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RESEARCH PAPER

Climatic niche evolution in turtles is characterized by phylogenetic conservatism for both aquatic and terrestrial species

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Abstract

Understanding how the climatic niche of species evolved has been a topic of high interest in current theoretical and applied macroecological studies. However, little is known regarding how species traits might influence climatic niche evolution. Here, we evaluated patterns of climatic niche evolution in turtles (tortoises and freshwater turtles) and whether species habitat (terrestrial or aquatic) influences these patterns. We used phylogenetic, climatic and distribution data for 261 species to estimate their climatic niches. Then, we compared whether niche overlap between sister species was higher than between random species pairs and evaluated whether niche optima and rates varied between aquatic and terrestrial species. Sister species had higher values of niche overlap than random species pairs, suggesting phylogenetic climatic niche conservatism in turtles. The climatic niche evolution of the group followed an Ornstein–Uhlenbeck model with different optimum values for aquatic and terrestrial species, but we did not find consistent evidence of differences in their rates of climatic niche evolution. We conclude that phylogenetic climatic niche conservatism occurs among turtle species. Furthermore, terrestrial and aquatic species occupy different climatic niches but these seem to have evolved at similar evolutionary rates, reinforcing the importance of habitat in understanding species climatic niches and their evolution.

KEYWORDS
climatic optimum, evolutionary models, habitat, niche evolution, niche overlap, phylogenetic niche conservatism, Testudines

1 | INTRODUCTION

The climatic niche (also called Grinnellian niche) may be defined as the set of climatic conditions within which a species is able to survive (Soberón, 2007). In recent years, much attention has been directed towards understanding patterns of climatic niche evolution in various taxa, mainly asking whether these niches are conserved (or not) through the evolutionary history of clades and what are the implications of this phylogenetic niche conservatism for different biological phenomena (Pyron, Costa, Patten, & Burbrink, 2015; Wiens & Donoghue, 2004; Wiens et al., 2010). Prediction of biological invasions (Broennimann & Guisan, 2008; Broennimann et al., 2012) and the impacts of climatic change (Ihlow et al., 2012) as well as the causes behind diversification patterns (Wiens, 2011) are examples of research areas that have benefited from considering and evaluating evolutionary patterns of climatic niches and their causal processes.

Although evolutionary patterns of species' climatic niches have been recently evaluated in many taxa (Duran, Meyer, & Pie, 2013; Duran & Pie, 2015; Mcnyset, 2009; Peixoto, Villalobos, & Cianciaruso, 2017; Peterson, 2011; Pie, Campos, Meyer, & Duran, 2017), few studies have tested whether patterns of climatic niche evolution are related to other taxon traits. In mammals, for example, species occurring in the tropics, with small range sizes or with specialized diets have climatic niches that are more conserved than temperate, widely distributed and diet-generalist mammals (Cooper, Freckleton, & Jetz, 2011). In addition, life history strategies in flowering plants also influence the evolution of their climatic niches, with herbaceous species having higher rates of niche evolution than trees and shrubs (Smith & Beaulieu, 2009). Thus, understanding how species traits influence climatic niche evolution is a relevant question in niche evolution studies (Lavergne, Mouquet, Thuiller, & Ronce, 2010).

Aquatic and terrestrial systems have different physical and chemical conditions, which seem to influence the biology and diversity of the organisms living in each of these habitats (Grosberg, Vermeij, & Wainwright, 2012; Shurin, Gruner, & Hillebrand, 2006; Vermeij & Dudley, 2000). Whether species are aquatic or terrestrial (hereafter simply habitat) is a species trait commonly used in functional diversity studies (Sobral, Lees, & Cianciaruso, 2016; Wilman et al., 2014) and often related to species diversity (Kozak & Wiens, 2016; Rodrigues & Diniz-Filho, 2016; Wiens, 2015). However, despite this great importance of habitat to species biology, until now no study has evaluated whether niche evolution is similar between aquatic and terrestrial species. Aquatic organisms live in an environment with less-steep physical gradients, less structural complexity and higher stability than a terrestrial environment (Grosberg et al., 2012). Such differences in stability between aquatic and terrestrial habitats, particularly over large temporal scales, may influence how the climatic niche of organisms associated with each habitat evolves. Phylogenetic conservatism of climatic niches in tropical lineages is, for example, a commonly cited hypothesis to explain high species richness in the tropics, with one of the underlying reasons being the higher long-term climatic stability of tropical regions compared to temperate regions over time (Wiens & Donoghue, 2004). Thus, considering a similar difference in long-term stability between aquatic and terrestrial habitats (Grosberg et al., 2012) influencing niche evolution, climatic niches of aquatic organisms would be expected to be phylogenetically conserved or at least evolve at slower rates (Ackerly, 2009; Cooper et al., 2011) than those of their terrestrial counterparts, which would be expected to be more labile.

