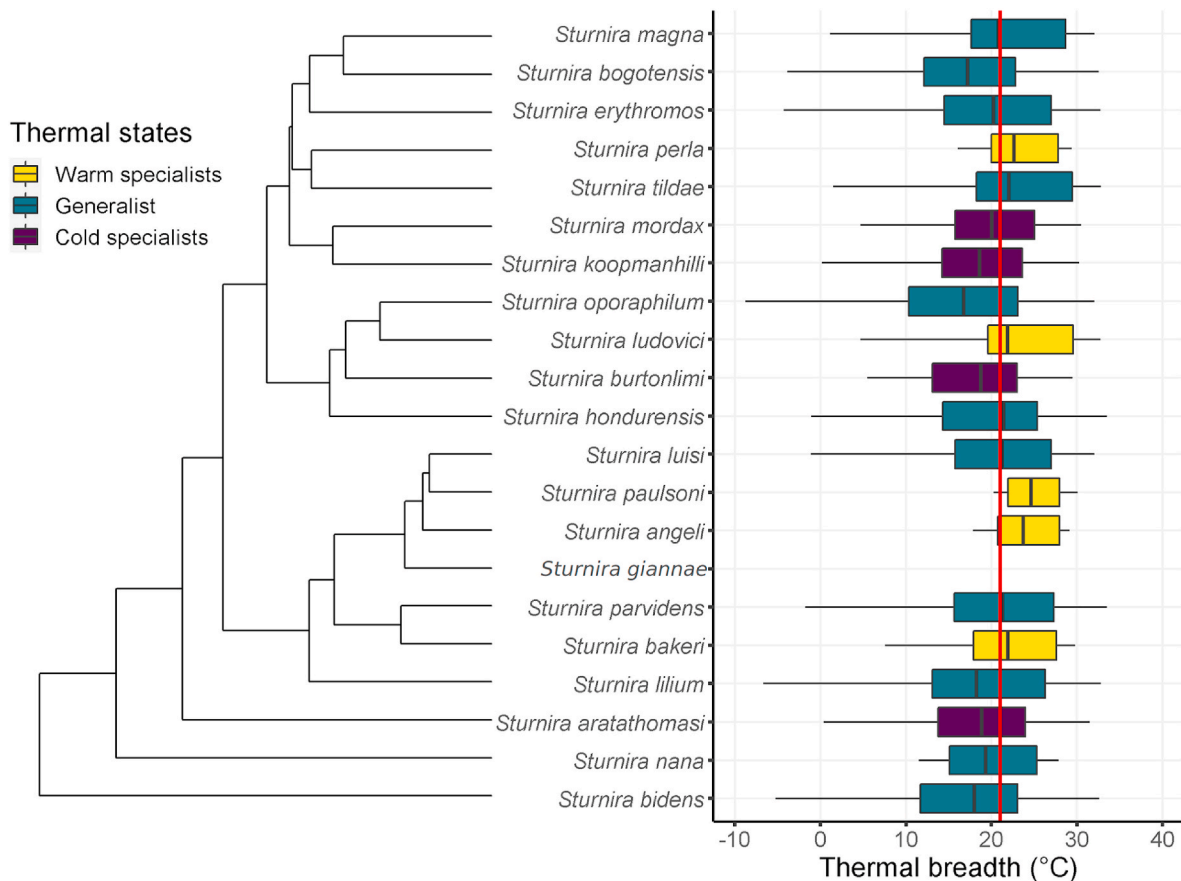


Fig. 2. Thermal states of *Sturnira* species and their phylogeny. Each box plot's interquartile range represents its individual species' thermal breadth. The red line is the genus' thermal median (i.e., 20.99 °C) which was used to classify the specialist species according to their thermal as a cold and warm specialist. *Sturnira giannae* is a nameless species at the moment (Velazco and Patterson, 2013). The phylogenetic tree was based on Velazco and Patterson (2013). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

model, lineages differ in diversification rates according to their thermal niches; in this model, the changes in thermal niches experienced by a lineage are tightly linked to shifts in diversification. Note that this process is independent of thermal niche shifts being coupled or not to speciation events themselves (see previous paragraph).

