RESEARCH ARTICLE

Niche conservatism over deep timescales and diverse niche axes in land vertebrates

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Abstract

Aim: There has been considerable interest in niche conservatism, the idea that ecological variables are similar among related species. Much research has focused on climatic niches of recently diverged species, rather than deeper timescales or nonclimatic niche axes. Furthermore, it has been suggested that conservatism disappears over deeper timescales, and is greater in alpha niche traits (like diet and microhabitat) than beta niche variables (like climate). Here, we test these latter two ideas by comparing patterns of phylogenetic conservatism among 10 niche variables across major clades of land vertebrates.

Location: Global.

Time Period: Present to 350 million years ago.

Major Taxa Studied: Tetrapods, including amphibians, mammals, lepidosaurs (including lizards and snakes), turtles, crocodilians and birds.

Methods: The 10 niche variables included four alpha niche components (diet, diel activity, habitat, body temperature) and six beta niche components (related to climatic temperature and precipitation). We analysed these variables on time-calibrated phylogenies with similar taxon sampling (~1700 species), using phylogenetic signal (lambda) to estimate conservatism, along with the *D* statistic and estimates of evolutionary rates.

Results: Phylogenetic signal was generally strong across all variables, with lambda generally >0.80 (with 1.0 representing maximum signal). Nevertheless, mean phylogenetic signal was lower in beta niche traits than alpha niche traits (based on lambda and especially the *D* statistic), and alpha niche traits showed significantly slower rates of evolution.

Main Conclusions: We address two long-held views in the literature on niche conservatism, rejecting one but supporting the other. We show that phylogenetic signal does not disappear over deep timescales for many important niche variables, even over 350 million years. We also generally support greater conservatism in alpha niche traits than beta niche traits over hundreds of millions of years, a pattern that was previously suggested (but not explicitly tested) based on closely related species.

KEYWORDS
climate, diet, ecology, habitat, niche conservatism, phylogeny, vertebrate

1 | INTRODUCTION

Do ecological traits of a species resemble those of their close relatives? Do these traits remain similar among species over time? If so, how long does this last? How much do the answers to these questions depend on which ecological variable is measured? These fundamental questions lie at the intersection of ecology and evolutionary biology, and have implications for many of the most important and urgent questions in these fields. For example, the tendency for species climatic niches to remain similar over time (or not) may have important implications for species responses to global warming (Román-Palacios & Wiens, 2020; Sinervo et al., 2010; Tingley et al., 2009), the spread of invasive species (Atwater et al., 2018; Liu et al., 2020; Peterson, 2003; Petitpierre et al., 2012), the origins of the latitudinal diversity gradient and other richness patterns (Crisp et al., 2009; Kerkhoff et al., 2014; Neves et al., 2021; Rangel et al., 2007; Smith et al., 2012; Wiens et al., 2006), the origin of species (Cadena et al., 2012; Hua & Wiens, 2013) and the assembly of ecological communities (Stephens & Wiens, 2009).

There has been extensive debate about whether ecological niches show a pattern of conservatism (i.e., similarity among closely related species over time), which aspects of the niche do and do not, and over what timescales (Crisp & Cook, 2012; Losos, 2008; Losos et al., 2003; Pearman et al., 2008; Peterson, 2011; Peterson et al., 1999; Wiens et al., 2010; Wiens & Graham, 2005). Two unresolved questions are: (1) whether niches remain conserved when including deep timescales of hundreds of millions of years or more, and (2) which aspects of the niche tend to be more conserved. Here we address these questions using tetrapods (land vertebrates) as a model system.

Niche conservatism is often thought to erode over deeper timescales. For example, in a well-cited review, Peterson (2011) stated that: "niche conservatism seems to break down more on the scale of diversification of species within genera" (p. 825). In that study, deeper timescales were considered to be 1–10 million years ago. However, only climatic niches were considered, and timescales >10 million years were not included. Other studies have found evidence for niche conservatism at much deeper timescales, but not necessarily in climatic niche variables. For example, some mutualisms appear to have been maintained for >1 billion years (Zeng & Wiens, 2021).

Previous studies have also suggested that different aspects of the niche might show different levels of divergence and conservatism at different timescales. Ackerly et al. (2006) suggested that there might be differences in the levels of conservatism between alpha niche variables and beta niche variables. Those authors defined the alpha niche as those niche components related to local-scale ecology, including microhabitat, diet and species interactions. This overlaps with the Eltonian niche concept (Soberón, 2007). Conversely, the beta niche pertains to climate and other factors related to large-scale distributions (similar to the Grinnellian niche concept; Soberón, 2007). Ackerly et al. (2006) suggested that there was earlier divergence in alpha niche variables, and more recent divergence in beta niche variables. This implies that alpha niche variables may be more conserved than beta niche variables, especially over deeper timescales. They proposed this pattern based on the long-standing idea that closely related species tend to co-occur less often than expected by chance (given competition and their similar alpha niche traits; e.g., Cavender-Bares et al., 2004; Elton, 1946; Gotelli & Graves, 1996; Williams, 1964), whereas close relatives diverge in the beta niche instead. Ackerly et al. (2006) supported this pattern based on their results in plants (*Ceanothus*), and suggested that this applied broadly, based on studies in plants (e.g., oaks; Cavender-Bares et al., 2004) and animals (e.g., warblers: *Phylloscopus*; Richman, 1996; Richman & Price, 1992; other vertebrates; Streelman & Danley, 2003). However, to our knowledge, there have not been explicit statistical tests of these potential differences in conservatism between these two types of niche traits using multiple traits. Moreover, these examples were drawn from relatively recent clades (e.g., genera). It is unclear if such differences also occur when deeper timescales are included.

These studies suggest tantalizing variation in levels of conservatism, both over time and among traits. However, most studies have not analysed diverse types of traits in the same taxa. There are some exceptions. For example, a study (Bohning-Gaese & Oberrath, 1999) tested 21 ecological traits among 151 German bird species and found significant phylogenetic signal in 13 traits. Prinzing et al. (2001) found significant conservatism in all six ecological traits examined among 100 European plant species. Losos et al. (2003) analysed 7 ecological variables in 11 species of *Anolis* lizards from Cuba, but found little conservatism. Kamilar and Cooper (2013) examined 31 diverse variables among primates and found significant signal in 28 traits. Our listing here is neither a comprehensive nor systematic review, nor do we describe the many tests used. Instead, these examples illustrate that past studies of diverse traits have often been limited in taxonomic scale, geographic scale or both. Moreover, none of these studies explicitly compared levels of conservatism in alpha versus beta niche traits.