Turtles represent an ideal group to evaluate patterns of climatic niche evolution related to habitat differences. The group has terrestrial as well as aquatic species and this habitat difference commonly influences many characteristics of turtle life history such as body size (Jaffe, Slater, & Alfaro, 2011), home range (Slavenko, Itescu, Ihlow, & Meiri, 2016), extinction risk (Slavenko, Tallowin, Itescu, Raia, & Meiri, 2016) and diversification rates (Rodrigues & Diniz-Filho, 2016). Indeed, a recent study comparing climatic data of terrestrial and aquatic groups between fossil and extant turtle taxa found that aquatic climatic niches seem to be phylogenetically more conserved (Waterson et al., 2016). However, due to fossil limitations in that study, all aquatic and terrestrial taxa were pooled into two general groups (terrestrial or aquatic) whose climatic niche was compared between present and past, an approach that does not take into account the phylogenetic relationships between species and consequently did not explicitly incorporate the evolutionary history of habitat preferences. More importantly, under the assumption of climatic niche conservatism, another recent study suggested that turtle species richness and distribution may decrease as a result of climate change affecting species' climatic niches (Ihlow et al., 2012). However, no previous study has evaluated climatic niche evolution for the whole group of nonmarine turtles (but see Almpanidou, Schofield, & Mazaris, 2017 for a general evaluation of niche conservatism in sea turtles) and climatic niche comparisons conducted so far have been mainly focused on invasive species (Liu et al., 2017; Rödder, Schmidtlein, Veith, & Lötters, 2009; Rodrigues, Coelho, & Diniz-Filho, 2016; Rodrigues, Coelho, Varela, & Diniz-Filho, 2016) with mixed results of niche conservatism and shifts. Therefore, studying niche evolution patterns in turtles represents an interesting opportunity with theoretical (understanding whether species habitat could influence climatic niche evolution) and conservation (understanding whether turtles could be able to deal with anticipated climatic changes) implications.

This study aimed to evaluate the evolutionary patterns in the climatic niche of turtles and, more specifically: (a) evaluate whether phylogenetic niche conservatism occurs across the whole clade; (b) evaluate temporal dynamics in the climatic niches of turtles; and (c) evaluate whether climatic niche evolution differs between aquatic and terrestrial species. We first evaluated climatic niche evolution in turtles irrespective of species habitat in order to provide a general scenario for the group, and then, compared the patterns of aquatic versus terrestrial species. We found that phylogenetic climatic niche conservatism occurs within closely related groups and that the evolution of the climatic niche is directed towards an optimum that differs between aquatic and terrestrial clades. Despite such habitat-related differences in optima, species from both habitat types had similar rates of climatic niche evolution.

2 | MATERIALS AND METHODS

2.1 | Species distributional and phylogenetic data

We used distribution data for 261 turtle species (tortoises and freshwater turtles, hereafter only "turtles") obtained from the Turtle Taxonomy Work Group (van Dijk, Iverson, Rhodin, Shaffer, & Bour, 2014). Range maps were projected onto a cylindrical equal-area projection and overlaid with a grid of 100 × 100 km. Considering potential commission errors present in range maps, this grid resolution is recommended for macroecological analyses using these type of maps (Hurlbert & Jetz, 2007) and although it might seem a bit coarse, previous studies have been able to observe climatic niche conservatism patterns at this or even coarser scales (Hof, Rahbek, & Araújo, 2010; Peixoto et al., 2017).