The combination of all the types of thermal niche evolution, speciation mode, and diversification dependence yielded 105 models. We assumed equal rates of extinction across models. To minimize the chances of finding a local optimum rather than a global one during the likelihood optimization, we used three different starting points. Because models differed in the number of free parameters (e.g., the Unique Rate model has one speciation rate, whereas the Variable Rate and Thermal Dependent model have three), we used AICweights for comparison across models.

2.4. Model validation

Tree size and other factors can impact the detectability of macroevolutionary processes during the analysis (Mynard et al., 2023). We conducted a simulation-inference analysis to describe our results' statistical robustness and limitations. We used the parameters that maximize the likelihood of the best-supported model to simulate the evolution of 200 phylogenetic trees along with thermal niche evolution. Therefore, the simulated datasets are structurally similar to our *Sturnira* tree. Half of the simulations featured an underlying evolutionary model of Variable Rate, whereas the other half was Thermal Dependent. We then used SecSSE to fit Variable Rate and Thermal Dependent models (in combination with Thermal Conserved and Specialization-Trigged

modes of speciation) to each simulated dataset and compared them using AIC. The best statistically possible scenario in this analysis is when 1) the SecSSE inference selects Variable Rate (over Thermal Dependent) in the 100 simulated datasets where Variable Rate was indeed the generating model and 2) the SecSSE inference selects Thermal Dependent in the 100 simulated datasets, where Thermal Dependent was the generating model.

2.5. Ancestral states reconstruction

Due to the SecSSE framework generating a diversification-dependent reconstruction of the ancestral states, we decided to build a diversification-independent reconstruction for comparison. The diversification-independent reconstruction was conducted using the function ace of the phytools package (Revell, 2012), which based its estimation on maximum likelihood. The function ace does not accept NA values; therefore, we made three different ancestral reconstructions assuming the three thermal states (i.e., thermal generalist, cold specialist, and warm specialist) for *Sturnira giannae*, the only species with unknown thermal state.

3. Results

3.1. Thermal niche evolution and diversification rates

We found that *Sturnira* shows significant heterogeneity in diversification rates across time and lineages, so Unique Rate models of diversification had lower statistical support than models including Variable

Table 1

Thermal niche evolution models implemented in SecSSE. Lineages shifted across the three categories (Warm specialist WS, Cold specialist CS, and Generalist G) at different rates (i.e., the frequency of shifting events per time unit). Different rates are shown using letters (a, b, c). See Fig. 3.

Model name	Assumptions
Simple null model (SNM)	All change rates are equal
Complex null model (CNM)	All change rates are different
Two-way specialist (TWS)	Adaptation to high temperature can be limited (Bennett et al., 2021); therefore, this model assumes the same rate of change from CS or WS to G (a), but a different rate from G to either specialist (b), and the rate from CS to WS, and vice versa, will be zero.
Stay-cold (strict) (SCS)	The upper limit of the thermal niche is conserved in the species. In contrast, the lower limit is more flexible (Araújo et al., 2013), which means that for species, it is easier to change to a cold climate, but it is difficult to change to a warm climate. Therefore, strictly speaking, this model assumes that the change rate from CS to G or WS will be zero, while the other rates are different from zero but equal to each other (a).
Stay-cold (flexible) (SCF)	This model is a more flexible version of the previous one [Stay-cold (strict)] and assumes that all change rates will be different from zero, but there will be a difference between the rates from WS to G or CS (a), and the other rates (b).
One-way generalist (OWG)	Bennett et al. (2021) indicates that tolerance to low temperatures evolves faster than tolerance to heat in endotherms. Therefore, this model assumes two different rates of change, one for the transition from G to CS (a) and another for G to WS (b), and vice versa. Moreover, the rate of change will be zero for WS to CS and vice versa.
Warm-restricted (WR)	Physiological restrictions make tolerance to high temperatures difficult to attain (Bozinovic et al., 2014), so the change rate for CS to WS will be zero. Therefore, we expect four different rates of change: G to WS (a), WS to G (b), WS to CS (c), and G to WS, or vice versa (d).

Rates. Models, where heterogeneity in diversification is related to the evolution of thermal niche breadth (Thermal Dependent), were statistically preferred over models without this feature. In other words, thermal niche breadth evolution drives diversification rates in *Sturnira* (Table 2). According to our best model, macroevolutionary dynamics are vastly dominated by the high speciation rates of warm specialists (0.317). In contrast, cold specialists and generalists species have a far lower probability of forming new species (<0.0001).

