

## RESEARCH ARTICLE

# Diet Evolution and Body Temperature in Tetrapods: Cool Old Carnivores and Hot Young Herbivores

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## ABSTRACT

**Aim:** Diet is a key aspect of life in animals. There have been numerous independent origins of herbivorous diet across animals, but the factors that explain these origins remain poorly understood. One potentially crucial factor is body temperature ( $T_b$ ), as the gut-dwelling bacteria that help digest cellulose in many herbivores are thought to require high temperatures. However, analyses in birds, lizards and mammals found only limited evidence for higher  $T_b$  in herbivores than in carnivores. These analyses tested whether diet explains  $T_b$  evolution. Here, we focus instead on testing whether  $T_b$  helps explain the evolution of diet across tetrapods.

**Location:** Global.

**Time Period:** Past 350 million years.

**Major Taxa Studied:** Tetrapods.

**Methods:** We analysed 1712 species with matched data on diet and  $T_b$  using diverse phylogenetic methods.

**Results:** Ancestral reconstructions indicated that tetrapods likely had a carnivorous ancestor, followed by repeated transitions to omnivory and herbivory, especially in the last 110 million years. Thus, extant herbivorous lineages in tetrapods are relatively young, in contrast to many older carnivorous lineages. They are also relatively unstable in that reversals from herbivory back to omnivory and from omnivory back to carnivory were as frequent as the origins of herbivory and omnivory. Using phylogenetic logistic regression, we support the hypothesis that higher  $T_b$  helps explain the evolution of herbivory across tetrapods and within birds, mammals, lepidosaurs and turtles. Phylogenetic path analyses suggest that  $T_b$  generally drives the evolution of herbivory, and not vice versa. Our analyses also suggest that  $T_b$  is more important for the evolution of herbivory than large body size or diurnal diel activity, which are both significant predictors of herbivory in some cases.

**Main Conclusions:** Our results show for the first time that  $T_b$  is a significant predictor of diet evolution among and within many major animal clades.

## 1 | Introduction

What an animal species eats is a crucial aspect of its biology, with many possible implications for its ecology, evolution, anatomy, physiology, behaviour and conservation (Schwenk 2000; Pough, Janis, and Heiser 2009; Hickman et al. 2012; Karasov and Martínez

del Rio 2020). Yet, large-scale patterns of evolution in animal diet remain poorly understood. Recent analyses suggest that the common ancestor of living animals was carnivorous (feeding on heterotrophs), and that herbivory (feeding on autotrophs) evolved repeatedly across animal phylogeny (Román-Palacios, Scholl, and Wiens 2019). This pattern raises the question: what explains these

evolutionary changes in diet? More specifically, why has herbivory evolved in certain lineages and not others?

Here, we address these questions in land vertebrates (tetrapods). Herbivory has evolved several times across major tetrapod clades, including in birds (Olsen 2015; Burin et al. 2016), mammals (Price et al. 2012) and squamates (Cooper and Vitt 2002; Espinoza, Wiens, and Tracy 2004; Lafuma et al. 2021). Body temperature ( $T_b$ ) has been suggested as a potentially important variable that may help explain the evolution of herbivory. Herbivory is thought to require symbiotic gut microbes that can enzymatically digest the cellulose in plant cell walls, as many animals lack the ability to digest cellulose themselves (McBee 1971; Sues and Reisz 1998; Ley et al. 2008). It is hypothesised that these gut microbes function more effectively at higher internal  $T_b$ , which could make high  $T_b$  necessary for the evolution of herbivory (e.g., Zimmerman and Tracy 1989; Mountfort, Campbell, and Clements 2002; Espinoza, Wiens, and Tracy 2004; Rimmer and Weibe 2006). Many potential factors might influence the origin of herbivory each time it evolves. However,  $T_b$  could be a particularly widespread factor that potentially spans the diverse ecologies, physiologies and morphologies of herbivorous animals. Other factors may be far more specific to particular groups (e.g., body size and physiology in herbivorous mammals will be very different from those in herbivorous insects).

Previous research has shown mixed support for an association between  $T_b$  and diet in mammals and birds (Clarke and O'Connor 2014). In that study, carnivorous mammals and birds had lower  $T_b$  than both herbivorous and omnivorous species. However, the pattern in birds was not significant after phylogenetic correction. Clarke and O'Connor (2014) also found that folivorous mammals and birds (defined as consuming primarily grass and leaves) had higher  $T_b$  than those that consumed fruit, flowers and nectar. Breakdown of plant cell walls could be especially important for folivorous species. This was a groundbreaking study, but the scope was limited to endotherms and the support for an association between herbivory and  $T_b$  was variable (i.e., supported in mammals, but not consistently in birds). Furthermore, that study used phylogenetic generalised least-squares regression (PGLS; Martins and Hansen 1997) to test the influence of diet (and body size) on  $T_b$ . This test addresses whether diet explains  $T_b$  evolution, and not the other way around. Therefore, they did not directly address whether  $T_b$  helps explain the evolution of herbivory, the question of interest here.

A relationship between  $T_b$  and herbivory has also been discussed in squamate reptiles (lizards and snakes). Herbivorous lizards are thought to have higher  $T_b$  than carnivorous lizards (Espinoza 2002; Espinoza, Wiens, and Tracy 2004). In an extensive analysis of >800 lizard species, Meiri et al. (2013) found that the mean body temperatures of herbivorous lizards were higher than those of carnivorous and omnivorous species, but the differences were not significant. Again, these analyses addressed whether diet potentially explains  $T_b$  evolution (using PGLS regression), but not whether  $T_b$  helps explain the evolution of herbivory.

Here, we test the hypothesis that higher  $T_b$  helps explain the evolution of increasingly herbivorous diets across all tetrapods (amphibians, mammals, lepidosaurs, turtles, crocodylians and birds). We assemble matched data on diet (Figure 1) and  $T_b$  (Figure 2) for 1712 tetrapod species, with all species represented

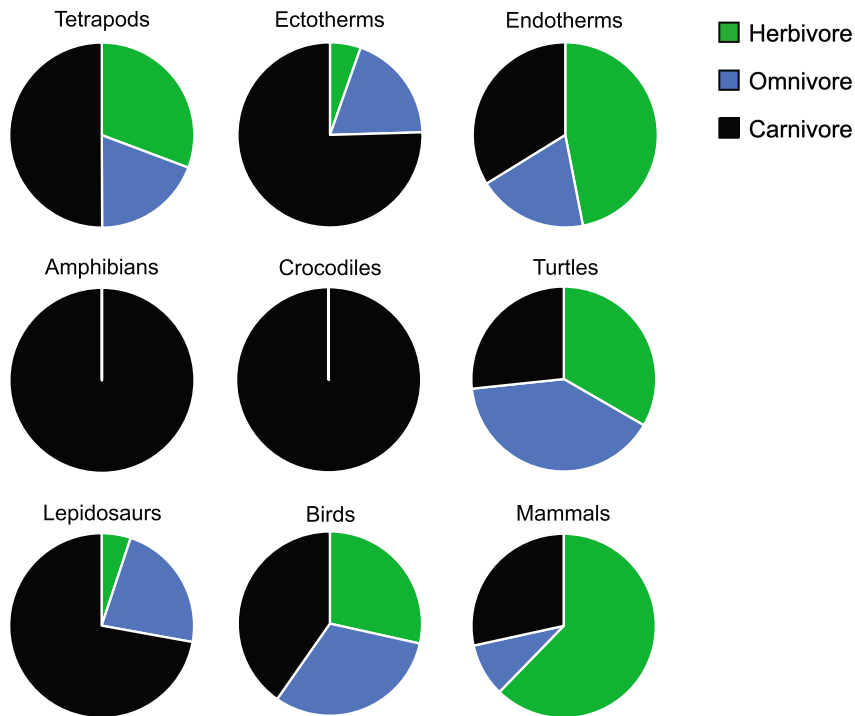
in large-scale, time-calibrated phylogenies (Figure 3). We then perform several analyses to analyse diet evolution and its relationship to  $T_b$  (Table 1). We primarily test the hypothesis that  $T_b$  helps explain diet evolution, using phylogenetic logistic regression (Ives and Garland 2010). This approach models the evolution of a categorical dependent variable (i.e., diet) that is potentially influenced by a continuous independent variable (i.e.,  $T_b$ ). We also perform matched analyses using phylogenetic ANOVA (implemented with the residual randomisation in permutation procedure [RRPP]; Adams and Collyer 2018). We used this approach to evaluate whether diet (independent variable) instead helps explain the evolution of  $T_b$  (dependent variable). This analysis is similar to the PGLS analyses of previous studies (e.g., Clarke and O'Connor 2014; Meiri et al. 2013) but is designed to test the effect of a categorical independent variable on a continuous dependent variable, and allowed us to evaluate whether our data support their conclusions. We also test whether herbivory is associated with diurnal activity (given that diurnal activity is related to higher  $T_b$ ; Moreira, Qu, and Wiens 2021) and with larger body size (e.g., as suggested in lizards; Pough 1973), and whether those associations (if present) are stronger than those between herbivory and  $T_b$ . We also use phylogenetic path analyses (von Hardenberg and Gonzalez-Voyer 2013) to help sort among these variables and their potential effects. Lastly, we use ancestral-state reconstructions to analyse large-scale patterns in diet evolution in tetrapods. Importantly, these latter analyses suggest that a major pattern in diet evolution within tetrapods is a tendency towards increasing herbivory, starting from carnivorous ancestors (Figure 3). To the best of our knowledge, our study represents the taxonomically broadest phylogenetic analysis of the predictors of diet evolution.