We used a recently published maximum clade credibility tree (MCC), which covers almost 80% of turtle species, estimating relationships using five loci (two nuclear and three mitochondrial) and calibrated using turtle fossil calibrations in a Bayesian framework in BEAST (Rodrigues & Diniz-Filho, 2016). All species used in our study were included in this phylogeny.

Turtle classification as either terrestrial or aquatic was extracted from a previous study (Jaffe et al., 2011) and complemented with additional studies (see Supporting Information Table S1). Habitat classification was based on where the species spends the greatest amount of its lifetime.

2.2 | Climatic data

To describe the climatic niches of turtle species, we used a set of environmental variables that have been previously suggested to adequately describe turtles niches (Ihlow et al., 2012): Mean diurnal range (Mean of monthly (maximum temperature − minimum temperature)); minimum temperature of coldest month; Mean Temperature of Wettest Quarter; mean temperature of driest quarter; Mean Temperature of Warmest Quarter; Precipitation Seasonality (Coefficient of Variation); Precipitation of Wettest Quarter; Precipitation of Driest Quarter; Precipitation of Warmest Quarter; Precipitation of Coldest Quarter. These variables were downloaded from the WorldClim database version 2.0 (www.worldclim.org) (Fick & Hijmans, 2017) at the 10 arcmin resolution and projected onto the cylindrical equal-area projection using the raster R package (Hijmans, 2015). Then, for each 100 × 100 km grid cell, we calculated the mean value of each environmental variable. This allowed us to have a multivariate representation of the climatic conditions that characterized the geographic distribution of species (Hutchinson's duality; Colwell & Rangel, 2009). Given that such representation of species niches considers only those climatic conditions that species actually use, after considering the effects of negative interactors (Soberón & Nakamura, 2009), our description essentially represents the realized climatic niches (hereafter, climatic niches, for simplicity) of species instead of their fundamental niches (Soberón, 2007; Soberón & Nakamura, 2009).

We note that using temperature data from terrestrial conditions to describe species' aquatic niches may seem controversial, but recent studies have shown that water temperatures are highly correlated with terrestrial ones at the scale of species geographic distributions (Frederico, De Marco, & Zuanon, 2014; Livingstone & Lotter, 1998). In fact, several recent studies evaluating climatic niche and distribution patterns of aquatic organisms, such as fishes (Culumber & Tobler, 2016; Edeline, Lacroix, Delire, Poulet, & Legendre, 2013; Emmrich et al., 2014) and turtles (Fagundes, Vogt, & De Marco Júnior, 2016; Ihlow et al., 2012; Rödder et al., 2013; Rodrigues, Olalla-Tárraga, Iverson, Akre, & Diniz-Filho, 2017; Waterson et al., 2016), have been performed using data on terrestrial conditions. Furthermore, it is important to highlight that even aquatic turtles also depend on terrestrial environments for activities such as basking and nesting, which are in turn environmentally influenced, reinforcing the relevance of terrestrial environmental conditions on their niches.

2.3 | Climatic niche evolution

The definition of phylogenetic niche conservatism (PNC) and the use of certain methods for evaluating its occurrence in clades are currently under debate (Münkemüller, Boucher, Thuiller, & Lavergne, 2015; Pyron et al., 2015). Evaluating for the presence of phylogenetic signal (PS), conducting species distribution models and comparing their outputs as well as fitting and comparing evolutionary models are among the most common methods for testing the existence of PNC (Cooper, Jetz, & Freckleton, 2010; Münkemüller et al., 2015; Wiens et al., 2010). Of these, and despite being highly employed in previous studies, phylogenetic signal has been much criticized because many processes related to PNC may not necessarily generate PS (Revell, Harmon, & Collar, 2008). Given such debate, we performed and compared two different approaches to evaluate the evolutionary patterns of turtles' climatic niches in a more robust way.

First, we evaluated phylogenetic niche conservatism patterns based on pairwise niche comparisons between sister species based on their geographic distributions, where higher niche overlaps between sister species compared to those of random species pairs represent evidence of PNC (Peixoto et al., 2017; Wiens et al., 2010). Although this method might seem similar to evaluating PS, this species-pair approach is of interest owing to its consideration of the complete climatic variability across the species' geographic ranges, reducing potential issues related to spatial patterns of climatic conditions that could lead to misleading ecological patterns (Warren, Cardillo, Rosauer, & Bolnick, 2014).