We found that generalism is an intermediate state between both modes of specialization during thermal niche evolution. Generalism, even though it is a transient condition, is not a short-duration stage as the rate towards either specialization type is relatively low (see Fig. 4). We find that warm specialist lineages in their evolutionary time adapt to

Table 2

Dynamic models differ in assumptions on how thermal niche breadth evolves (second column; see Table 1 for further details) over time and impacts diversification events (first and third columns). Unlike thermal-dependent models, where diversification rates increase and decrease as lineages shift across generalist and cold/warm-specialist states, variable rate models assume that lineages differ in diversification rates, but this is unrelated to the thermal niche. We also considered that during speciation, the inheritance of the parental niche breadth to daughter lineages could be perfect (Thermal Conserved, third column) or be associated with simultaneous changes in thermal preference, as explained in methods. This table shows the ten best-performing models according to the AIC weight value (AICw). The rest can be found in Table S1.

Variation in Speciation	Transition mode	Speciation mode	Loglik	Free parameters	AICw
Thermal dependent	TWS	Thermal Conserved	-66.66	7	0.194
Thermal dependent	TWS	Specialization-Triggered	-66.83	7	0.164
Thermal dependent	SCF	Thermal Divergence	-68.45	6	0.089
Thermal dependent	WR	Thermal Conserved	-66.76	8	0.065
Thermal dependent	TWS	Thermal Divergence	-67.97	7	0.053
Thermal dependent	WR	Specialization-Triggered	-67.00	8	0.051
Variable rate	WR	Thermal Displacement	-67.18	8	0.043
Thermal dependent	SCF	Thermal Conserved	-69.34	6	0.036
Thermal dependent	SCF	Specialization-Triggered	-69.49	6	0.031
Variable rate	SCF	Thermal Displacement + Divergence	-69.81	6	0.023
Thermal dependent	WR	Thermal Divergence	-67.86	8	0.022

a generalist condition at a rate = 0.247 and, once this state is attained, it is unlikely to return to a warm specialist state (rate = < 0.0001). Moreover, generalist species can become cold specialists at a rate = 0.137. This rate is lower than changing from a cold specialist to a generalist condition (rate = 0.247; Fig. 4a).

Models that assumed the Thermal Conserved mode of speciation had the highest support, which means that both daughter lineages inherit the same thermal niche state as the parental one. This suggests that there is no evidence of speciation events being triggered or linked to transition events (i.e., switching from one niche state to another), albeit warm specialists have a far higher rate of speciation than species with other thermal preferences.

Our simulation-inference analysis shows that in all datasets simulated under the Thermal Dependent Model, SecSSE correctly pointed to the Thermal Dependent model as the best supported. However, in 23% of the datasets other than the Thermal Dependent Model were used to simulate, Thermal Dependent was incorrectly selected. In other words, the signal of thermal dependency in phylogenetic trees with similar characteristics to the *Sturnira* tree is strong enough to be recovered by our SecSSE analysis with reasonable rates of Type I error.

3.2. Ancestral states reconstruction

The diversification-independent (i.e., Variable Rates model) ancestor states reconstruction assigns the most basal nodes in *Sturnira* phylogenetic tree equal probability for warm specialists, cold specialists, and generalists. However, when the two main subclades that group most contemporary species arose (Fig. 5), the status assigned to the *Sturnira giannae* influences the estimation of ancestral status. When this species is assumed to be a warm specialist, the various ancestors of the *luisi-lilium* clade are inferred to have been warm specialists. (Fig. 5a).

The ancestral reconstruction in Fig. 5 considers niche breadth evolution independently of diversification events. When reconstructing the ancestral history under the Thermal Dependent model, we find that both reconstructions differ significantly. Consistently with our finding that only warm specialists speciate, all ancestral nodes are reconstructed to be warm specialist lineages, as shown in Fig. 4b.