## 2 | Materials and Methods

### 2.1 | Data Assembly

We started from a dataset of 1721 tetrapod species previously assembled by Moreira, Qu, and Wiens (2021), who compiled published information on body temperatures ( $T_b$ ), diel activity and phylogeny for each species. As discussed by Moreira, Qu, and Wiens (2021), the species sampling within each major clade (Table 2) was broadly proportional to the clade's overall extant species richness (i.e., many amphibians, birds, mammals and lepidosaurs, but few crocodylians and turtles). However, relative to strictly proportional sampling, mammals were somewhat overrepresented and amphibians underrepresented. This reflected the relative abundance and scarcity of available  $T_b$  data in these two groups. These sampling biases should not be problematic, since we also performed separate analyses for each group for most tests (e.g., the number of mammals should not impact results within lepidosaurs). Our sampling of species was incomplete within all major groups, relative to their overall species richness. Nevertheless, we sampled most major clades in each group (except the rare, species-poor caecilians). We address taxon sampling further in the final section of the Methods.

Body temperature ( $T_b$ ) data for each species were generally averages from multiple sampled individuals and were taken from summaries in Qu and Wiens (2020) and Moreira, Qu, and Wiens (2021). Data for ectotherms were generally from active



**FIGURE 1** | Pie chart showing the proportion of species of each diet type among the sampled species of the major groups of tetrapods. Raw numbers are given in Table 2.

(thermoregulating) animals in the field. Data for endotherms were from both the lab and field, from individuals that were awake but not actively exercising (since exercise generally increases  $T_b$  in endotherms). Moreira, Qu, and Wiens (2021) found no significant differences between data from the lab and field for ectotherms or endotherms.

We then assembled a dataset on diet for these same 1721 species (Dataset S1). Note that all supplementary tables and appendices are available in the Supporting Information document, whereas supplementary figures and datasets (and the Supporting Information) are accessible on figshare (<https://figshare.com/s/944b7700d69e65750ca5>). We used the following classification (from Meiri 2018) to assign a diet to each species: carnivorous: >90% animal matter in diet; omnivorous: 10%–50% plant matter; herbivorous: >50% plant matter. We applied this criterion to all types of quantitative data on diet, depending on which data were available in the original study (e.g., volume, mass, frequency), following Meiri (2018). A summary of diets across species among major groups is shown in Figure 1. A summary of  $T_b$  across diets and diel activities is given in Tables S1–S3. We give the details of how the diet data were obtained from the literature in Appendix S1 (following Saban, Qu, and Wiens 2023). Major sources for diet information included Pough et al. (2016) for amphibians, crocodylians and snakes, Meiri (2018) for lizards, and Wilman et al. (2014) for birds and mammals. There were nine species that lacked adequate diet data (eight lizards and one mammal; Appendix S1), and so diet analyses across tetrapods included only 1712 species.

We recognise that these three diet states do not reflect all of the extensive variation in diets within and among species. Nevertheless, these three states should be the most relevant to

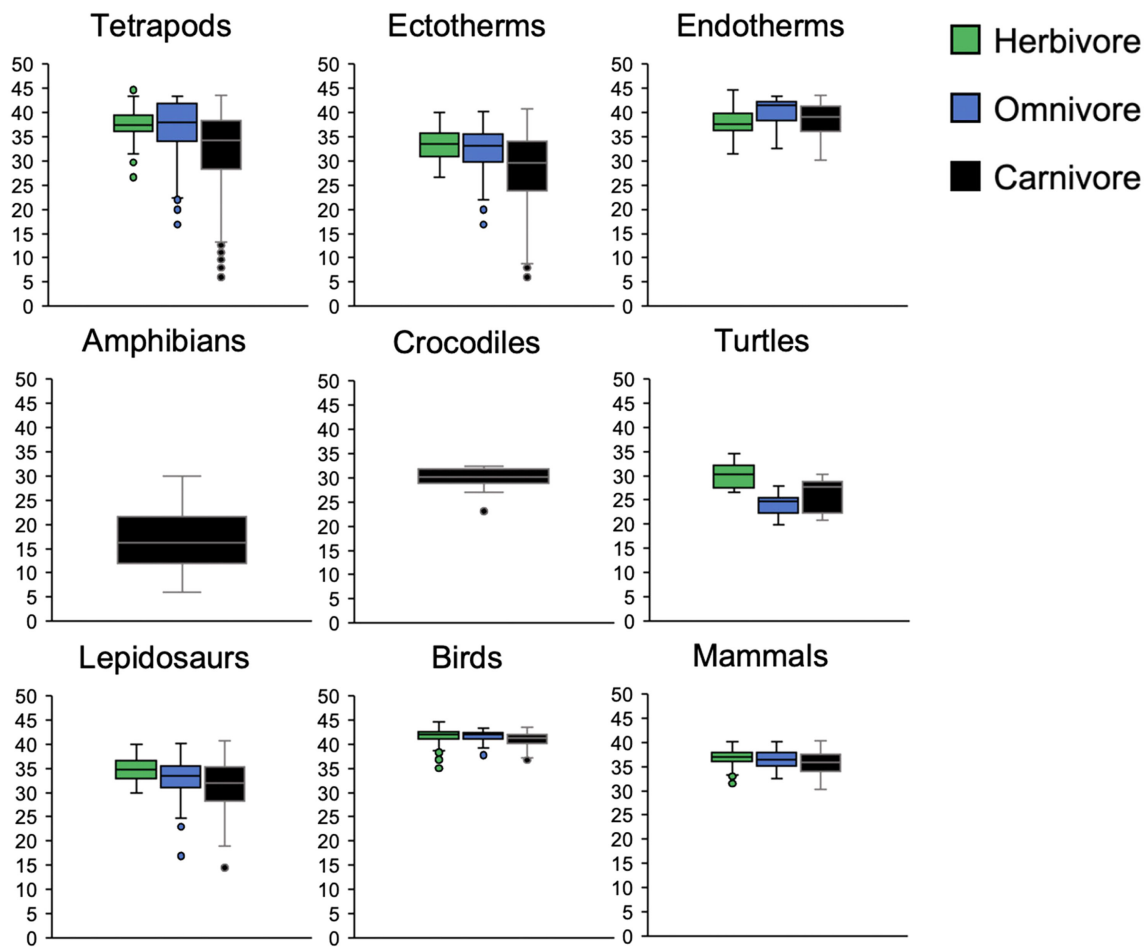
our main hypothesis (i.e., the evolution of herbivory from non-herbivorous states). Their usage is also widespread in large-scale ecological and evolutionary studies (e.g., Price et al. 2012; Román-Palacios, Scholl, and Wiens 2019).

We also tested whether the evolution of herbivorous diets is related to diurnal diel activity (and if diel activity is more important than  $T_b$ ). Most diel-activity data were from the compilation in Anderson and Wiens (2017). These authors defined four diel-activity states: arrhythmic (ARR), crepuscular (CRE), diurnal (DIU) and nocturnal (NOC). However, most sampled tetrapod species were either diurnal or nocturnal (87%; Table S2). 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 were defined as primarily active at dusk or twilight.

We also tested for relationships between diet and body size (i.e., adult body mass), as previously hypothesised (see Introduction). Full details of the methods and results for body size are reported in Appendix S2. Estimates of body mass were obtained for all 1712 species with diet data and are presented in Dataset S2.

## 2.2 | Phylogenies Used

We performed all analyses on two time-calibrated phylogenies, but the results presented in the main text are based on the primary tree (Dataset S3) and not the alternative tree (Dataset S4). The details of these phylogenies are given in Appendix S3. In short, the primary phylogeny is based on trees estimated in



**FIGURE 2** | Box plots depicting the distribution of body temperatures (in °C) associated with each diet in each group in this study. The coloured boxes depict the data between the 25th and 75th quantiles with the median represented by the middle line. The upper and lower horizontal lines represent the 95th and 5th quantiles. Dots represent outliers. Means are given in Table S1 and raw data are in Dataset S1.

separate analyses within each major group of tetrapods (amphibians, birds, lepidosaurs, mammals, crocodylians and turtles) and then compiled into a supertree. The alternative tree used a different phylogeny within each of the four largest clades (amphibians, birds, lepidosaurs and mammals), each based on a separate phylogenetic analysis within that group. Note that the secondary tree included 1700 species with matched data. We used these two trees rather than a distribution of trees because: (a) such a distribution of trees (spanning all sampled tetrapod species) is not available, and (b) the trees from separate phylogenetic analyses are potentially more different from each other than those from a distribution of trees from one phylogenetic analysis. Thus, these two trees may better capture the sensitivity (or robustness) of the results to variation in the topology than a summary of results from a distribution of trees from a single phylogeny-estimation study.