Here, we test 10 diverse ecological variables among vertebrate species, incorporating very deep timescales. We focus on tetrapods (land vertebrates), which include amphibians, mammals, lepidosaurs (lizards and snakes), turtles, crocodilians and birds. We compare the same measures of signal and conservatism across all variables (see Methods). This allows us to test the prediction that alpha niche traits show greater conservatism than beta niche variables. Our results generally show strong phylogenetic signal across all variables, but with more signal and slower rates in alpha niche traits. These results are inconsistent with the idea that conservatism breaks down over deeper timescales, but do support the hypothesis of greater conservatism in alpha niche traits.

2 | METHODS

2.1 | Overview

We assembled data on climate, body temperature, diel activity, diet and habitat for a matched set of species sampled across tetrapods. These species were initially selected for a study on body temperatures

(Moreira et al., 2021). The distribution of species among major clades and families is summarized in Table S1. Two time-calibrated phylogenies were available for these species (Appendix S1). The primary phylogeny included 1721 species and the secondary tree included 1712 species.

The variables that were included spanned the most obvious aspects of the niche, including where species occur (climate), when they are active (diel activity), what habitat they utilize and what they feed on. Body temperature is a crucial ecological variable that potentially determines exactly when and where species are active (e.g., morning vs. afternoon, sun vs. shade) and for ectotherms can impact almost all aspects of their behaviour, ecology, life history and physiology (e.g., Angilletta, 2009; Angilletta et al., 2002). For endotherms (e.g., birds, mammals), much of their energy goes into maintaining relatively constant body temperatures (Bennett & Ruben, 1979; Fristoe et al., 2015).

We first quantified levels of phylogenetic signal (lambda; Pagel, 1999) for these species for all traits. We then tested if there are significant differences in levels of signal among alpha niche traits (diet, habitat, diel activity, body temperature) and beta niche variables (the six climatic variables). We also included an alternative measure of phylogenetic signal designed for discrete traits (D statistic; Fritz & Purvis, 2010) and estimates of evolutionary rates.

There has been debate about whether phylogenetic signal reflects phylogenetic niche conservatism. Phylogenetic signal reflects the tendency of closely related species to share similar trait values (Pagel, 1999) and is consistent with a Brownian motion (BM) model of trait evolution. Niche conservatism has also been defined as the tendency of closely related species to share similar trait values (Losos et al., 2003). However, conservatism and signal can diverge if a trait is largely invariant among species (i.e., the trait may be conserved but will not have signal; Revell et al., 2008). Therefore, the presence of signal is potential evidence of conservatism, but the absence of signal does not necessarily reject conservatism. There has been considerable emphasis on the idea that rate and signal can be decoupled (Losos, 2008; Revell et al., 2008). But this may apply primarily to continuous variables (Revell et al., 2008). Therefore, we also performed analyses in which we recoded all continuous variables as discrete, and we also included comparisons of rates. Furthermore, many researchers do consider the greater similarity of more closely related species (i.e., phylogenetic signal) to be evidence of niche conservatism (Losos et al., 2003; Wiens et al., 2010). We do not think that traits must be more conserved than a BM model to have niche conservatism.

Note that the presence of strong phylogenetic signal (BM) does not necessarily mean that a trait evolves randomly according to a neutral model of genetic drift (see O'Meara et al., 2006). Instead, the BM model is also consistent with other processes, such as directional selection with a changing optimum over time and punctuated models that combine both long-term stasis and abrupt change (Hansen & Martins, 1996). The latter seems especially relevant to niche conservatism. Many traits included here seem very unlikely to evolve through drift alone (e.g., climatic niche, diet, microhabitat,

body temperature). Finally, we do not know of empirical evidence that genetic drift within populations can generate a pattern of strong phylogenetic signal among hundreds of species over tens or hundreds of millions of years.

As an alternative approach to comparing conservatism between types of niche traits (alpha vs. beta), we also analysed transition rates. Again, some authors consider rates to be a more appropriate measure of conservatism than signal (Revell et al., 2008). However, it is unclear what specific rate values indicate conservatism versus lability. Instead, we compared mean rates between the alpha and beta niche traits. To do this, we coded the continuous variables as discrete, so that all variables were discrete and therefore comparable (note that recoding discrete variables as continuous was not possible for all discrete traits analysed here).

2.2 | Assembling datasets

2.2.1 | Climatic data

We obtained climatic data for 1721 species (those analysed by Moreira et al., 2021) for six variables: annual mean temperature (Bio1), maximum annual temperature (Bio5), minimum annual temperature (Bio6), annual precipitation (Bio12) and precipitation of the wettest quarter (Bio16) and driest quarter (Bio17). These reflect overall climate (Bio1, Bio12) and yearly extremes of temperature (Bio5, Bio6) and precipitation (Bio16, Bio17).

Most climatic data were obtained from previous studies of amphibians (Qu & Wiens, 2020), squamates (Pie et al., 2017), birds (Cooney et al., 2016) and mammals (Castro-Insua et al., 2018). These data were primarily from fine-scale range maps, with data for each species based on the mean across grid cells where that species occurs. There were 17 amphibian species and 77 reptile species that had data for temperature variables, but lacked precipitation data. A total of 186 reptile species, 129 bird species and 75 mammal species lacked all climate data. We obtained additional climatic data from distribution maps for birds (BirdLife International, 2017). For other species we obtained georeferenced locality information from GBIF.org (which we considered strongly preferable to excluding these species). We then assessed whether these localities were within the native range of the species, using information from Uetz et al. (2018) and IUCN (2021). Any localities outside the known range of each species were excluded. We used QGIS (QGIS Development Team, 2018) to extract climatic data for each locality or grid cell from the WorldClim dataset (Hijmans et al., 2005) at 30″ spatial resolution (for 1950–2000). Both maps and point localities reflect locations where each species occurs, and use of one or the other should have limited impact on the estimates of mean climatic niche values for each species (e.g., a species occurring in a mesic tropical climate should be correctly characterized as such using both approaches). For both, we used mean values across localities for each species. One species lacked adequate locality information (*Cryptomys/Fukomys amatus*) and was excluded. Climatic data

(Dataset S1) consisted of 1720 species for the primary tree and 1709 for the secondary tree. All datasets (Datasets S1–S17) and other supplementary materials are available as Supporting Information and on Dryad (Saban et al., 2023).