Second, considering that the species-pair approach only includes the most recent part of the phylogenetic history of a clade and its slight resemblance to the criticized PS approach, we also evaluated phylogenetic conservatism of climatic niches by fitting evolutionary models across the whole tree, thus including the clade's complete phylogenetic history (Ackerly, 2009; Cooper et al., 2010; Kozak & Wiens, 2010; Münkemüller et al., 2015). Under such whole-tree approach, we were able to evaluate different scenarios of climatic niche evolution, from that independent of species relationships to a constrained evolution more consistent with PNC (see below; Münkemüller et al., 2015), in explaining the observed variation among species climatic niches. In addition, this approach allowed us evaluating the tempo of niche evolution by considering rates of niche change. Such rates can then be associated with the "degree of PNC" (Cooper et al., 2011), allowing the comparison of which group of species had the faster niche evolution (Münkemüller et al., 2015). Comparing the results of species-pair and whole-tree approaches is a more robust way to evaluate patterns of niche evolution and thus more appropriately discuss phylogenetic niche conservatism (Münkemüller et al., 2015; Peixoto et al., 2017).

2.3.1 | Species-pair approach

We used pairwise niche comparisons following a well-established approach to evaluate species climatic niche overlap (Broennimann et al., 2012), which has been frequently used in niche conservatism studies (de Medeiros, Guisan, & Lohmann, 2015; Peixoto et al., 2017; Waterson et al., 2016). This method employs kernel smoothers of species occurrences and climatic factors in a gridded space, which are then used to calculate standardized species and climatic distributions. We used the PCA-env approach in a grid size of 100 × 100 cells and the Schoener's D index to evaluate niche overlap among species pairs. This index varies from 0 (no overlap) to 1 (complete overlap). The background or accessible area for each species was defined as the set of ecoregions (Olson et al., 2001) covered by the species' distribution. Using the species distributions along with their potentially accessible areas allows the reliable estimation of niche differences between species pairs (Broennimann et al., 2012). In our study, species occurrences were defined as the centroids of the cells where they occurred.

We conducted a detailed inspection of the phylogenetic structure of species niche overlap by focusing solely on pairs of sister species instead of the whole phylogeny. To do so, we compared the mean niche overlap among sister species with the niche overlap among random species pairs taken from the phylogeny. For this, we randomly drew 74 species pairs (the same number of sister species in the phylogeny used in this study) 1,000 times in order to generate a null distribution of mean overlap values to be compared with the observed species' overlap values. Higher values of niche overlap among sister species would suggest less divergence, and thus PNC (Ackerly, 2009; Cooper et al., 2011), compared to random species pairs. We preferred this species-pair approach instead of using a standard Mantel test, which would evaluate the relationship between climatic niche overlap and divergence times (i.e., niche vs. phylogenetic distance) because the Mantel approach essentially estimates phylogenetic signal under the assumption of a linear relationship between niche overlap and divergence time, a pattern that might not occur if niche evolution does not follow a Brownian Motion model (Münkemüller et al., 2015).

To evaluate whether climatic niche overlap among sister pairs of aquatic species differed from that among terrestrial species, we compared the mean niche overlap between sister species of aquatic and terrestrial species using an ANOVA. Higher values of niche overlap among sister species of one of the habitats would suggest less divergence, and thus a lower rate of niche evolution compared to the sister species of the other habitat. Alternatively, similar values of niche overlap between the two groups of species would simply suggest that sister species within both groups have similar niche evolutionary patterns in the degree of PNC (Cooper et al., 2011).