4. Discussion

We found support for thermal niche evolution driving diversification dynamics in *Sturnira* species. This relationship is likely associated with *Sturnira*'s broad geographic range and mountain origin, which results in significant variation in altitude and temperature range. Previous studies have shown that lineages with a broad niche (generalists) might have higher chances of speciating through peripatric speciation processes. In contrast, Sexton et al. (2017) proposed that narrow-niched species



Fig. 3. Thermal niche models implemented in SecSSE framework as the function of their thermal state change rates (i.e., Generalist, Warm Specialist, and Cold Specialist), represented in a transition table. Each model is represented by an acronym (e.g., SNN, CNM, and TWS; see Table 1 for the full list of acronyms). The transition events are represented by the inner boxes in the figure (i.e., six inner boxes, excluding the diagonal), and the color of the model boxes indicate a change rate value. For example, the simple null model (SNM), is present in all the transition events (6) but its boxes have the same color which means that SNM has a change rate value for every transition event but all the rates are the same (i.e., same color; grey). In other words, the change rate values in SNM are independent of the thermal state and the transition direction (i.e., constant rate value for all transitions). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

(specialists) could undergo speciation at high rates when passing through adaptive peaks that promote diversification. Our results support the latter hypothesis, as we found strong statistical support for warm specialists changing to generalist conditions more often than the reverse across the evolution of the genera. In the following sections, we discuss the implications of these results in light of the role of thermal niche breadth on the diversification process.

4.1. Why is being a generalist advantageous?

Generalist *Sturnira* species, in contrast to specialist species, are characterized by a more extensive geographic range (Slatyer et al., 2013), except for *S. nana*, which in its small distribution covers a great variety of temperatures (see Fig. 1). We found that specialized lineages (cold specialist and warm specialist) change to a generalist condition at a higher pace than they do in the opposite direction (Fig. 4), which yields a high proportion of generalist species. In previous studies, with non-chiropterans organism, it have been found that generalist species also have greater tolerance to variations in environmental conditions and phenotypic plasticity (Griffith and Sultan, 2012; Spitze and Sadler,

1996), and greater ability to compete for resources (e.g., intercepting sunlight; Denelle et al., 2020). *Sturnira* bats and their thermal specialization's degree (generalist, cold specialist or warm specialist) might be an example of that. Previous studies show how *Sturnira* species, classified as thermal generalists in our study, have adapted to various environmental conditions and resources. For example, *S. tildae*, *S. lilium*, and *S. parvidens*, all of them thermal generalist species, have a wide trophic niche breadth and occupy a great number of different ecosystems (Mosquera-Izquierdo et al., 2022; Saldaña-Vázquez et al., 2015), which is not observed in specialists species (cold specialist and warm specialist) such as *S. aratathomasi*, *S. perla*, and *S. bakeri*. In addition, Castaño et al. (2018) find that species such as *S. bogotensis*, *S. erythromos*, and *S. hondurensis*, classified as generalists in our current study, are capable of feeding on a large variety of plant species (over ten plant families) which is not observed in *S. aratathomasi*, classified as a cold specialist, with only one plant species in its diet.