These variables reflect the realized climatic niche. Thus, values in each species may be influenced by non-climatic factors (e.g., dispersal barriers, other species) and not simply the climatic conditions that can be physiologically tolerated (fundamental niche; Soberón, 2007). This might introduce noise in the climatic variables and weaken their phylogenetic signal, but should not create broad-scale phylogenetic signal when none exists. Realized climatic niche variables have been central to discussions about niche conservatism for decades. They are also essential for comparing alpha and beta niche traits (since alpha niche traits are also based on realized niches). We are here testing for conservatism in the large-scale climatic distributions of these species. Incorporating the spatial accessibility of different climates for each species is somewhat impractical when testing for signal across trees over hundreds of millions of years.

2.2.2 | Diet data

We assembled diet data for these same 1721 species. We give the details of the assembly of this dataset in Appendix S2. We primarily assigned a diet to each species using the following classification (from Meiri, 2018): carnivorous: >90% animal matter in diet; omnivorous: 10%–50% plant matter; herbivorous: >50% plant matter. Diet data for mammals and birds were obtained largely from Wilman et al. (2014) and for lepidosaurs from Meiri (2018).

We were unable to obtain adequate diet data for nine species (eight lizards, one mammal). Therefore, the diet dataset included 1712 species for the primary tree and 1700 for the secondary tree. Diet data (along with supporting references) are given in Dataset S2.

For some analyses (see below), we treated diet as a binary variable. For these analyses, we treated omnivorous species as either carnivorous (maximum carnivory coding) or herbivorous (maximum herbivory coding).

We also performed alternative analyses within birds and mammals using more fine-scaled data, with 10 diet states (including states for species that predominantly eat fruit, nectar, seeds, other plant material, invertebrates, fish, endothermic tetrapods, ectothermic tetrapods, vertebrates in general and scavenge). Details of these codings are in Appendix S2 and the bird and mammal data are in Datasets S3 and S4 respectively. We did not perform these analyses in other groups because such fine-scale data were not broadly available and because most adult amphibians and lepidosaurs are generalist insectivores (Pough et al., 2016).

2.2.3 | Habitat data

For habitat, we initially focused on whether species were marine or terrestrial (with terrestrial here including freshwater). We again used

the tree for 1721 species (Moreira et al., 2021) to select species. We assigned species to habitats using data compiled by Miller and Wiens (2017). That dataset did not include amphibians, but all extant amphibians were here considered non-marine (Pough et al., 2016). The habitat dataset (Dataset S5) consisted of 1721 species for the primary tree and 1709 for the secondary tree.

We considered habitat to be an alpha niche trait, given that the transition from terrestrial to marine habitats can occur over a few metres (unlike climate or biomes) and since they are part of a continuum of variation among microhabitats. We recognize that marine and terrestrial habitats can also vary over large spatial scales (but so can other microhabitats, like rocks, trees and freshwater).

We also performed analyses using more fine-scale microhabitat data, such as states for species that are active in vegetation (arboreal), on the ground (terrestrial) and on rocks (saxicolous). However, the available data were not standardized across groups, and so we did not combine them. Nevertheless, these analyses allowed us to test the impact of different codings of microhabitat on phylogenetic signal within each major group (i.e., amphibians, birds, lepidosaurs, mammals, turtles). We give the details of how these datasets were assembled in Appendix S3. The data and references are in Datasets S6–S10.

2.2.4 | Diel activity data

We used the diel activity dataset of Moreira et al. (2021), which was largely from a previous compilation (Anderson & Wiens, 2017). We used the four diel activity states as defined by those authors (Anderson & Wiens, 2017): arrhythmic, crepuscular, diurnal and nocturnal. However, most (>75%) sampled tetrapod species were diurnal or nocturnal (Moreira et al., 2021). Diurnal species are primarily active between sunrise and sunset. Nocturnal species are primarily active after sunset and before sunrise. Arrhythmic species are similarly active during day and night or show major seasonal changes (e.g., active by night during summer, but by day during spring and fall). Crepuscular species are primarily active at dusk or twilight. We performed analyses of phylogenetic signal analysing all four states, and two analyses in which crepuscular and arrhythmic species were either treated as diurnal (maximum diurnal coding) or nocturnal (maximum nocturnal coding). For our comparison among variables, we used the mean value of phylogenetic signal across these three coding schemes for each tree. The diel activity dataset (Dataset S11) consisted of 1721 species for the primary tree and 1709 for the secondary tree.

2.2.5 | Body temperature

We used previously compiled body temperature (T_b) data (Moreira et al., 2021). We refer readers to that article for the criteria for including species and data. Data are given in Dataset S12.

2.3 | Statistical analyses

We primarily assessed the level of phylogenetic signal in each ecological variable. We first estimated Pagel's (1999) lambda for each variable, using the R package *Geiger* version 2.0.7 (Harmon et al., 2008; Pennell et al., 2014). We used the function "fitContinuous" for continuous variables (climate, T_b) and "fitDiscrete" for discrete variables (diet, habitat, diel activity). Our main focus was on comparing lambda values among variables, rather than testing the fit of the data to alternative models (e.g., white noise, Ornstein–Uhlenbeck [OU]). Many alternative models, such as OU, cannot be applied to discrete variables. Moreover, the strong phylogenetic signal found for all variables across tetrapods suggested that these alternative models did not have the best fit to these data (e.g., white noise implies a lambda of 0). However, we did test the fit of the data to alternative models within crocodilians and turtles, in which sample sizes were small and estimated lambda was highly variable. For these two groups, we compared the sample-size corrected AIC (AICc; Burnham & Anderson, 2002) for the estimated lambda and white noise models for each variable, using fitContinuous and fitDiscrete in *Geiger*. We also used an alternative measure of signal and conservatism, the *D* statistic, and compared estimated rates between the different types of variables (see below).