2.3.2 | Whole-tree approach

To better understand climatic niche evolution in turtles, we also evaluated which evolutionary models best explained the temporal dynamics of their climatic niches. First, we estimated species climatic niches using the Outlying Mean Index (OMI) (Dolédec, Chessel, & Gimaret-Carpentier, 2000), a multivariate approach recently used satisfactorily to describe species climatic niches (Gouveia et al., 2014; Pearman et al., 2014; Peixoto et al., 2017). The OMI applies an ordination procedure resulting in uncorrelated niche axes without assuming particular species response curves (Thuiller, Lavorel, & Araújo, 2005). We used the species scores from the first axis of the OMI analysis to estimate the climatic niche position of turtles. This score describes the distance of each species' niche conditions from the average niche of the whole group (i.e., a theoretical niche describing the mean conditions within the combined distribution of all considered species; Gouveia et al., 2014; Peixoto et al., 2017).

We then evaluated which evolutionary model best fits the distribution of species climatic niche positions along the phylogeny. We compared four commonly used alternative models: (a) the white noise (WN) model, where niche evolution is independent of species relationships; (b) the Brownian motion (BM) model, where niche differences among species accumulate over time under a single evolutionary rate (i.e., divergence proportional to time; Felsenstein, 1985); (c) the Ornstein–Uhlenbeck (OU) model, where differences among species are due to (a) a single evolutionary rate, (b) an optimum representing a niche value where species fitness is highest and towards which niche values tend to converge, and (c) an attractor force towards such an optimum (Butler & King, 2004; Hansen, 1997); and (d) the early burst (EB) model, where evolutionary rate may decrease over time (Harmon et al., 2010). A better fit of an OU model over the other models can be considered as evidence of PNC, given that this model represents niche evolution as constrained around an optimal value and not just as a function of time. These models were compared using the Akaike information criterion (AIC) and AIC weights (AICw) to determine the best fit model. Only models with AIC difference (delta AIC) larger than 2 were considered as different models (Burnham & Anderson, 2002). These models were fitted using the Geiger package in R (Harmon, Weir, Brock, Glor, & Challenger, 2008).

In addition to evaluating different scenarios of niche evolution, we also tested for differences in evolutionary rates between the climatic niches of aquatic and terrestrial turtles. To do so, we evaluated whether the parameters of the OU model (the best model according to AIC comparisons; see Section 3)—optimum and evolutionary rate—varied between aquatic and terrestrial species. We compared three OU models: a general OU model that does not account for rate differences between habitat types; an OU model allowing for variation in optima between these species groups (OUm); and an OU model allowing for variation in optima and in evolutionary rates between habitat types (OUmr). These models were fitted using the R Package OUwie (Beaulieu, Jhwueng, Boettiger, & O'Meara, 2012) and compared using AIC. We reinforce that we compared evolutionary rates in order to evaluate differences in the speed of niche evolution or degree of PNC between the groups and not to evaluate the existence of PNC (see Münkemüller et al., 2015).

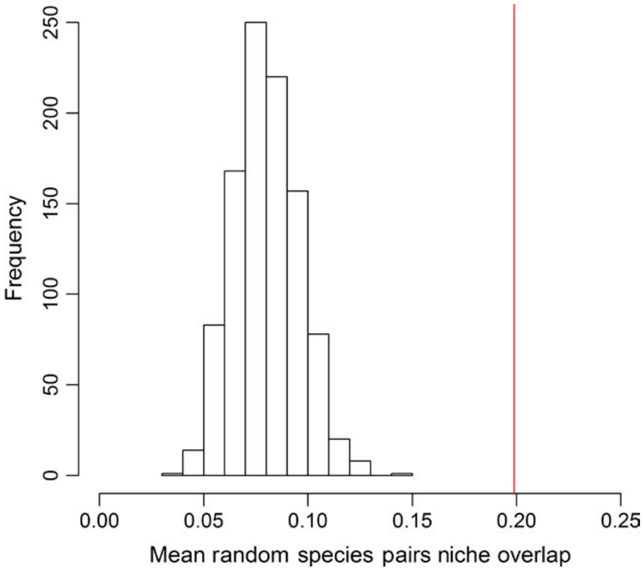

FIGURE 1 Distribution of mean climatic niche overlap between species pairs randomly selected in the phylogeny. We randomly selected 74 species pairs (the same number of sister species) 1,000 times. The red line represents the observed mean climatic niche overlap of sister species

3 | RESULTS

Niche overlap between sister species was higher than between random species pairs (mean sister = 0.199, mean random = 0.078, $p < 0.001$, Figure 1), suggesting higher niche similarity and thus phylogenetic conservatism between sister species. In addition, mean sister species niche overlap was not different between aquatic (mean = 0.20, min = 0, max = 0.68) and terrestrial species (mean = 0.22, min = 0, max = 0.61) ($F_{1,70} = 0.2$, $p = 0.656$), suggesting similar patterns of niche evolution between aquatic and terrestrial species.