4.2. Why do warm specialists have consistently high rates of speciation?

The estimated transition rates indicate a higher probability of change

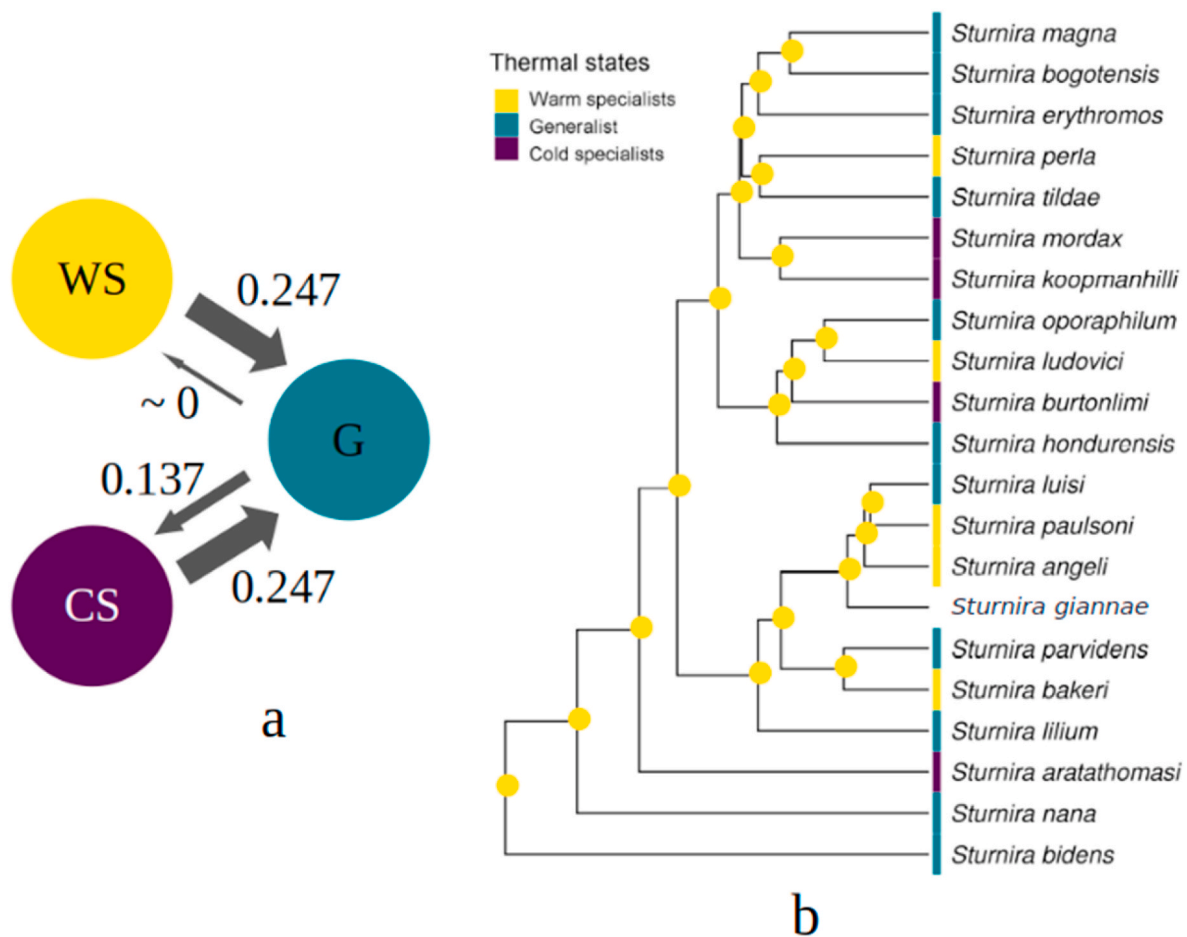


Fig. 4. A) Thermal state change rates of the *Sturnira* species in their evolutionary time, being a WS Warm specialist, G Generalist, and CS Cold specialist. b) Diversification-dependent ancestral states reconstruction of the thermal states of the *Sturnira* species.

from a warm specialist to a generalist and from this state to a cold specialization, with most of those transitions taking place in the recent history of *Sturnira*. There is a tendency to change from warm specialist to cold specialist eventually. This pattern is consistent with what Bennett et al. (2021) found on a global scale in endotherms and ectotherms: increases in thermal niche breadth have shown a trend of significant change in the lower limits, while in the upper limits of thermal tolerance, there has been slower and more constant change during evolution. The absence of variability in the upper limit of thermal tolerance has been reported for several groups of endothermic vertebrates (Araújo et al., 2013; Bennett et al., 2021), possibly associated with a physiological restriction of thermal stress in membranes, proteins, and cell function (Araújo et al., 2013). However, more significant variability has been found in the lower limits of the thermal niche. Endothermic vertebrates have developed numerous adaptation strategies in regions with low temperatures. This pattern has been documented in nectar-feeding bats, in which there is a wide variation in the amplitude of thermal niches. However, the upper limits of these species ($32.5 \pm 1.6\text{C}$) tend to have less variation than the lower thermal limits ($5.5 \pm 5.3\text{C}$; Ortega-García et al., 2017). This pattern of variation was also found in our data (Fig. 3).

The common ancestor of *Sturnira* arose in the mid-Miocene (14.2 Ma) in the Central or Northern Andes, while the first lineages of the genus appeared in the late Miocene (approximately 7 Ma) in the Northern Andes and Choco region (Velazco and Patterson, 2013). The subsequent radiation of the genus is estimated to have occurred in the Quaternary period in the context of glacial and interglacial periods. Interglacial periods of high temperatures and glacial periods with low temperatures

and forest refugia set the stage for geographical isolation (Torres-Morales et al., 2019) for *Sturnira* and many other taxa. The warm specialist ancestors, with a low but significant probability, would transition to generalists and eventually to cold specialists, but not in the opposite direction. This would explain the current variation observed in the width of the thermal niche of extant species.