### 2.3 | Data Analysis

The major analyses performed here are summarised in Table 1. We primarily tested the hypothesis that higher body temperatures ( $T_b$ ) promote the evolution of herbivorous diet using phylogenetic logistic regression (Ives and Garland 2010). Diet represented the discrete dependent variable, assuming that

$T_b$  (continuous independent variable) potentially determines which diet can evolve in a given species. Phylogenetic logistic regression was run using the R package *phylolm* (Ho and Ané 2014) in R version 4.0.5. The ‘*phylolm*’ function and ‘*logistic\_MPLE*’ method were used. Phylogenetic logistic regression generally allows only two states per discrete variable. Therefore, we performed alternative sets of analyses in which we re-assigned omnivorous species to either carnivory (called maximum carnivory coding) or herbivory (maximum herbivory coding). Carnivory was coded as 1, and herbivory and folivory were coded as 0 (Dataset S1). Under maximum carnivory, omnivory was also coded as 1. Under maximum herbivory, omnivory was coded as 0 instead. Thus, a negative relationship between diet and  $T_b$  would indicate that herbivory was associated with higher  $T_b$ . We also performed analyses in which only folivores were considered herbivorous (details in Appendix S1). We do not show plots of logistic regression results since these plots themselves do not necessarily depict the evolutionary patterns of interest here. R code used in these and all other analyses are given in Dataset S5.

Analyses were performed across all tetrapods, and within each major clade, including birds, mammals, lepidosaurs and turtles. We did not analyse crocodylians or amphibians separately, since they are almost exclusively carnivorous as adults. We also

performed analyses of all ectotherms combined and all endotherms combined, given the possibility that physiological differences between these groups influence the relationships between  $T_b$  and diet (although neither group is monophyletic). For each table of tests, we applied a table-wide sequential Bonferroni

correction (Holm 1979) and flagged  $p < 0.05$  that were not significant after correction.

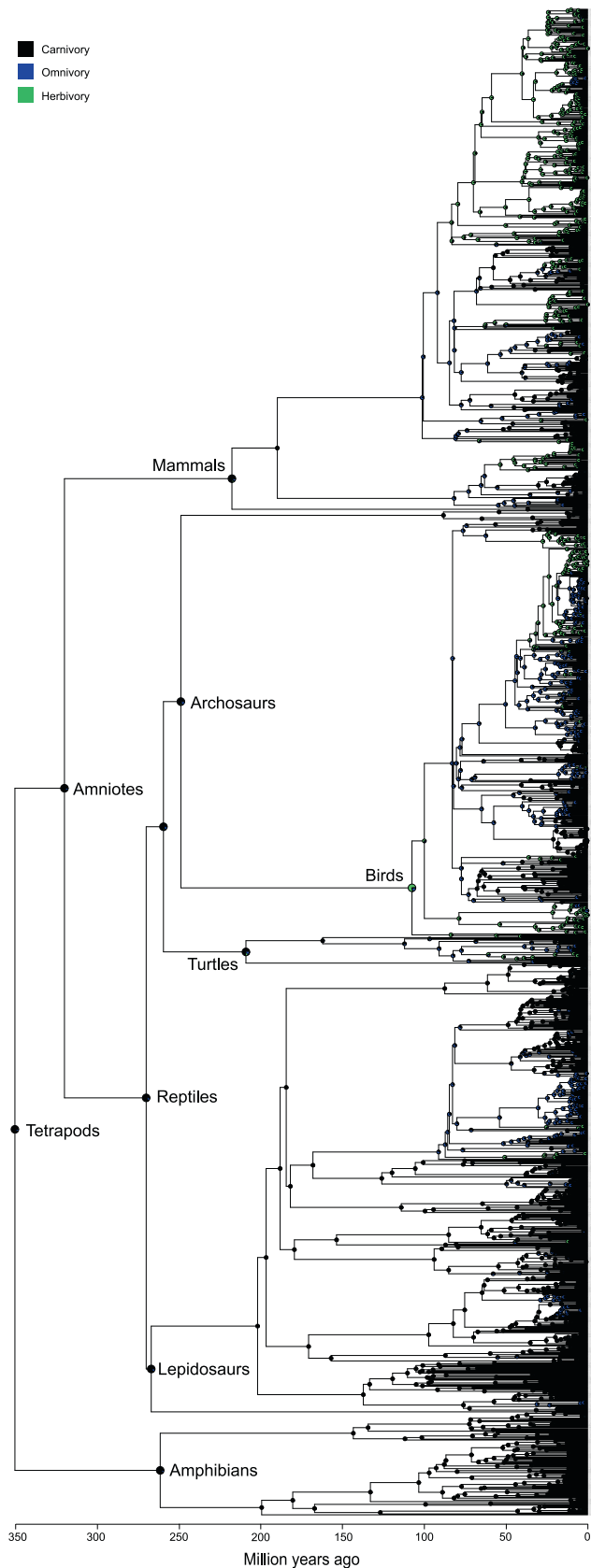
Instead of assuming that  $T_b$  potentially drives diet, as in the logistic regression, we also tested whether  $T_b$  (dependent variable) was instead influenced by diet (independent variable). A phylogenetic analysis of variance (phylogenetic ANOVA; Garland et al. 1993) was run using the RRPP approach (Adams and Collyer 2018) implemented in the R package *RRPP* (Collyer and Adams 2018). Species diets were coded as carnivorous (C), omnivorous (O) or herbivorous (H). For each group, we performed an overall analysis using 1000 simulation replicates to assess whether diet significantly influenced  $T_b$ . We then examined  $p$  values from post hoc tests to look for significant differences in  $T_b$  between each pair of diet states (i.e., C vs. H, C vs. O, O vs. H).

We then tested two other potential correlates of diet evolution (diel activity, body size) besides  $T_b$ . We tested each of these variables separately for relationships to diet and then together (in multiple regression and path analyses). This set of analyses was essential to identify whether  $T_b$  was an important predictor of diet evolution relative to other variables, and whether apparent correlations between diet and  $T_b$  merely reflected another variable instead.

We first tested diel activity, with diet as the dependent variable (i.e., assuming that diel activity influences diet evolution). Phylogenetic logistic regression was run using the ‘*phylglm*’ function and ‘*logistic\_MPLE*’ method. Since phylogenetic logistic regression allows only two states for discrete variables, we recoded intermediate states for diel activity (crepuscular, arrhythmic) as either nocturnal (maximum nocturnal) or diurnal (maximum diurnal). Nocturnality was assigned a state of 1 and diurnality 0.

Another potential correlate of diet evolution is body mass. We assembled a dataset on body mass (details in Appendix S2). Then we used phylogenetic logistic regression (see above), with diet as the categorical, dependent variable and body mass as the continuous, independent variable. Initial analyses showed no significant relationships between diet and raw body mass but some relationships were found after  $\log_{10}$  transforming body mass (across tetrapods, in ectotherms and in lepidosaurs). We used  $\log_{10}$ -transformed body mass to better approximate a normal distribution, and given that body mass varies over many orders of magnitude (details in Appendix S2).

We then tested for potential associations between diet and these three predictor variables ( $T_b$ , diel activity, body mass) across



**FIGURE 3** | Ancestral reconstructions of diet on a time-calibrated phylogeny of tetrapods. Colours within each pie diagram represent the proportional likelihoods of each of the three diet states at each node. The scale at the bottom is in millions of years ago. This figure illustrates that the earliest nodes are inferred to be carnivorous (expanded pie charts), and that herbivory evolved among extant lineages only within the last ~110 Myr. The results shown are based on the primary tree and the all-rates different model for observed states. Results from alternative trees and models are described in Appendix S5 (and Figures S2–S4; Tables S54–S60).

**TABLE 1** | Summary of the main questions and analyses used in this study.

| Question  | Dependent variable | Independent variable            | Method  |
|---|--------------------|---------------------------------|---|
| Does higher $T_b$ drive the evolution of herbivory?                         | Diet               | $T_b$                           | Phylogenetic logistic regression                        |
| Are origins of herbivory associated with increases in $T_b$ ?               | NA                 | NA                              | Ancestral reconstructions                               |
| Does herbivory drive the evolution of $T_b$ ?                               | $T_b$              | diet                            | Phylogenetic ANOVA                                      |
| Do diel activity, body size and/or $T_b$ drive the evolution of herbivory?  | Diet               | Diel activity, body size, $T_b$ | Multiple phylogenetic logistic regression               |
| What are the relationships among diet, $T_b$ , diel activity and body size? | Depends on model   | Depends on model                | Phylogenetic path analysis                              |
| When did herbivory evolve among living tetrapods?                           | NA                 | NA                              | Ancestral-state reconstructions on time-calibrated tree |
| What are the rates of change between herbivory, omnivory and carnivory?     | NA                 | NA                              | Maximum-likelihood rate estimation                      |

tetrapods, ectotherms and lepidosaurs using multiple phylogenetic logistic regression. We also tested whether there was a relationship between body mass and  $T_b$  using PGLS regression (Martins and Hansen 1997). PGLS was conducted using the R package *caper* version 1.0.1 (Orme et al. 2013). We assumed that  $T_b$  was the dependent variable and that body mass was independent.