We selected Pagel's (1999) lambda to quantify signal for two main reasons. First, this index may be unique in providing an easily interpretable index that can be obtained for both continuous and discrete variables. Second, simulations show that this estimator is relatively accurate for estimating the level of phylogenetic signal and has particularly low rates of Type I error (Munkemuller et al., 2012). We recognize that this approach is not estimating different rates of change in different parts of the tree for each variable, but our goal was to estimate overall signal for each variable across the tree and then compare levels of signal across diverse variables. We also performed analyses within each major tetrapod clade, which help address variability across the tree (see below).

We also performed analyses in which continuous variables were made discrete. These addressed whether lambda is impacted by treating quantitative variables as discrete. We also used these recoded variables to allow for direct comparison with the discrete variables for the *D* statistic and for evolutionary rates. To make continuous variables discrete, we calculated the average value among species for each variable and assigned species above or below the average to alternative states. There are many other ways that the continuous variation could be subdivided into states. However, almost any approach would require a similar arbitrary division in continuous variation among species. Use of binary coding (two states) was also necessary to estimate the *D* statistic.

Analyses were performed using two time-calibrated tetrapod trees (from Moreira et al., 2021). These trees used a time-calibrated phylogeny of tetrapods to which was grafted detailed time-calibrated trees from separate studies within amphibians, mammals, lepidosaurs, turtles, crocodilians and birds. The two trees differed in that different studies within amphibians, mammals, lepidosaurs were used (with different backbone trees within birds). The primary tree included 1721 species, whereas the alternative tree included only 1709 species. Details of these trees (and associated references) are given in Appendix S1. The two trees are given in Datasets S13 and S14.

We analysed these two trees rather than a distribution of trees for two main reasons. First, a distribution of trees (spanning all sampled tetrapod species) was simply not available. Second, trees from separate phylogenetic analyses are potentially more different from each other than those from a distribution of trees from one analysis. Therefore, the two trees may better capture the robustness of the results to variation in topology and branch lengths than a distribution of trees from a single analysis.

We also analysed phylogenetic signal in these 10 variables within the major clades of tetrapods, including amphibians, mammals, lepidosaurs, turtles, crocodilians and birds. However, diet and two-state habitat were not analysed in amphibians because they share the same state for these variables. Similarly, diet and diel activity in crocodilians shared the same state and were not analysed. These analyses were performed on the primary and secondary trees for amphibians, lepidosaurs, birds and mammals. For turtles and crocodilians, the primary tree and alternative trees were identical. However, we note that results within these six clades should be taken with some caution for at least two reasons. First, our sampling may be less representative within these clades than among them (e.g., we include all major groups of tetrapods, but not every major group of amphibians). Second, the absolute numbers of species sampled within crocodilians and turtles are limited, and so these results are potentially unreliable (Fritz & Purvis, 2010; Munkemuller et al., 2012).

To test whether signal decreased over time, we tested for a negative correlation between lambda and the crown group ages of these six clades. We analysed the mean lambda for the alpha and the beta niche variables for each tree (rather than all 10 variables separately). We also included tetrapods as a seventh, older data point. We used non-parametric Spearman correlation in R. We did not perform a phylogenetic correction (given that six clades are nested inside tetrapods), but our primary interest was in evaluating whether the correlation is negative or positive. Additional younger clades could potentially be included within these major groups, but our question was whether signal disappears at the deepest timescales, as previously predicted.

We statistically compared mean levels of signal between alpha niche traits (T_b, diel activity, diet, habitat) and beta niche traits (climatic variables). We used an unpaired *t* test in R. This test is not corrected for phylogeny, because we are comparing variables, not taxa (there is no phylogeny among variables). We performed one analysis (*t* test) based on the results for each tree. Estimates of signal were generally similar between the two trees. We also compared means of the alpha and beta niche variables within each clade. We recognize that some variables may not be fully independent (see Discussion).