Turtle niche position, as described by the OMI analysis, had a strong negative correlation with values of extreme precipitation and minimum temperature (Table 1). Accordingly, species with high OMI scores had climatic niches characterized by low minimum temperature and low maximum and minimum precipitation. When comparing the fit of evolutionary models, the OU model had the lowest AIC (AIC = 703.30) and the highest AICw (AICw = 1) among the candidate models (Table 2), reinforcing the climatic niche conservatism found in the species-pair approach. Using the OUwie method, we found that the model that only considered differences in niche optimum between terrestrial and aquatic species (OUm) had the lowest AIC (AIC = 684.91), but it had similar support to the model considering differences in niche optimum and evolutionary rates between the two habitats (OUmr; delta AIC = 0.38; Table 3 and Figure 2). Aquatic species have climatic niche optimum in areas with higher minimum temperatures and higher amount of minimum and maximum precipitation when compared to terrestrial species (Table 3).

4 | DISCUSSION

We found that climatic niches seem to be conserved among turtle sister species and that their evolution followed an OU evolutionary model with different niche optima between aquatic and terrestrial species. In spite of such difference in climatic niche optima, niche evolutionary rates seem to be similar between both groups of turtles, given that the inclusion of this variation in the model did not consistently improve the model when considering the only variation in climatic niche optima. This suggests comparable degrees of phylogenetic conservatism between species climatic niches from different habitats, which is also in accordance with findings from the species-pair approach.

Our study represents, to our knowledge, the first one evaluating the existence of phylogenetic conservatism of climatic niches across the whole turtle clade. Climatic niche conservatism is a well-studied subject in several vertebrate groups (Duran & Pie, 2015; Duran et al., 2013; Mcnyset, 2009; Peixoto et al., 2017; Peterson, 2011; Pie et al., 2017), but in turtles, it is still poorly explored. The few studies that have evaluated niche conservatism in this group found a mix of evidence for both divergence and conservatism, mainly in the biological invasions scenario (Liu et al., 2017; Rödder et al., 2009; Rodrigues, Coelho, & Diniz-Filho, 2016; Rodrigues, Coelho, Varela, et al., 2016). However, another study using the fossil records from some turtle families also found evidence for niche

TABLE 1 Correlation between climatic variables and species climatic niche (first axis of Outlying Mean Index [OMI] scores)

Variable	Contribution
Mean diurnal range	0.298
Minimum temperature of coldest month	−0.387
Mean temperature of wettest quarter	−0.243
Mean temperature of driest quarter	−0.270
Mean temperature of warmest quarter	−0.137
Precipitation seasonality	0.095
Precipitation of wettest quarter	−0.437
Precipitation of driest quarter	−0.373
Precipitation of warmest quarter	−0.339
Precipitation of coldest quarter	−0.396

conservatism in Testudines (Waterson et al., 2016), reinforcing our findings using only extant taxa under a phylogenetic approach. Yet another study also found that niche conservatism may have determined the distribution of some emydid turtles in North America (Stephens & Wiens, 2009). In summary, all these findings along with ours suggest that climatic niche conservatism is common among turtles.

Phylogenetic niche conservatism among sister species suggests that recent cladogenetic processes generate species pairs that maintain similar climatic requirements or have not had time to accumulate differences (Peterson, 2011). Such phylogenetic climatic niche conservatism can be related with a predominance of an allopatric speciation mode determining diversification within a clade, where ancestors of sister species were split into separate populations due to a geographic barrier, without the influence of species climatic preferences (Kozak & Wiens, 2006; Peterson, Soberón, & Sánchez-Cordero, 1999; Pyron et al., 2015; Warren et al., 2014; Wiens & Graham, 2005). The predominance of such allopatric speciation in the diversification of the turtle clade has not been evaluated but it could provide an additional explanation for PNC to our findings on niche overlap as well as evolutionary scenarios and rates.