We performed phylogenetic path analysis to test potential cause-and-effect relationships among these variables (von Hardenberg and Gonzalez-Voyer 2013). We implemented phylogenetic path analysis in the R package *phylopath* version 1.1.3 (van der Bijl 2018). We compared a total of nine models to address the potential relationships among diet,  $T_b$ , body size and diel activity. Full details of the methods and results of these analyses are provided in Appendix S4.

We also carried out a limited series of maximum-likelihood ancestral-state reconstructions, primarily to visualise the overall patterns of diet evolution. We provide the full details of the methods and results of these analyses in Appendix S5. In short, we performed initial analyses that compared different models for transition rates among the three diet states (C, O and H), including equal rates (a single rate for all transitions among states), symmetrical rates for transitions among states (three rates total) and an all-rates-different model (a different rate for each possible transition type between each pair of states, with six rates in total). We then explored hidden-rate models (Beaulieu, O'Meara, and Donoghue 2013) using the R package *corHMM* (Beaulieu and O'Meara 2016). These models account for possible hidden rate categories within each observed state, rather than assuming that transition rates are constant throughout the tree. However, some transition rates

from these latter analyses seemed problematic, possibly because of the problem of rare states (see Appendix S5; Schluter et al. 1997). For brevity, we focus mainly on the analyses of the observed states in the main text, but the hidden-state models yielded similar reconstructions overall. We acknowledge that a more complete analysis of diet evolution could include many more species (beyond those with  $T_b$  data analysed here). Such an analysis could also incorporate the potential impact of diversification rates on reconstructions of diet evolution (Maddison, Midford, and Otto 2007). Our goal here was to visualise the major patterns of diet evolution among the sampled species, to address whether repeated origins of herbivory was a widespread pattern across tetrapods (as in animals in general; Román-Palacios, Scholl, and Wiens 2019). This is relevant to whether the impact of  $T_b$  on the origins of herbivory is important for diet evolution in tetrapods overall. Nevertheless, we present these results last because they are somewhat tangential to our main question.

Finally, we utilised these ancestral reconstructions to undertake a limited set of confirmatory analyses that addressed whether the repeated origins of herbivory were associated with repeated increases in  $T_b$ . We describe these analyses and their full results in Appendix S6 (data in Datasets S6 and S7; Figure S4).

## 2.4 | Taxon Sampling

We acknowledge that our taxon sampling spanned only a limited number of tetrapod species, especially relative to the overall number of tetrapod species (~37,000; Moreira, Qu, and Wiens 2021). However, recent analyses suggest that our results should be robust to incomplete sampling (Moreira, Qu, and

Wiens 2021; Emberts and Wiens 2022). Those studies examined the impact of sampling only 10% of the sampled species on their analyses, using tetrapod phylogenies almost identical to those used here. They found that limited taxon sampling generally had little impact on their statistical analyses and ancestral reconstructions. However, some statistical results (phylogenetic ANOVA and logistic regression) that were significant with full sampling were non-significant under reduced sampling. There were no cases in which subsampling led to significant results that conflicted with those based on full sampling. These results were consistent with simulations (Ackerly 2000), which suggest that limited taxon sampling can reduce statistical power but rarely leads to inferring false positives.

### 3 | Results

#### 3.1 | Does $T_b$ Help Explain Diet Evolution?

Our species-level sampling among all groups and diet categories is summarised in Table 2. The frequencies of different diets among the sampled species within each group are summarised in Figure 1. The distribution of  $T_b$  among sampled species with each diet in each group is summarised in Figure 2. Major patterns of diet evolution are summarised in Figure 3, and are described in the final section of the Results.

Our main question in this study was whether origins of herbivory were related to high  $T_b$ . Across tetrapods, phylogenetic logistic regression analyses revealed that the evolution of herbivory was associated with higher  $T_b$  (Table 3). Using both coding schemes (maximum carnivory and maximum herbivory), there was a significant negative relationship between diet and  $T_b$  (maximum carnivory:  $p < 0.001$ , coefficient estimate [CE] =  $-0.108$ ; maximum herbivory:  $p < 0.001$ , CE =  $-0.123$ ). We also confirmed that origins of herbivory were significantly associated with increases in  $T_b$  using ancestral reconstructions (Appendix S6). The significant negative relationship was found across all ectotherms (Table 3) and in the four major groups that vary most extensively in diet (Table 4), including birds, mammals, lepidosaurs and turtles (but the relationship in turtles was non-significant under maximum-herbivory coding). Surprisingly, endotherms showed a significant

positive relationship under maximum carnivory coding (Table 3), indicating that carnivores were associated with higher  $T_b$  than herbivores and omnivores. Using maximum herbivory coding in endotherms, the relationship was negative but not significant.

We expected the strongest relationship between  $T_b$  and herbivory to involve folivory. Surprisingly, there was no significant relationship between diet and  $T_b$  when folivory was equated with herbivory in the single analysis across all tetrapods (Table S4). However, using this coding (Table S4), folivory was associated with higher  $T_b$  in ectotherms ( $p = 0.028$ , CE =  $-0.151$ ) but with lower  $T_b$  in endotherms ( $p = 0.019$ , CE =  $0.201$ ). Folivory was associated (Table S5) with higher  $T_b$  in lepidosaurs ( $p = 0.024$ , CE =  $-0.202$ ) and turtles ( $p = 0.012$ , CE =  $-0.788$ ), but these results were not significant after correction for multiple tests. There were no significant associations found for folivory in birds (Table S5). In mammals, there was a significant association between folivory and higher  $T_b$  ( $p < 0.001$ , CE =  $-0.253$ ) under the 50% threshold for folivory, but not the 100% threshold (Table S5). Results were similar using an alternative tree (Tables S6–S9).

#### 3.2 | Does Diet Help Explain the Evolution of $T_b$ ?

We also tested the question addressed in earlier studies: does diet help explain  $T_b$  evolution? Based on the phylogenetic ANOVA (using RRPP) across tetrapods (Table S10),  $T_b$  varied significantly among diets ( $p = 0.001$ ), with significantly higher  $T_b$  in herbivores than in carnivores (Table S11). The mean  $T_b$  across all carnivores was  $32.3^\circ\text{C}$ , whereas the mean across all herbivores was  $37.8^\circ\text{C}$  (Table S1; Figure 2). Different diets were also significantly associated with different  $T_b$  within most groups, including ectotherms, endotherms, turtles, birds and mammals (but not lepidosaurs; see Tables S11–S17 for pairwise comparisons among diets within groups). Results were similar using an alternative tree, except that differences were significant in lepidosaurs (Tables S18–S24).

#### 3.3 | Diet, Diel Activity, Body Mass and $T_b$

We also tested whether other variables besides  $T_b$  predicted the evolution of herbivory (including diel activity and body mass),

**TABLE 2** | Summary of the number of sampled species with each diet in each clade.

|              | <b>Total</b> | <b>Herbivore</b> | <b>Omnivore</b> | <b>Carnivore</b> |
|--------------|--------------|------------------|-----------------|------------------|
| Tetrapods    | 1712         | 526 (31%)        | 329 (19%)       | 857 (50%)        |
| Amphibians   | 117          | —                | —               | 117 (100%)       |
| Lepidosaurs  | 510          | 26 (5%)          | 116 (23%)       | 368 (72%)        |
| Crocodylians | 11           | —                | —               | 11 (100%)        |
| Turtles      | 30           | 10 (33%)         | 12 (40%)        | 8 (27%)          |
| Ectotherms   | 668          | 36 (5%)          | 128 (19%)       | 504 (75%)        |
| Birds        | 474          | 135 (28%)        | 148 (31%)       | 191 (40%)        |
| Mammals      | 570          | 355 (62%)        | 53 (9%)         | 162 (28%)        |
| Endotherms   | 1044         | 490 (47%)        | 201 (19%)       | 353 (34%)        |

*Note:* The percentage of the sampled species with each diet state is given in parentheses. Note that the species were only included if they also had data available on their body temperatures, and if they were also included in one or both of the time-calibrated phylogenies used.