As an alternative measure of signal for discrete variables, we used the *D* statistic (Fritz & Purvis, 2010). We applied this statistic across
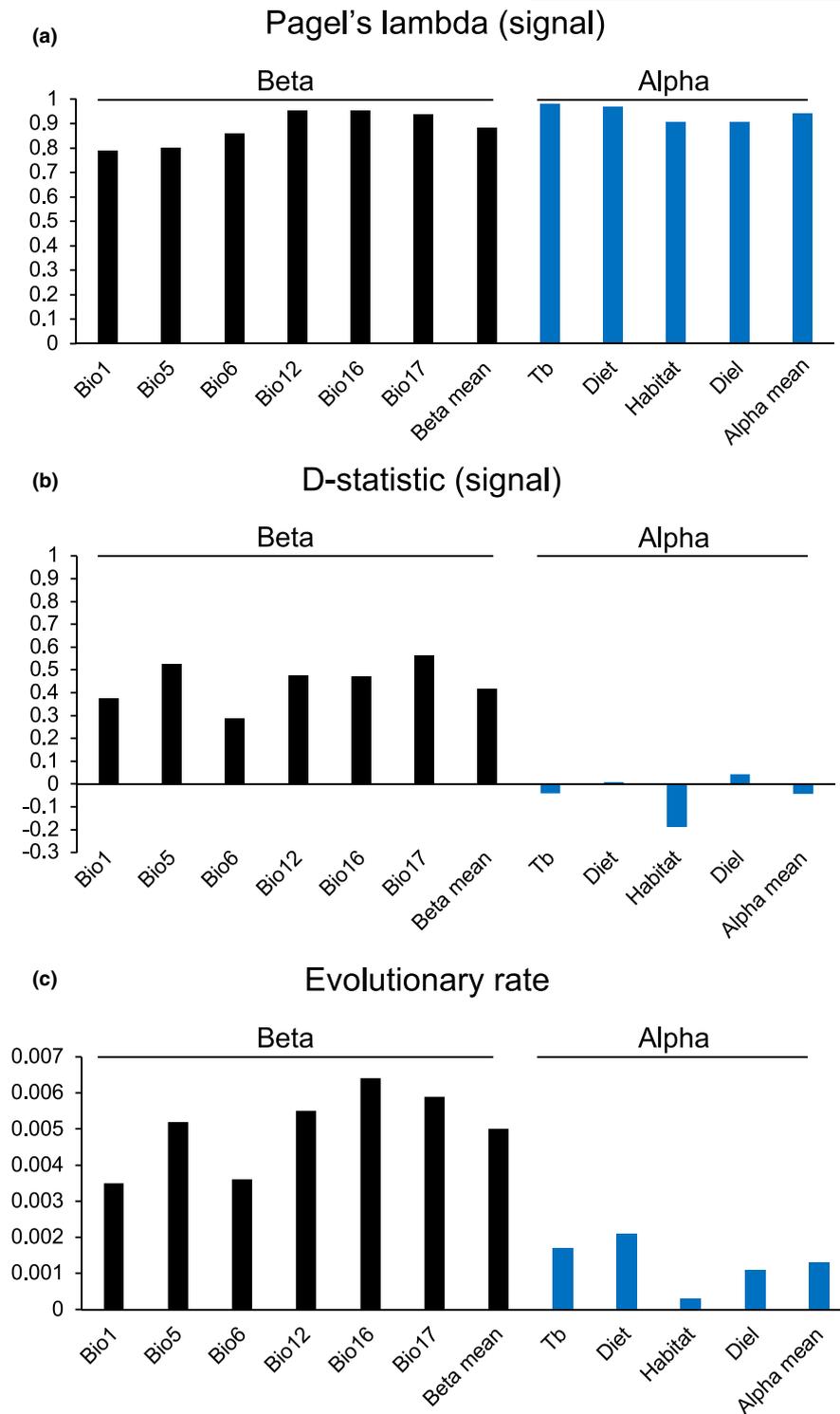
FIGURE 1 Niche conservatism in beta and alpha niche variables across tetrapods. Beta variables are in black and alpha variables are in blue. All results are for the primary tree. (a) Phylogenetic signal based on Pagel's (1999) lambda (values in Table 1). For diet, lambda is based on the three-state diet coding. For diel activity, the mean lambda from the maximum nocturnal, maximum diurnal, and four-state diel codings is shown. (b) Phylogenetic signal based on the *D*-statistic (values in Table S3). The *D*-statistic uses discrete, binary variables. Therefore, all climate variables and body temperature (T_b) have been made discrete. Diet is based on the mean of the binary maximum carnivory and maximum herbivory codings. Diel activity is based on the mean of the binary maximum nocturnal and maximum diurnal codings. (c) Evolutionary rates, given in changes per million years (values in Table 2). Climatic variables and T_b were made discrete prior to estimating rates, to allow direct comparison to the other variables. The rate for diet is taken from the three-state coding. The rate for diel activity is from the four-state coding.

TABLE 1 Estimates of phylogenetic signal (lambda) for diverse ecological niche axes in tetrapods.

Variable	Primary tree	Secondary tree
Beta niche		
Bio1 (continuous)	0.789	0.808
Bio5 (continuous)	0.803	0.837
Bio6 (continuous)	0.861	0.884
Bio12 (continuous)	0.954	0.956
Bio16 (continuous)	0.954	0.958
Bio17 (continuous)	0.939	0.935
Beta mean	0.883	0.896
Alpha niche		
Body temperature (continuous)	0.981	0.979
Diet (three states)	0.969	0.971
Habitat (two states)	0.905	0.928
Diel activity (mean)	0.908	0.937
Diel activity (four states)	0.872	0.937
Diel activity (maximum nocturnal)	0.916	0.923
Diel activity (maximum diurnal)	0.937	0.951
Alpha mean	0.941	0.954

TABLE 2 Estimated evolutionary rates in alpha and beta niche variables across tetrapods.

Variable	Primary tree	Secondary tree
Beta niche		
Bio1 (discretized)	0.0035	0.0038
Bio5 (discretized)	0.0052	0.0060
Bio6 (discretized)	0.0036	0.0043
Bio12 (discretized)	0.0055	0.0058
Bio16 (discretized)	0.0064	0.0068
Bio17 (discretized)	0.0059	0.0067
Beta mean	0.0050	0.0056
Alpha niche		
Body temperature (discretized)	0.0017	0.0017
Diet (three states)	0.0021	0.0023
Habitat (two states)	0.0003	0.0003
Diel activity (four states)	0.0011	0.0012
Alpha mean	0.0013	0.0014

Note: The units are changes per million years. The difference between alpha and beta traits was significant for both trees (based on Welch's two-sample t test; primary tree: $T = -5.909$; df $= 7.995$; $p < 0.001$; secondary tree: $T = -6.333$; df $= 7.962$; $p < 0.001$). Model selection results are in Dataset S15. The lambda model had the best fit and was used here. Other models (constant rate, delta) gave a similar dichotomy in rates between alpha and beta niche variables (Dataset S15). Note that a delta model of changing rates over time did not have the best fit, and the estimated delta values were positive (implying increasing rates at more recent timescales).

all tetrapods and within individual clades, using the R package *caper* (Orme et al., 2013). The *D* statistic is only applicable to discrete, binary variables. Diet and diel activity have three and four states respectively. Therefore, we used the two binary versions of these variables (maximum diurnal and maximum nocturnal; maximum carnivory and maximum herbivory). We also used the continuous variables that were recoded as discrete across tetrapods. As for lambda, the *D* statistic cannot be calculated in clades that are invariant for a given character.