4.3. Speciation and niche breadth

Although our results suggest that speciation rate heterogeneity across *Sturnira* lineages depends on variation in thermal niche breadth, the speciation events themselves are not triggered by niche evolution (i. e., they do not take place simultaneously); the insights of this finding is twofold. On the one hand, if species' ecology is linked to niche breadth, ecological speciation might not be a driving force in *Sturnira*'s evolution. Speciation in *Sturnira* might be geographically mediated where barriers (e.g., Andes) could separate populations which would diverge but maintain a similar thermal niche. Even if divergence rates are uncoupled from population isolation (Singhal et al., 2022), the dynamic topography of the region can still create the stage for species formation by providing a wide array of microhabitats (Badgley, 2010) and, therefore, opportunities for specialization. On the other hand, the duration of the transition of a lineage from one thermal niche state to another might be brief. This suggests that all the populations of a given lineage evolve their thermal preference at the same time and in the same direction, which decreases the chances of intraspecific variation in the thermal niche and precludes divergence across populations.

Our analysis differs from previous efforts to test the nature of the

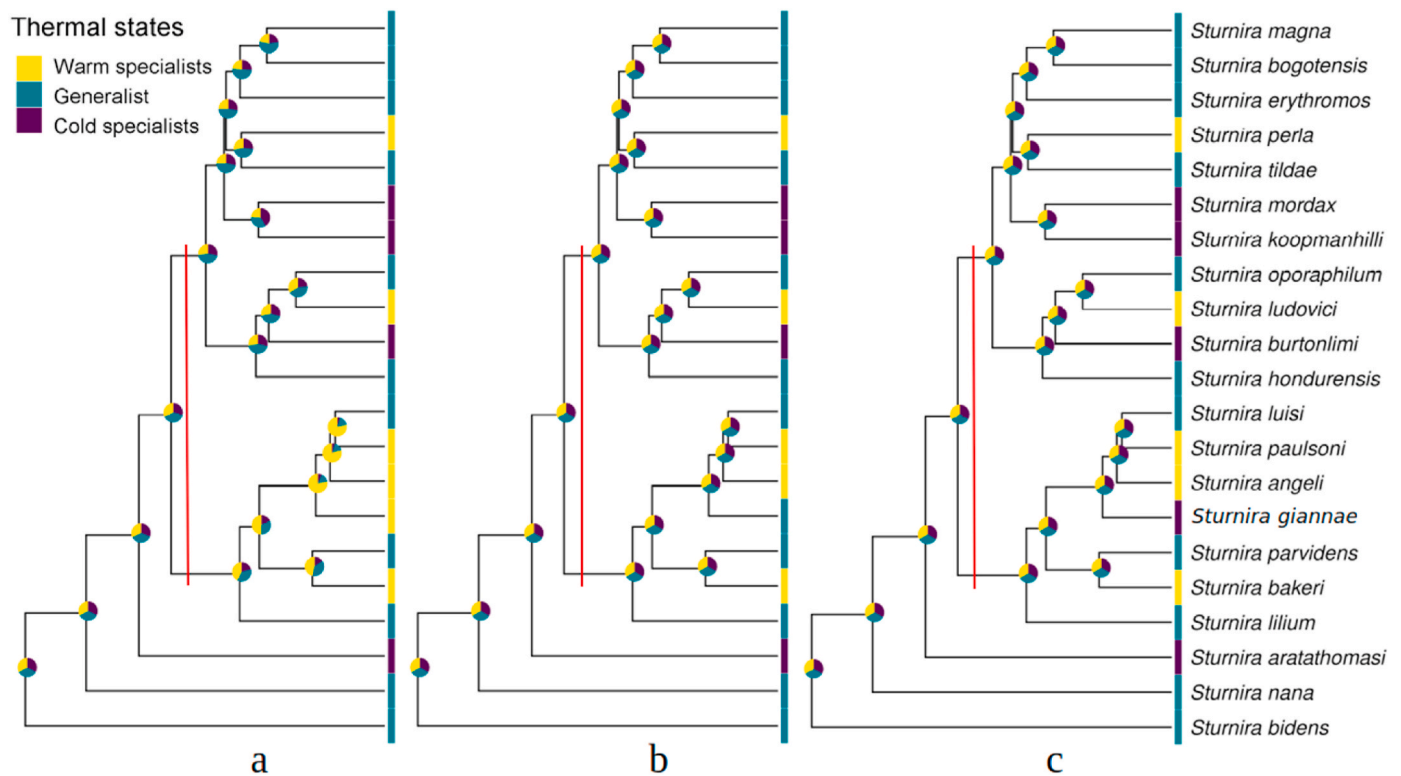


Fig. 5. Ancestral state reconstruction, where diversification is independent of thermal niche evolution for the *Sturnira*. Panels differ in assumptions on possible thermal states for *Sturnira giannae*: a) Warm specialist, b) Generalist, and c) Cold specialist. The red line indicates where the change in probability of the node's thermal states occurs. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

relationship between niche and diversification rates in bats. We found at least two differences in our study compared with [Pie et al. \(2021\)](#) and [Castro-Insua et al. \(2018\)](#). The first one is the data used for modeling thermal niche, both used the bioclimatic variables without considering that Neotropical bats are nocturnal. They used the climatic information BIO1 (annual mean temperature), BIO5 (maximum temperature of the warmest month), and BIO6 (minimum temperature of the coldest month) among others. These variables little reflect about how *Sturnira* and the environment interact because they are weakly related to the time of the day when bats are active. In comparison, we model the *Sturnira* thermal niche using the lowest among minimum temperatures and the lowest among maximum temperatures, the rationale behind the latter is that bats use shelters during the day, so they are not exposed to the maximum temperatures ([Ortega-García et al., 2017](#)).