**TABLE 3** | Results of phylogenetic logistic regression between diet and body temperature across major groups, using the primary phylogeny.

|            | Maximum carnivory | Maximum herbivory |
|------------|-------------------|-------------------|
| Tetrapods  |                   |                   |
| <i>p</i>   | <b>&lt;0.001</b>  | <b>&lt;0.001</b>  |
| CE         | -0.108 (±0.024)   | -0.123 (±0.018)   |
| CI         | -0.115 to -0.103  | -0.132 to -0.118  |
| Ectotherms |                   |                   |
| <i>p</i>   | <b>0.014</b>      | <b>&lt;0.001</b>  |
| CE         | -0.144 (±0.058)   | -0.140 (±0.019)   |
| CI         | -0.160 to -0.131  | -0.149 to -0.130  |
| Endotherms |                   |                   |
| <i>p</i>   | <b>&lt;0.001</b>  | 0.246             |
| CE         | 0.134 (±0.038)    | -0.040 (±0.034)   |
| CI         | 0.121-0.145       | -0.052 to -0.012  |

Note: Maximum carnivory indicates that omnivores were coded the same as carnivores (state 1). Maximum herbivory indicates that omnivores were coded the same as herbivores (state 0). Significant results are boldfaced ( $p < 0.05$ ). All results are significant after a sequential Bonferroni correction. Abbreviations: CE = coefficient estimate (± standard error), CI = bootstrap 95% confidence interval (lower to upper).

and whether the relationship between  $T_b$  and diet remained significant when these other variables were included in the analysis. Phylogenetic logistic regression analyses between diet and diel activity yielded significant results, but only in some cases. Across all tetrapods, there were significant associations between herbivory and diurnality when omnivorous species were coded as herbivores (Table S25). This pattern also occurred in ectotherms, but not endotherms (Table S25). There were also significant associations between herbivory and diurnality in lepidosaurs (under most coding schemes; Table S26) and in birds (when treating omnivores as herbivores and crepuscular and arrhythmic species as diurnal; Table S26). There were no significant associations between folivory and diel activity (Tables S27 and S28). Similar results were obtained using an alternative tree (Tables S29–S32). For groups that showed significant relationships between diel activity and diet (tetrapods, ectotherms, lepidosaurs), we also conducted multiple regression analyses that included diel activity and  $T_b$  (Tables S33–S38). These analyses consistently supported the importance of  $T_b$  when it was included in the model, and models with  $T_b$  had better fit than those with diel activity alone (based on the AIC).

Phylogenetic logistic regression between body mass and diet yielded significant relationships, but only in some groups and under some codings for diet (Appendix S2; Tables S39–S42). Specifically, there were significant relationships in tetrapods under maximum herbivory coding, in ectotherms under maximum carnivory coding and in lepidosaurs under both codings. These relationships indicated that herbivory was associated with larger body sizes, as expected.

**TABLE 4** | Results of phylogenetic logistic regression between diet and body temperature within four major tetrapod clades, using the primary phylogeny.

|             | Maximum carnivory | Maximum herbivory |
|-------------|-------------------|-------------------|
| Lepidosaurs |                   |                   |
| <i>p</i>    | <b>0.012</b>      | <b>&lt;0.001</b>  |
| CE          | -0.196 (±0.078)   | -0.136 (±0.024)   |
| CI          | -0.216 to -0.183  | -0.147 to -0.126  |
| Turtles     |                   |                   |
| <i>p</i>    | <b>0.007</b>      | 0.664             |
| CE          | -0.766 (±0.285)   | -0.050 (±0.114)   |
| CI          | -0.803 to -0.726  | -0.151 to 0.056   |
| Birds       |                   |                   |
| <i>p</i>    | <b>0.005</b>      | <b>&lt;0.001</b>  |
| CE          | -0.208 (±0.073)   | -0.406 (±0.090)   |
| CI          | -0.221 to -0.201  | -0.415 to -0.396  |
| Mammals     |                   |                   |
| <i>p</i>    | <b>&lt;0.001</b>  | <b>&lt;0.001</b>  |
| CE          | -0.273 (±0.047)   | -0.307 (±0.059)   |
| CI          | -0.284 to -0.262  | -0.317 to -0.295  |

Note: Significant results are boldfaced ( $p < 0.05$ ). All results are significant after a sequential Bonferroni correction. Abbreviations: CE = coefficient estimate (± standard error), CI = bootstrap 95% confidence interval (lower to upper).

We also performed single and multiple regression analyses with  $T_b$ , diel activity and body mass as predictors of diet for tetrapods, ectotherms and lepidosaurs. These are three groups in which diel activity and body mass were significantly related to diet (at least in some analyses; see above). The details of these analyses are given in Tables S43–S48 and summarised in Appendix S2. Importantly, in multiple logistic regression models that included both  $T_b$  and body mass, the effect of  $T_b$  on diet was almost always significant whereas the effect of body mass was often not (and there were no cases when mass was significant and  $T_b$  was not). Furthermore, there were no significant associations between body mass and  $T_b$  across tetrapods, ectotherms and lepidosaurs (Tables S49 and S50). In summary, the effects of diel activity and body mass on the evolution of diet depended on the group, the coding of diet and whether  $T_b$  was also included in the model.  $T_b$  was the most consistent predictor of diet evolution in tetrapods.

Finally, we performed phylogenetic path analysis (Appendix S4) to further address which predictor variables ( $T_b$ , diel activity, body mass) were related to diet and whether diet depends on  $T_b$  or whether  $T_b$  depends more strongly on diet. We performed an extensive series of analyses to incorporate different binary codings of diet and diel activity, different transformations of size and  $T_b$ , different trees and different groups (Dataset S8). The results often differed among these analyses, and we briefly summarise the results here (see also Tables S51 and S52). Across



tetrapods, the models most frequently supported as best fitting were those in which the evolution of diet depended on both  $T_b$  and body size (Model 6) or on  $T_b$ , body size and diel activity (Model 7). Using maximum-carnivory coding of diet, Models 6 and 7 tended to be the only ones with strong support (best fit or within 2 CICc units of the best-fit model). However, there was a minority of cases in which other models were supported as best (such as Models 2, 5 and 9), and many cases in which additional models had similar support (within 2 CICc units of the best-fit models). In the majority of analyses across tetrapods, a model in which  $T_b$  depended on diet was not among the best-fit models. Models 6 and 7 were also the most frequently supported as the best-fitting among ectotherms, endotherms, birds and mammals. In turtles, the model most frequently found to be best fitting was one in which diet depended only on  $T_b$  (Model 1). In lepidosaurs, no single model was the most frequently supported as best-fitting. In summary, the phylogenetic path analyses generally confirmed the other results in showing that  $T_b$  has a significant influence on diet evolution.

### 3.4 | Major Patterns of Diet Evolution

We used ancestral reconstructions to infer the overall patterns of diet evolution, especially the timescale over which herbivory evolved and the rates of change between herbivory and other diet states. The results of the model-selection analyses for the primary tree are given in Tables S53–S55. The reconstructions using the best-fitting model (all-rates different) for the observed states on the primary tree are shown in Figure 3. These reconstructions suggest that the most recent common ancestor of living tetrapods (i.e., crown-group node) was most likely ancestrally carnivorous, as were the crown-group ancestors of many major clades within tetrapods, including amphibians, amniotes, mammals, reptiles, lepidosaurs, squamates, snakes, archosaurs, turtles and crocodylians (but not birds, which were inferred as ancestrally herbivorous). These reconstructions also suggest that there were many origins of omnivory and herbivory among extant tetrapod lineages (specifically mammals, birds, lizards and turtles), but that these origins were all relatively recent, in the last 110 million years. The estimated rates among observed states suggest that there were many transitions between omnivory and the other two states (Table S53) but very few direct transitions between carnivory and herbivory (Table S53). Surprisingly, transitions back to carnivory from omnivory and back to omnivory from herbivory were at least as common as origins of omnivory and herbivory (based on the estimated rates). Overall, broadly similar results were found using hidden-rate models (Figure S1; Tables S54–S56) and using the alternative tree (Figures S2 and S3; Tables S57–S60).

## 4 | Discussion

### 4.1 | $T_b$ and Diet

Animal diets vary extensively, but why animal species have the diets that they do is generally unclear. Here, we estimated large-scale patterns of diet evolution in tetrapods and found that higher  $T_b$  was significantly associated with the evolution of herbivory in nearly every major tetrapod group. This result was predicted given the hypothesis that herbivory requires high  $T_b$ , since the gut

bacteria that are required to break down plant cell walls (and thus extract nutrition from many types of plant matter) are thought to require high temperatures in order to function.