We also tested for differences in overall evolutionary rates between alpha and beta niche traits. For this analysis, we used the discrete traits and the continuous variables that were recoded as discrete (rates for discrete and continuous variables are otherwise not directly comparable). We used the "fitDiscrete" function in *Geiger* to estimate the overall transition rate under the equal-rates (ER) model for each variable. We used the ER model for two main reasons. First, the all-rates-different model can give problematic rate estimates when one or more states are rare among species (e.g., Schluter et al., 1997), which is the case for some variables here. Second, we were interested in obtaining a single estimate of overall change for each trait across tetrapods, not transition rates between individual states. This is also why we did not explore differences in rates among clades. For each variable on each tree, we compared the fit of the constant rate, lambda and delta (rates changing over time) tree-transformation models using the AICc (results in Dataset S15). We then estimated overall transition rates from the best-fit model. After obtaining the overall rate for each character, we then performed a t test comparing rates between the alpha and beta niche variables.

Finally, we assessed how our estimates of phylogenetic signal were impacted by incomplete taxon sampling. We analysed lambda for tetrapods and major tetrapod clades for each variable using 10 randomly sub-sampled trees (from Moreira et al., 2021). Each tree included ~10% of the species in the primary tree (172 species). Species were sampled from each major clade roughly in proportion to their richness in the full sampled tree (details in Moreira et al., 2021). Species from groups within these clades were also proportionally sampled, including groups within amphibians (frogs, salamanders), mammals (monotremes, marsupials, placentals), lepidosaurs (tuatara, snakes, gekkotans, other lizards) and birds (paleognaths, neognaths). Therefore, the overall sampling of species across the tree was not fully random, but the selection of species within these major groups was. These 10 trees are provided in Dataset S16. For each variable, we evaluated whether lambda from the full tree was within the 95% confidence interval of the 10 sub-sampled replicates. The R codes used in these and all other analyses are given in Dataset S17.

3 | RESULTS

Estimates of lambda for each variable are summarized in Figure 1a and Table 1. Results were generally very similar between the primary

FIGURE 2 Bar charts depicting the mean phylogenetic signal (lambda) in beta and alpha niche variables within major tetrapod clades. Results are for the primary tree. Values for each variable in each major clade are given in Tables S5–S10. For all clades, diet is coded with up to three states and diel activity with up to four. Silhouettes are from PhyloPic (phylopic.org).
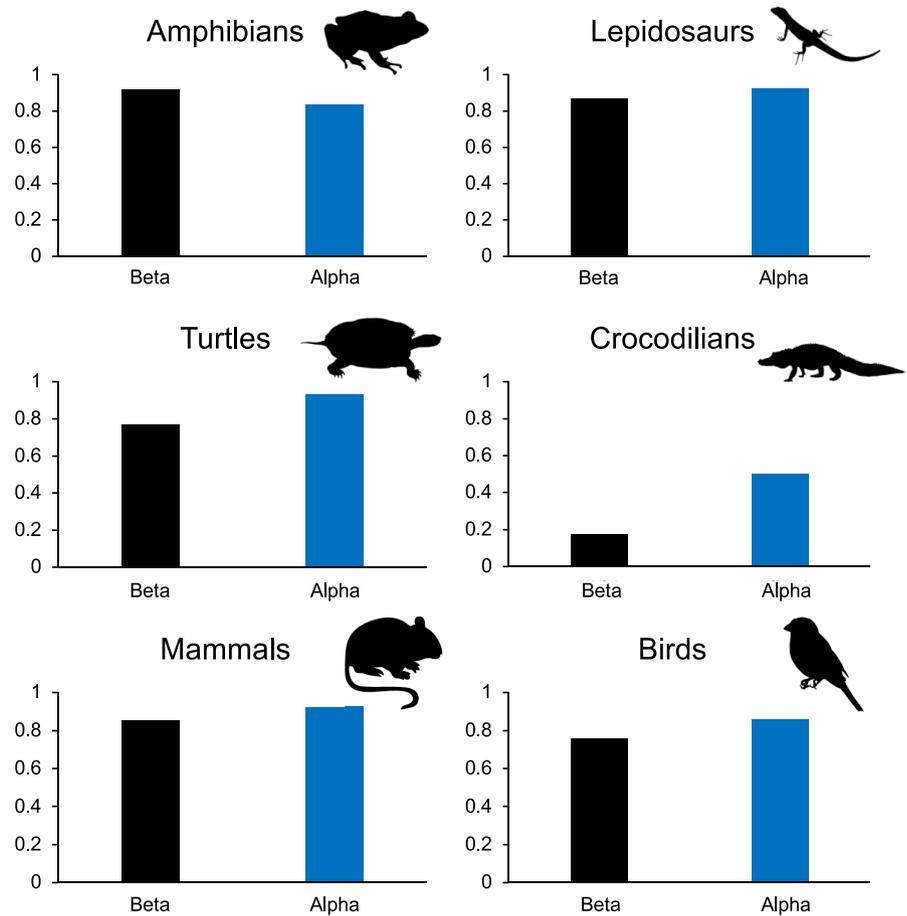
and alternative trees (Table 1). There was strong signal in every variable, with all values >0.75 and many >0.90. Results were generally similar after discretizing continuous variables (Table S2), with all lambdas for discretized variables from 0.90 to 0.95 (and roughly equal numbers of increases and decreases relative to the continuous data). Estimated *D* for the discrete alpha niche variables (Figure 1b; Table S3) was generally low (−0.189 to 0.120; indicating strong conservatism) and significantly different from a white noise model (no signal) but not from a BM model (strong signal). For the discretized climatic variables (Figure 1b), *D* was higher (0.285–0.575; less conserved) and significantly different from both a white noise model and also a BM model. Discretized T_b also showed low *D* (−0.040 to −0.032) and was not significantly different from BM (strongly suggesting that the higher *D* in the discretized climatic variables is not an artefact of their being made discrete).

There was no significant difference in estimated lambda between alpha and beta niche variables in tetrapods ($p=0.160$ and $p=0.087$ for the primary and alternative trees; Figure 1a; Table S4). However, mean lambda values for beta niche variables were lower, as predicted. Alpha niche variables had significantly lower *D* (more conserved) for both trees ($p<0.001$; Figure 1b; Table S3). Rates of change were significantly higher for beta niche variables than for alpha niche variables ($p<0.001$; Figure 1c; Table 2).