The second difference comes from the statistical method for evaluating the relationship between niche and diversification rates. [Pie et al. \(2021\)](#) used a non-parametric approach, which aims to find a correlational link between diversification rates and niche breadth. Because the evolution of niche breadth and changes in diversification rates are not jointly modeled in [Pie et al.](#) it cannot be claimed that those variables have been associated across the entire evolutionary history of the clade but only in recent times. Such a non-parametric approach could also suffer from issues of phylogenetic non-independence ([van Els et al., 2021](#)). In contrast, our SSE modeling, by coupling niche evolution and branching pattern in the phylogenetic tree, tests whether diversification rate variation has entirely depended on changes in niche breadth (i.e., causality relationship) since the clade's origin (14.2 Ma; [Velazco and Patterson, 2013](#)) to the present.

Finally, we acknowledge that similar to other studies, our research has limitations regarding the use of geographic data (i.e., the geographic range of the species and temperature layers) as an indirect measure of the realized thermal niche. This approach relies on the assumption that climate temperature data correlates with body temperature. While

temperature undoubtedly influences species distributions, other factors such as the geographic variation of microhabitat use, thermoregulatory effectiveness, resource availability, competition, and habitat suitability also play significant roles ([Gvoždík, 2018](#)). However, the categorization strategy we employed may mitigate an overestimation of the thermal niche's breadth. Therefore, we believe that our work represents a reasonably accurate modeling of the realized thermal niche of *Sturnira* species, despite the inherent limitations of our study.

5. Conclusion

We explore whether the evolution of the thermal niche in *Sturnira* bats is related to macroevolutionary dynamics. Our results show that *Sturnira* species arise as warm specialists, their niche breadth broadens throughout their evolutionary time, and just a subset of those species becomes cold specialists. These transition patterns may be related to an upper thermal limit associated with a physiological restriction of thermal stress. We found that the evolution of thermal niche breadth causes fluctuations in per-lineage rates of diversification, where warm specialists boast the highest speciation rates. However, we found no evidence of these changes in the niche, neither triggering nor resulting from speciation events.

Author contribution

RASV, FV, and LHA: Conceptualization, Supervision; JDCM, RASV, FV, and LHA; Methodology, Writing – Original Draft, Writing – Review & Editing; JDCM and LHA: Formal analysis; JDCM and FV: Investigation, Visualization; JCDM: Data Curation.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Other (please explain: e.g. 'I have shared the link to my data as an attachment').

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jtherbio.2023.103697>.

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