Superficially, it might appear that previous studies addressed this question. For example, Clarke and O'Connor (2014) found associations between diet and  $T_b$  in mammals and birds, which paralleled ours (i.e., lower  $T_b$  in carnivorous species, but their results in birds were not significant after phylogenetic correction). Similarly, Meiri et al. (2013) did not find that diet significantly predicted  $T_b$  in lizards. Yet, both tested whether diet was a significant predictor of  $T_b$ , whereas our analyses also tested whether  $T_b$  predicts diet evolution. Using phylogenetic logistic regression, we found that high  $T_b$  was a significant predictor of the evolution of herbivory across tetrapods, ectotherms, mammals, birds, lepidosaurs and turtles. Our results suggest that herbivory originates among non-herbivorous lineages that already have relatively high  $T_b$  (i.e., high  $T_b$  helps explain the evolution of herbivory) and herbivores generally have high  $T_b$  (Figure 2). Consistent with this interpretation, we did not find that all species with high  $T_b$  were herbivores (Figure 2). Furthermore, our phylogenetic path analyses across tetrapods generally supported the idea that  $T_b$  is a potential driver of diet evolution, whereas the best-fit models did not support the idea that diet drives the evolution of  $T_b$ . In summary, the earlier studies (Clarke and O'Connor 2014; Meiri et al. 2013) tested whether diet can help explain variation in  $T_b$  (and found that it often cannot), whereas we found that  $T_b$  helps explain the evolution of diet. Of course, these results do not prove causation (a limitation shared with all phylogenetic comparative analyses), and we do show that other variables are also important predictors in some cases (i.e., body size, diel activity), along with  $T_b$ .

A somewhat surprising and discordant result is that among all sampled endotherms, the relationship between  $T_b$  and diet was reversed. Thus, phylogenetic logistic regression showed that herbivory was associated with lower  $T_b$  than omnivory and carnivory (Figure 2; Table 3), but only when omnivory was considered part of carnivory (maximum carnivory coding). This is especially surprising because both birds and mammals (when analysed separately) show the expected negative relationship between carnivory and  $T_b$  (Table 4). The most likely explanation for this pattern is that mammals have lower mean  $T_b$  than birds for all three diets (Figure 2; Table S1), and mammals are dominated by herbivorous species whereas birds are not (Figure 1). Therefore, when birds and mammals are analysed together, herbivorous endotherms have somewhat lower mean  $T_b$  overall (Figure 2), given the predominance of herbivorous mammals relative to birds. Note that Clarke and O'Connor (2014) did not address this pattern, because they only analysed birds and mammals separately. However, endotherms do not form a monophyletic group, and this anomalous pattern does not overturn the general association between herbivory and high  $T_b$  found across tetrapods, ectotherms and within birds and mammals.

### 4.2 | Diel Activity, Body Mass and Diet

We also tested whether diel activity was a significant predictor of diet evolution (Tables S25–S32). Diel activity is potentially

important because it is related to variation in  $T_b$  in tetrapods (Moreira, Qu, and Wiens 2021), with higher mean  $T_b$  in diurnal species in every group (albeit with some variation in significance levels). We found that when we analysed diel activity with phylogenetic logistic regression, it sometimes predicted the evolution of diet, with herbivory associated with diurnal activity (e.g., in tetrapods, ectotherms and lepidosaurs). Significant relationships were absent in mammals, turtles and in most comparisons in birds (Table S26). The latter three are all groups in which  $T_b$  significantly predicted the evolution of diet (Table 4). Given these overall results, we suggest that the diel activity influences the evolution of  $T_b$  (Moreira, Qu, and Wiens 2021) and  $T_b$  then influences the evolution of herbivory. Nevertheless, there could be other constraints of nocturnality on herbivory besides  $T_b$ . For example, fruits and leaves can have a combination of visual and olfactory cues that indicate ripeness to herbivores (Lev-Yadun, Ne'eman, and Izhaki 2009; Stutz et al. 2016, 2017). These visual cues may be ineffective at night. Thus, diurnality may be a prerequisite for herbivorous diets to evolve in some cases (but there are many diurnal species that are not herbivorous). Some authors have also suggested that diet and trophic interactions help drive diel-activity patterns in mammals (e.g., Vallejo-Vargas et al. 2022), but our results do not support a relationship between these variables in mammals.

We also tested for an effect of body size (=mass) on diet. Previous authors (e.g., Pough 1973) have hypothesised that herbivory is associated with larger body mass in lizards (but see Espinoza, Wiens, and Tracy 2004). This hypothesis (Pough 1973) posits that larger lizards cannot meet their metabolic demands by feeding on insects (e.g., too much energy expenditure relative to energy gain) whereas smaller lizards cannot meet theirs by feeding on plants (e.g., too little energy gained relative to their body mass). We found a significant relationship between body mass and diet in tetrapods, ectotherms and lepidosaurs. However, even in these three groups, this significant relationship was relatively fragile, and depended on how diet was coded (i.e., maximum herbivory vs. carnivory) and whether  $T_b$  was included in the model. Overall, our results do support the idea that herbivory is more likely to evolve in species with larger body sizes, especially in lizards. But our results also suggest that both  $T_b$  and size are generally important for diet evolution.

### 4.3 | Large-Scale Evolution of Diet in Tetrapods

Our analyses also estimated overall macroevolutionary patterns in tetrapod diet. These results should be considered preliminary, especially because our taxon sampling was designed specifically to address the relationship between  $T_b$  and diet. Nevertheless, all major groups were represented, and simply adding more species to these groups need not overturn our results (especially since diet shows strong phylogenetic signal, such that close relatives tend to have the same diet; Saban, Qu, and Wiens 2023). Furthermore, previous phylogenetic analyses support our inferences here (Figure 3) that carnivory (as defined here) is ancestral in mammals (Price et al. 2012) and lepidosaurs (Lafuma et al. 2021).

We found three intriguing patterns. First, tetrapods were most likely carnivorous ancestrally (Figure 3), as were many major

tetrapod clades. Thus, some presently carnivorous lineages appear to have maintained that diet through a continuous series of carnivorous ancestors going back hundreds of millions of years, showing strong evidence for niche conservatism in diet (see also Román-Palacios, Scholl, and Wiens 2019; Saban, Qu, and Wiens 2023). Second, we found many independent origins of omnivory and herbivory among extant tetrapod lineages (e.g., in mammals, lizards, turtles and birds) but all within the last ~110 million years (Figure 3), despite the much greater overall age of extant tetrapods (~350 million years). Fossil evidence suggests that angiosperms came to dominate plant communities ~100 million years ago (e.g., Knoll 1986). Although there are many older inferred herbivorous tetrapod lineages in the fossil record (e.g., many non-avian dinosaurs and older groups; Sues and Reisz 1998), these lineages have not persisted to the present day. Third, our rate estimates (e.g., Table S53) suggest that reversals from herbivory back to omnivory and from omnivory back to carnivory were as common or more common than origins of herbivory and omnivory. These frequent reversals suggest that plant-based diets are relatively unstable among extant tetrapod lineages (see also dedicated studies within many tetrapod groups; e.g., Price et al. 2012; Burin et al. 2016; Lafuma et al. 2021).

### 4.4 | Areas for Future Research

Our results suggest many areas for future research. First, many other factors besides  $T_b$  could help explain the evolution of herbivory and omnivory in particular lineages. For example, in lizards, these may include body size, climate and dentition (e.g., Cooper and Vitt 2002; Espinoza, Wiens, and Tracy 2004; Meiri et al. 2013; Lafuma et al. 2021). More broadly, additional factors could include competition among animals for different dietary resources (both plant and non-plant), the plant clades present at a given timepoint (angiosperms vs. non-angiosperms), and adaptations of these plant clades that function to encourage (e.g., fruits, flowers) and discourage (e.g., toxins, spines) their consumption by animals. We emphasised one factor here ( $T_b$ ), but that factor may be the most general (within tetrapods and across animals overall). Numerous other factors are likely more specific to particular groups (e.g., behaviour, metabolism, habitat, dentition). Thus, we are seeking here the broadest potential explanation for the evolution of herbivory, not all the different factors that contribute to the origin of herbivory each time that it evolves.

Second, more research is needed to determine if the relationships between temperature and diet evolution found here also apply to other groups. If herbivory is widely dependent on the temperature requirements of gut bacteria, then the relationship between herbivory and temperature could be very widespread across animals (Clarke and O'Connor 2014). Among other vertebrates, this relationship may also be present in fish (Gaines and Lubchenco 1982). More research is needed in invertebrates. Insects are especially important, since ~25% of eukaryotic species are estimated to be herbivorous insects (Bernays 1998). Symbiotic gut bacteria may be broadly important in herbivorous insects, although some insects have acquired the genes for cellulose digestion from these symbionts (Engel and Moran 2013; Paniagua Voiron et al. 2018). Previous

studies have shown that both ambient temperature and host-plant choice affect fitness in herbivorous insects (Clissold and Simpson 2015), and that there are interactions between diet and temperature in marine invertebrates (Brockington and Clarke 2001). However, we do not know of broad-scale comparative studies linking diet evolution and  $T_b$  among invertebrate species. This should also be a priority for future research.