There was strong phylogenetic signal (lambda) within most major clades for most variables (Figure 2; Tables S5–S10). The *D*

statistic within clades also generally supported significant signal for most variables (Tables S11–S16), but with some exceptions (e.g., habitat in lepidosaurs and crocodilians). However, lambda values within clades were sometimes lower and more variable than for tetrapods (especially for climatic variables in crocodilians and birds; Figure 2; Tables S5–S10). The beta niche variables had significantly lower mean values (Table S4) within birds ($p=0.042$) for the primary tree. Crocodilians showed very low signal for some variables (lambda=0.00). This was most likely an artefact of the limited number of sampled species in this clade (see Discussion). Mean values of lambda for alpha niche variables were generally higher than for beta niche variables among these clades and trees (Figure 2).

Subdividing microhabitat into additional states yielded very similar estimates of signal (lambda) relative to only two states in these major clades (Table S17). Similarly, subdividing diet into 10 states in mammals and birds produced lambda values similar to analysing only three states (Table S18).

We found that correlations between clade age and mean phylogenetic signal (lambda) among these clades were positive but non-significant for alpha niche variables (primary tree: rho=0.4286, $p=0.3536$; secondary: rho=0.0714, $p=0.9063$) and positive and significant for beta niche variables (primary tree: rho=0.8929, $p=0.0123$; secondary: rho=0.9286, $p=0.0067$; data in Table S19). These results do not support the idea that signal disappears at deeper timescales (which should yield negative correlations).

We found that sampling only 10% of the species in the full tree tended to reduce estimated signal (lambda) relative to the full tree (Tables S20–S22). This decrease was strong for the beta niche variables (mean across variables = 0.883 for full sampling, mean = 0.597 for sub-sampled replicates) and weaker for the alpha niche variables (from 0.941 to 0.869). The decrease was significant for all but one (Bio12) of the beta niche variables and one of four alpha niche traits (Table S21). This difference in the effects of sub-sampling led to significant differences between alpha and beta niche variables in 4 of the 10 replicates (Table S22).

4 | DISCUSSION

The question of whether related species share similar ecological niches (i.e., niche conservatism) has been extensively debated for more than 20 years. Two important ideas in this discussion have been that niche conservatism disappears over deeper timescales (e.g., Peterson, 2011; Peterson et al., 1999) and that different kinds of ecological traits show different patterns of conservatism (e.g., alpha niche traits are more conserved than beta niche traits; Ackerly et al., 2006). Here we addressed these questions across multiple traits over a timescale of hundreds of millions of years. We found that all 10 variables generally showed a strong pattern of phylogenetic signal and conservatism over the 350 million year time span of tetrapod evolution. Thus, we found no evidence that conservatism disappeared over this deep timescale. By contrast, we generally supported greater conservatism in alpha niche traits than beta niche traits (Figure 1). Mean lambda was somewhat higher for alpha niche traits (Table 1), and *D* was significantly lower. Further, mean rates for alpha niche traits were more than three times slower than for beta niche traits (Table 2). In the paragraphs that follow, we discuss the implications of these results, methodological concerns and areas for future research.

These results show that there is a strong imprint of phylogenetic history on many aspects of the ecological niches of land vertebrates. Niche conservatism in these variables may help explain many other ecological patterns such as phylogenetic conservatism in food webs (Cattin et al., 2004), differences in species richness between habitats (Miller & Wiens, 2017; Wiens, 2015) and the latitudinal diversity gradient (Smith et al., 2012). For example, niche conservatism may contribute to differences in richness between habitats (and climatic zones) by limiting transitions among them, which helps maintain the richness gradient over time, especially if the primary cause of the gradient is the difference in colonization time between habitats and regions. Similarly, conservatism may also contribute to trait-based richness patterns (i.e., which states are most common in a clade), patterns that are often determined by the long-term persistence of the ancestral state (Wiens, 2023). Patterns of conservatism in alpha niche traits may also be important for community assembly (Ackerly et al., 2006), as discussed below. Finally, it has been suggested that alpha niche traits may be more important for explaining patterns of diversification among older

clades than beta niche traits (Wiens, 2017), specifically because alpha niche traits are more conserved. Our results offer partial support for this hypothesis.

Our results on climatic niche conservatism might seem to contradict the idea that climatic niche divergence is important for speciation within many tetrapod clades (e.g., Castro-Insua et al., 2018; Cooney et al., 2016; Hernández-Hernández et al., 2021). One possible resolution of this conflict is that the deep-scale patterns of climatic niche conservatism documented here may reflect dramatic, large-scale differences in climatic distributions (e.g., tropical vs. temperate; deserts vs. rainforests), whereas climate-driven speciation may involve more subtle differences in climate within large-scale climatic regions occupied by closely related species (e.g., different elevations in the mesic tropics). This basic idea might also apply to other traits, such as diet or microhabitat.

Our results generally confirm the initial prediction that alpha niche variables are more conserved than beta niche variables (Ackerly et al., 2006). We tested this idea across multiple variables (possibly for the first time) and showed that this dichotomy holds over hundreds of millions of years, not only among closely related species. This prediction was based on the idea that closely related species tend not to co-exist (e.g., Cavender-Bares et al., 2004; Elton, 1946), presumably because they share similar alpha niche traits that would lead to competitive exclusion, whereas divergence in beta niche traits may drive allopatric speciation of closest relatives. Of course, recent divergence in alpha niche traits might facilitate local co-existence of closely related species. Our results are less consistent with this idea, but it is also possible that more subtle differentiation in alpha niche traits contributes to local co-existence. Overall, our results suggest that many of the most important ecological differences among species in communities (in terms of activity patterns, body temperatures, diet and microhabitat) may have originated tens or hundreds of millions of years ago.

We recognize that some readers may have reasonable methodological concerns about our study. First, our sampling of species is not perfectly proportional among clades. We used almost identical taxon sampling of species across datasets to remove potential effects caused by selection of different species in different datasets. We set our sampling of species across traits to the trait with the fewest species (T_b). In this dataset, mammals are somewhat overrepresented and amphibians underrepresented (Table S1). However, this need not strongly impact our conclusions. Simulations show that Pagel's (1999) lambda rarely (if ever) infers signal to be present when it is actually absent (Munkemuller et al., 2012). It is especially unclear why we would falsely infer strong, incorrect signal across 10 variables on two trees. Furthermore, we generally found strong phylogenetic signal within most major clades for most variables (Figure 2). The results within these clades are independent of the sampling among clades. Overall, it seems unlikely that this issue explains our findings.