Climatic niche of turtles followed an OU evolutionary model, reinforcing the occurrence of niche conservatism in the group. Under this evolutionary model, a phylogenetic signal approach, such as a Mantel test between species niche overlap and phylogenetic distances, would be problematic (Münkemüller et al., 2015). Indeed, we ran this Mantel test and it was not significant ($r = -0.06$, $p = 0.99$), reinforcing the importance of using the species-pair approach when species climatic niche follows an OU evolutionary model.

TABLE 2 Comparison among the evolutionary models employed in our study to describe climatic niche evolution of turtles along their evolutionary history

Model	AIC	delta AIC	AICw
OU	703.30	0	1
White noise	713.87	10.57	0
BM	846.91	143.61	0
EB	848.95	145.65	0

Note. AICw: AIC weight; BM: Brownian motion; delta AIC: AIC difference between the model and the best model (lowest AIC); EB: early burst; OU: Ornstein–Uhlenbeck.

Our evidence supporting climatic niche conservatism in turtles reinforces the concern that climate change impacts, estimated using species distribution models (Ihlow et al., 2012), are a future potential problem that turtles might face. Considering that turtles also have reproductive traits commonly associated with delayed reproduction (Congdon, Dunham, & Van Loben Sels, 1993), which in turn are also related to high extinction risk, and that most species have temperature-dependent sex determination (TSD) (Ewert, Etchberger, & Nelson, 2004), global warming might be other important challenge that these species will face.

Terrestrial and aquatic turtles have different climatic niche optima in the OU model. This result is not surprising considering all the physical and chemical differences between these environments (Grosberg et al., 2012; Vermeij & Dudley, 2000). Although temperature might determine most of the niche of terrestrial species, aquatic species are more likely limited by water availability, reinforcing the importance of precipitation in their climatic niche (Waterson et al., 2016). In our study, climatic niches of aquatic species are mainly characterized by high amounts of precipitation, which increases water availability, a basic demand for this group that spends most of its lifetime in water. Precipitation is also strongly related to biogeographic delineation of aquatic turtles distribution (Ennen et al., 2017), suggesting the importance of the climatic niche pattern we found in the species distributions. Terrestrial turtles were mainly characterized by mesic niches (scores close to zero). Such mesic niches (and a lower richness when compared to aquatic turtles) help to explain why richness and biogeographic patterns of turtles as a whole are also strongly related to precipitation and thus similar to the patterns of aquatic species alone (Ennen, Agha, Matamoros, Hazzard, & Lovich, 2016; Ennen

TABLE 3 Comparison among the different variations of OU models employed in our study to evaluate whether climatic niche evolution of turtles might differ between aquatic and terrestrial species

Model	AIC	dAIC	AICw	Optimum	*SE*	Rate
OUm	684.91	0	0.55	**−0.671**	**0.074**	**0.329**
				0.101	0.150	0.329
OUmr	685.29	0.38	0.45	**−0.675**	**0.077**	**0.332**
				0.110	0.133	0.245
OU	703.30	18.39	0	**−0.515**	**0.070**	**0.342**
				−0.515	0.070	0.342

Note. Parameters in bold are from aquatic species, whereas those in normal fonts are from the terrestrial ones.

AICw: AIC weight; dAIC: AIC difference between the model and the best model (lowest AIC); Optimum: optimum value according to the OU model; OU: single-optimum Ornstein–Uhlenbeck; OUm: Ornstein–Uhlenbeck model with different climatic niche optimum for species of each habitat type; OUmr: Ornstein–Uhlenbeck model with different climatic niche optimum and evolutionary rates between species of the two habitat types; Rate: niche evolutionary rate; *SE*: standard error of the optimum value.