Third, more research is needed on the causes of the patterns found here, especially the potential role of gut microbes in linking herbivory and  $T_b$ . It is believed that symbiotic cellulose-digesting bacteria in herbivorous vertebrates require higher temperatures to function (e.g., Zimmerman and Tracy 1989; Mountfort, Campbell, and Clements 2002; Espinoza, Wiens, and Tracy 2004; Rimmer and Weibe 2006). However, to our knowledge, this claim still lacks experimental support. A quantitative analysis of the cellulose-digesting performance of these bacteria at a range of temperatures is paramount for determining if these bacteria do indeed impose a temperature constraint on the evolution of herbivory. Along these lines, our results suggest that there might be a minimum  $T_b$  necessary to be an herbivore. Specifically, we found almost no herbivores have  $T_b < 30^\circ\text{C}$  (Figure 2). The only exceptions are two turtle species, which nevertheless have  $T_b > 25^\circ\text{C}$ . Many species with non-herbivorous diets have lower  $T_b$ , including many amphibians, turtles and lepidosaurs. Herbivorous species can then have a range of different mean  $T_b > 30^\circ\text{C}$ , depending on the group (e.g., higher in birds) and the particular species. These patterns imply that a  $T_b$  near  $30^\circ\text{C}$  or higher is necessary for gut microbiota to function in digesting plant material (but again, direct experimental tests are needed). At the same time, our results do not suggest that there is a minimum mean  $T_b$  necessary to be an omnivore. For example, some omnivorous lepidosaurs have  $T_b < 20^\circ\text{C}$  (at least when their  $T_b$  was measured). We also note that these putative constraints of temperature and gut microbiota on diet evolution might only apply to some herbivorous diets. Fruit and nectar have high contents of simple sugars, which require less specialised digestion (Widdowson and McCance 1935). Therefore, frugivory and nectivory may not require specialised gut microbes or high  $T_b$ . Yet, we found similar results whether treating all plant-based diets as herbivory, or only treating folivores as herbivores. Surprisingly, many relationships with  $T_b$  were actually weaker when treating only folivory as herbivory.

Fourth, more work is needed on the broad-scale phylogenetic patterns found. The relatively high rate of reversals inferred from plant-based diets back to more animal-based diets should be an especially interesting subject for future research (and should be revisited with greater taxon sampling). Future studies should also explore the relationship between the origins of tetrapod herbivory and the rise of angiosperms, and the failure of older herbivorous tetrapod lineages to persist to the present day.

## 5 | Conclusions

In this study, we tested whether  $T_b$  helps explain the evolution of diet in tetrapods. We found that higher  $T_b$  significantly predicts the evolution of herbivory across all tetrapods and in every major group with herbivorous species (e.g., birds, mammals,

lepidosaurs, turtles).  $T_b$  is only one of many potential factors that influence diet evolution. However, the impact of  $T_b$  on diet may be particularly widespread across animals, especially if this relationship is determined by the thermal requirements of gut microbes needed to digest cellulose. Finally, our results suggest that plant-based diets are relatively recent and unstable among extant tetrapod lineages. Thus, we found that tetrapods are ancestrally carnivorous and that all origins of herbivory and omnivory among extant tetrapod lineages have been in the last ~110 million years. Yet, reversals from herbivory back to omnivory and from omnivory back to carnivory were at least as frequent as origins of herbivory and omnivory, suggesting that these latter two diets are surprisingly unstable once they evolve.

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## Conflicts of Interest

The authors declare no conflicts of interest.

## Data Availability Statement

All data are currently available as Datasets S1–S8 through a link on figshare: <https://figshare.com/s/944b7700d69e65750ca5> with the permanent DOI: [10.6084/m9.figshare.24961875](https://doi.org/10.6084/m9.figshare.24961875).

## References

- Ackerly, D. D. 2000. "Taxon Sampling, Correlated Evolution, and Independent Contrasts." *Evolution* 54: 1480–1492. <https://doi.org/10.1111/j.0014-3820.2000.tb00694.x>.
- Adams, D. C., and M. L. Collyer. 2018. "Phylogenetic ANOVA: Group-Clade Aggregation, Biological Challenges, and a Refined Permutation Procedure." *Evolution* 72, no. 6: 1204–1215.
- Anderson, S. R., and J. J. Wiens. 2017. "Out of the Dark: 350 Million Years of Conservatism and Evolution in Diel Activity Patterns in Vertebrates." *Evolution* 71, no. 8: 1944–1959. <https://doi.org/10.1111/evo.13284>.
- Beaulieu, J. M., and B. C. O'Meara. 2016. corHMM: Analysis of Binary Character Evolution. R package version 1.20. <https://CRAN.R-project.org/package=corHMM>.
- Beaulieu, J. M., B. C. O'Meara, and M. J. Donoghue. 2013. "Identifying Hidden Rate Changes in the Evolution of a Binary Morphological Character: The Evolution of Plant Habit in Campanulid Angiosperms." *Systematic Biology* 62, no. 5: 725–737. <https://doi.org/10.1093/sysbio/syt034>.
- Bernays, E. A. 1998. "Evolution of Feeding Behavior in Insect Herbivores." *BioScience* 48, no. 1: 35–44. <https://doi.org/10.2307/1313226>.
- Brockington, S., and A. Clarke. 2001. "The Relative Influence of Temperature and Food on the Metabolism of a Marine Invertebrate." *Journal of Experimental Marine Biology and Ecology* 258, no. 1: 87–99. [https://doi.org/10.1016/s0022-0981\(00\)00347-6](https://doi.org/10.1016/s0022-0981(00)00347-6).
- Burin, G., W. D. Kissling, P. R. Guimaraes, C. H. Sekercioglu, and T. B. Quental. 2016. "Omnivory in Birds is a Macroevolutionary Sink." *Nature Communications* 7, no. 1: 11250. <https://doi.org/10.1038/ncomm511250>.
- Clarke, A., and M. I. O'Connor. 2014. "Diet and Body Temperature in Mammals and Birds." *Global Ecology and Biogeography* 23, no. 9: 1000–1008. <https://doi.org/10.1111/geb.12185>.