Nevertheless, our overall sampling was limited, given that there are ~37,000 tetrapod species (Table S1). We addressed the impact of limited taxon sampling by sub-sampling only 10% of the included

species. We found that sub-sampling generally lowered the estimated levels of phylogenetic signal relative to the full dataset, especially for climatic variables. Thus, increasing our sample sizes beyond 1721 species might not strongly impact our conclusions, given that the estimated levels of phylogenetic signal were already high (Figure 1; Table 1). There is also evidence that very limited taxon sampling can lead to incorrectly inferring the absence of phylogenetic signal (Jezkova & Wiens, 2016). This may explain the lambda of 0 inferred for some variables in crocodilians (with 11 sampled species). It would be possible to include more species for some variables, but more difficult for others (especially T_b). We prioritized having largely identical taxon sampling among variables instead. Furthermore, simply estimating phylogenetic signal can become computationally very challenging when thousands of species are included.

We also note that some niche variables may not be fully independent of each other. For example, some climatic variables may be correlated (e.g., annual mean temperature vs. minimum temperature). Similarly, T_b may be influenced by diel activity patterns (Moreira et al., 2021) and T_b may influence diet (Clarke & O'Connor, 2014). In statistical terms, the most important consequence of this non-independence might be to incorrectly consider differences between groups of traits to be significant. Our comparison of alpha and beta niche traits was not significant for lambda but was for D. When we reduced the climatic variables to include only annual mean temperature (Bio1) and precipitation (Bio12), this difference remained significant (Table S3). Using multivariate methods to reduce the number of variables would only decrease the overall sample size of traits, and bias the results against finding significant differences.

Another reasonable concern is that traits might only appear to be conserved because their coding is oversimplified. We coded diel activity, diet and habitat as discrete variables, whereas these could also be considered continuous variables. Yet, we generally found similar lambda values when we recoded continuous variables as discrete (Table S2) and when we subdivided diel activity, diet and habitat into different numbers of states (Table 1, and Tables S17, S18).

We acknowledge that it is possible to obtain different results using different methods or considering different taxonomic scales. For example, analyses of conservatism in climatic niches are often based on species-distribution models (Peterson, 2011). Instead, we used approaches that allowed us to compare conservatism across diverse niche axes. Further, many discrete variables analysed here show strong conservatism based on ancestral reconstructions. For example, many extant species have retained the same states that were inferred for the most recent common ancestor of tetrapods (terrestrial habitat: Miller & Wiens, 2017; nocturnal diel activity: Anderson & Wiens, 2017; carnivorous diet: Román-Palacios et al., 2019).

Very different results might also be obtained at different taxonomic scales. For instance, analysing only closely related species might reveal limited phylogenetic signal. A simple explanation for this pattern might be that closely related species are relatively similar for a given variable, such that similarity does not increase with phylogenetic relatedness among them. This would reflect conservatism but not signal. Interestingly, Losos et al. (2003) found little signal in T_b among 11 sympatric *Anolis* species, whereas T_b shows strong signal across lepidosaurs (lambda=0.948) and across tetrapods (lambda=0.981; Moreira et al., 2021). Thus, these results for *Anolis* may reflect a lack of signal among the set of congeners that were analysed rather than a broader lack of conservatism in T_b.

Some of the traits analysed here are conserved at even deeper phylogenetic scales than across tetrapods. For example, diet shows strong signal across animals (lambda=0.79), a timescale of ~1 billion years (Román-Palacios et al., 2019). Habitat (i.e., marine vs. non-marine) also appears to be strongly conserved at this timescale (Wiens, 2015).

Note that our analyses are addressing phylogenetic conservatism across tetrapods at a timescale spanning ~350 million years (i.e., from 350 million years ago to the present). Our point here is that when we incorporate these very deep timescales, the pattern of signal and conservatism is maintained and does not disappear (despite past predictions). Our point is not that phylogenetic signal was especially strong at exactly 350 million years ago (or a broader, ancient time frame), when there was only one or relatively few tetrapod species present.

A final concern is that we did not consider every possible trait, and different variables might show different patterns from those found here. We focused here on crucial and widely studied components of the beta niche (climatic temperature and precipitation) and alpha niche (diet, habitat, diel activity, body temperature). Other patterns might well be found in other traits (e.g., range size, life-history variables).

Our results raise several areas for future research. First, these patterns should be tested in other groups of organisms, including plants and arthropods. Second, the causes of these patterns of conservatism should also be studied. There are numerous potential causes of niche conservatism (Crisp & Cook, 2012; Wiens et al., 2010). Two of the most important causes may be natural selection against individuals leaving the ancestral niche (for a given niche variable) and competition with other clades that currently occupy that niche (and that have occupied it for tens or hundreds of millions of years, as suggested here). Third, studies are needed that examine the same niche variables in the same group of organisms, but at different temporal scales, to identify if there are certain scales at which phylogenetic signal erodes and if there are generalities in these patterns of signal erosion across clades and variables. For example, our results here suggest that signal decreases at more recent timescales in climatic variables but not alpha niche traits.

5 | CONCLUSIONS

Niche conservatism is an intensively studied topic at the intersection of ecology and evolutionary biology. Two important ideas in this area are that niche conservatism erodes over deeper timescales and that traits related to local-scale ecology (alpha niche) are more

conserved than those related to large-scale distributions (beta niche). Our results for land vertebrates contradict the first but generally support the second. We show strong phylogenetic signal in 10 diverse ecological traits across a clade that is ~350 million years old. We also test whether alpha and beta niche variables differ in their phylogenetic conservatism at this scale (possibly for the first time) and support the prediction that there is generally lower signal and faster rates in beta niche variables.

CONFLICT OF INTEREST STATEMENT
We have no competing interests to declare.

DATA AVAILABILITY STATEMENT
All data are currently available as Datasets S1–S17, and on Dryad (https://doi.org/10.5061/dryad.q573n5tpf).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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