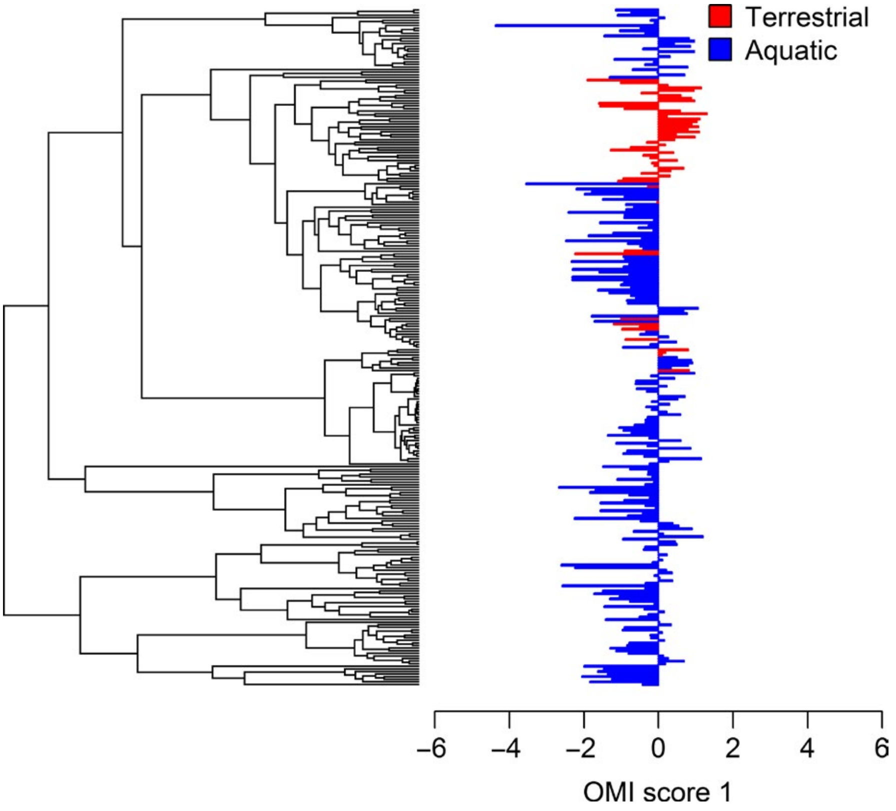

FIGURE 2 Niche position (first axis of Outlying Mean Index [OMI] scores) of terrestrial and aquatic turtle species

et al., 2017; Iverson, 1992; Rodrigues et al., 2017). Finally, previous studies have found that the ancestor of recent turtles was most likely aquatic (Jaffe et al., 2011; Joyce & Gauthier, 2004; Rodrigues & Diniz-Filho, 2016). Hence, when invading terrestrial environments, the new environmental conditions encountered likely drove the observed change in niche position during the aquatic to terrestrial transition in turtles.

Although species traits such as reproduction, range size and diet might influence evolutionary rates of climatic niches (Cooper et al., 2011; Smith & Beaulieu, 2009), and habitat has a strong influence on many turtle characteristics (Jaffe et al., 2011; Rodrigues & Diniz-Filho, 2016; Slavenko, Itescu, et al., 2016; Slavenko, Tallowin, et al., 2016), including their climatic evolutionary optimum, the importance of habitat on climatic niche evolutionary rate was not consistently found. The AIC difference between the model including differences in evolutionary rates of climatic niches and a more parsimonious version that ignored rate differences was very low (<2), suggesting that both models are similar. Despite different climatic niche optima between aquatic and terrestrial species, their evolutionary rates seem to be similar, suggesting that changes in these two components of niche evolution are not necessarily linked. Even when the model including rate variation showed a fit to the observed pattern similar to the model without it, both models support differences in niche optima between aquatic and terrestrial species, whereas the additional finding of similar patterns of sister species niche overlap between these two species groups reinforces similarity in their evolutionary rates. Indeed, if evolutionary rates were highly different between climatic niches of aquatic and terrestrial species, these two species groups would also show different values of sister species pairs niche overlap. For instance, faster evolutionary rates in one species group should result in smaller values of niche overlap between sister species when compared to the other group.

We conclude that phylogenetic climatic niche conservatism occurs among turtle species. Furthermore, terrestrial and aquatic species occupy different climatic niches but seem to have evolved at similar evolutionary rates, reinforcing the importance of habitat preference in understanding species climatic niches and their evolution.

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