- Clissold, F. J., and S. J. Simpson. 2015. "Temperature, Food Quality and Life History Traits of Herbivorous Insects." *Current Opinion in Insect Science* 11: 63–70. <https://doi.org/10.1016/j.cois.2015.10.011>.
- Collyer, M. L., and D. C. Adams. 2018. "RRPP: An R Package for Fitting Linear Models to High-Dimensional Data Using Residual Randomization." *Methods in Ecology and Evolution* 9, no. 7: 1772–1779. <https://doi.org/10.1111/2041-210X.13029>.
- Cooper, W. E., and L. J. Vitt. 2002. "Distribution, Extent, and Evolution of Plant Consumption by Lizards." *Journal of Zoology* 257, no. 4: 487–517. <https://doi.org/10.1017/S0952836902001085>.
- Emberts, Z., and J. J. Wiens. 2022. "Why Are Animals Conspicuously Colored? Evolution of Sexual Versus Warning Signals in Land Vertebrates." *Evolution* 76, no. 12: 2879–2892. <https://doi.org/10.1111/evo.14636>.
- Engel, P., and N. A. Moran. 2013. "The Gut Microbiota of Insects—Diversity in Structure and Function." *FEMS Microbiology Reviews* 37, no. 5: 699–735. <https://doi.org/10.1111/1574-6976.12025>.
- Espinoza, R. E. 2002. *Body Size, Temperature, and the Evolution of Herbivory in Reptiles*. University of Nevada at Reno: ProQuest Dissertations Publishing.
- Espinoza, R. E., J. J. Wiens, and C. R. Tracy. 2004. "Recurrent Evolution of Herbivory in Small, Cold-Climate Lizards: Breaking the Ecophysiological Rules of Reptilian Herbivory." *Proceedings of the National Academy of Sciences, United States of America* 101: 16819–16824. <https://doi.org/10.1073/pnas.0401226101>.
- Gaines, S. D., and J. L. Lubchenco. 1982. "A Unified Approach to Marine Plant–Herbivore Interactions. 2. Biogeography." *Annual Review of Ecology, Evolution, and Systematics* 13: 111–138. <https://doi.org/10.1146/annurev.es.13.110182.000551>.
- Garland, T., A. W. Dickerman, C. M. Janis, and J. A. Jones. 1993. "Phylogenetic Analysis of Covariance by Computer Simulation." *Systematic Biology* 42, no. 3: 265–292. <https://doi.org/10.1093/sysbio/42.3.265>.
- Hickman, C., L. Roberts, S. Keen, A. Larson, and D. Elsenhour. 2012. *Animal Diversity*. New York: McGraw-Hill.
- Ho, L. S. T., and C. Ane. 2014. "A Linear-Time Algorithm for Gaussian and Non-Gaussian Trait Evolution Models." *Systematic Biology* 63, no. 3: 397–408. <https://doi.org/10.1093/sysbio/syu005>.
- Holm, S. 1979. "A Simple Sequentially Rejective Multiple Test Procedure." *Scandinavian Journal of Statistics* 6: 65–70.
- Ives, A. R., and T. Garland. 2010. "Phylogenetic Logistic Regression for Binary Dependent Variables." *Systematic Biology* 59, no. 1: 9–26. <https://doi.org/10.1093/sysbio/syp074>.
- Karasov, W. H., and C. Martínez del Río. 2020. *Physiological Ecology: How Animals Process Energy, Nutrients, and Toxins*. Princeton, NJ: Princeton University Press.
- Knoll, A. H. 1986. "Patterns of Change in Plant Communities Through Geological Time." In *Community Ecology*, edited by J. Diamond and T. J. Case, 126–141. New York: Harper and Row.
- Lafuma, F., I. J. Corfe, J. Clavel, and N. Di-Poi. 2021. "Multiple Evolutionary Origins and Losses of Tooth Complexity in Squamates." *Nature Communications* 12, no. 1: 6001. <https://doi.org/10.1038/s41467-021-26285-w>.
- Lev-Yadun, S., G. Ne'eman, and I. Izhaki. 2009. "Unripe Red Fruits may be Aposematic." *Plant Signaling and Behaviour* 4, no. 9: 836–841. <https://doi.org/10.4161/psb.4.9.9573>.
- Ley, R. E., C. A. Lozupone, M. Hamady, R. Knight, and J. I. Gordon. 2008. "Worlds Within Worlds: Evolution of the Vertebrate Gut Microbiota." *Nature Reviews Microbiology* 6, no. 10: 776–788. <https://doi.org/10.1038/nrmicro1978>.
- Maddison, W. P., P. E. Midford, and S. P. Otto. 2007. "Estimating a Binary Character's Effect on Speciation and Extinction." *Systematic Biology* 56, no. 5: 701–710.
- Martins, E. P., and T. F. Hansen. 1997. "Phylogenies and the Comparative Method: A General Approach to Incorporating Phylogenetic Information Into the Analysis of Interspecific Data." *American Naturalist* 149, no. 4: 646–667. <https://doi.org/10.1086/286013>.
- McBee, R. H. 1971. "Significance of Intestinal Microflora in Herbivory." *Annual Review of Ecology, Evolution, and Systematics* 2: 165–176. <https://doi.org/10.1146/annurev.es.02.110171.001121>.
- Meiri, S. 2018. "Traits of Lizards of the World: Variation Around a Successful Evolutionary Design." *Global Ecology and Biogeography* 27, no. 10: 1168–1172. <https://doi.org/10.1111/geb.12053>.
- Meiri, S., A. M. Bauer, L. Chirio, et al. 2013. "Are Lizards Feeling the Heat? A Tale of Ecology and Evolution Under Two Temperatures." *Global Ecology and Biogeography* 22, no. 7: 834–845. <https://doi.org/10.1111/geb.12053>.
- Moreira, M. O., Y.-F. Qu, and J. J. Wiens. 2021. "Large-Scale Evolution of Body Temperatures in Land Vertebrates." *Evolution Letters* 5, no. 5: 484–494. <https://doi.org/10.1002/evl3.249>.
- Mountfort, D. O., J. Campbell, and K. D. Clements. 2002. "Hindgut Fermentation in Three Species of Marine Herbivorous Fish." *Applied and Environmental Microbiology* 68, no. 3: 1374–1380. <https://doi.org/10.1128/AEM.68.3.1374-1380.2002>.
- Olsen, A. M. 2015. "Exceptional Avian Herbivores: Multiple Transitions Toward Herbivory in the Bird Order Anseriformes and Its Correlation With Body Mass." *Ecology and Evolution* 5, no. 21: 5016–5032. <https://doi.org/10.1002/ece3.1787>.
- Orme, D., R. Freckleton, G. Thomas, et al. 2013. "The Caper Package: Comparative Analysis of Phylogenetics and Evolution in R." <https://cran.r-project.org/web/packages/caper/vignettes/caper.pdf>.
- Paniagua Voirol, L. R., E. Frago, M. Kaltenpoth, M. Hilker, and N. E. Fatouros. 2018. "Bacterial Symbionts in Lepidoptera: Their Diversity, Transmission, and Impact on the Host." *Frontiers in Microbiology* 9: 556. <https://doi.org/10.3389/fmicb.2018.00556>.
- Pough, F. H. 1973. "Lizard Energetics and Diet." *Ecology* 54, no. 4: 837–844. <https://doi.org/10.2307/1935678>.
- Pough, F. H., R. M. Andrews, M. L. Crump, A. Savitzky, K. D. Wells, and M. C. Brandley. 2016. *Herpetology*. Sunderland, MA: Oxford University Press.
- Pough, F. H., C. M. Janis, and J. B. Heiser. 2009. *Vertebrate Life*. 8th ed. San Francisco, CA: Pearson.
- Price, S. A., S. S. B. Hopkins, K. K. Smith, and V. L. Roth. 2012. "Tempo of Trophic Evolution and Its Impact on Mammalian Diversification." *Proceedings of the National Academy of Sciences* 109, no. 18: 7008–7012. <https://doi.org/10.1073/pnas.1117133109>.
- Qu, Y.-F., and J. J. Wiens. 2020. "Higher Temperatures Lower Rates of Physiological and Niche Evolution." *Proceedings of the Royal Society of London, Series B: Biological Sciences* 283: 20200823. <https://doi.org/10.1098/rspb.2020.0823>.
- Rimmer, D. W., and W. J. Weibe. 2006. "Fermentative Microbial Digestion in Herbivorous Fishes." *Journal of Fish Biology* 31, no. 2: 229–236. <https://doi.org/10.1111/j.1095-8649.1987.tb05228.x>.
- Román-Palacios, C., J. P. Scholl, and J. J. Wiens. 2019. "Evolution of Diet Across the Animal Tree of Life." *Evolution Letters* 3, no. 4: 339–347. <https://doi.org/10.1002/evl3.127>.
- Saban, K. E., Y.-F. Qu, and J. J. Wiens. 2023. "Niche Conservatism Over Deep Timescales and Diverse Niche Axes in Land Vertebrates." *Global Ecology and Biogeography* 32, no. 9: 1522–1534. <https://doi.org/10.1111/geb.13715>.

- Schluter, D., T. Price, A. O. Mooers, and D. Ludwig. 1997. "Likelihood of Ancestor States in Adaptive Radiation." *Evolution* 51, no. 6: 1699–1711. <https://doi.org/10.1111/j.1558-5646.1997.tb05095.x>.
- Schwenk, K., ed. 2000. *Feeding: Form, Function, and Evolution in Tetrapod Vertebrates*. London, UK: Academic Press.
- Stutz, R. S., P. B. Banks, N. Proschogo, and C. McArthur. 2016. "Follow Your Nose: Leaf Odour as an Important Foraging Cue for Mammalian Herbivores." *Oecologia* 182: 643–651. <https://doi.org/10.1007/s00442-016-3678-2>.
- Stutz, R. S., B. M. Croak, N. Proschogo, P. B. Banks, and C. McArthur. 2017. "Olfactory and Visual Plant Cues as Drivers of Selective Herbivory." *Oikos* 126, no. 2: 259–268. <https://doi.org/10.1111/oik.03422>.
- Sues, H. D., and R. R. Reisz. 1998. "Origins and Early Evolution of Herbivory in Tetrapods." *Trends in Ecology & Evolution* 13: 141–145. [https://doi.org/10.1016/s0169-5347\(97\)01257-3](https://doi.org/10.1016/s0169-5347(97)01257-3).
- Vallejo-Vargas, A. F., D. Sheil, A. Semper-Pascual, et al. 2022. "Consistent Diel Activity Patterns of Forest Mammals Among Tropical Regions." *Nature Communications* 13, no. 1: 7102. <https://doi.org/10.1038/s41467-022-34825-1>.
- van der Bijl, W. 2018. "Phylopath: Easy Phylogenetic Path Analysis in R." *PeerJ* 6: e4718. <https://doi.org/10.7717/peerj.4718>.
- von Hardenberg, A., and A. Gonzalez-Voyer. 2013. "Disentangling Evolutionary Cause-Effect Relationships With Phylogenetic Confirmatory Path Analysis." *Evolution* 67: 378–387. <https://doi.org/10.1111/j.1558-5646.2012.01790.x>.
- Widdowson, E. M., and R. A. McCance. 1935. "Available Carbohydrates of Fruits." *Biochemical Journal* 29, no. 1: 151–156. <https://doi.org/10.1042/bj0290151>.
- Wilman, H., J. Belmaker, J. Simpson, C. de la Rosa, M. M. Rivadeneira, and W. Jetz. 2014. "EltonTraits 1.0: Species-Level Foraging Attributes of the World's Birds and Mammals." *Ecology* 95, no. 7: 2027. <https://doi.org/10.1890/13-1917.1>.
- Zimmerman, L. C., and C. R. Tracy. 1989. "Interactions Between the Environment and Ectothermy and Herbivory in Reptiles." *Physiological Zoology* 62, no. 2: 374–409. <https://doi.org/10.1086/physzool.62.2.30156176>.

### Supporting Information

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