



Do Geographic Range Sizes Evolve Faster in Endotherms?

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Abstract

Changes in geographical distributions underlie a variety of fundamental ecological and evolutionary processes, from allopatric speciation to local extinction. However, little is known about general principles governing the evolution of range sizes at macroevolutionary scales. In this study we measure rates of geographical range size and position in a large-scale dataset of nearly 20,000 species including mammals, birds, squamates and anurans to test three predictions regarding the relationship between endothermy and geographical range evolution, namely whether endotherms show (1) larger geographical ranges; (2) faster rates of range size evolution; and (3) faster changes in the geographical position of their ranges. We found evidence in favor of all of these predictions, suggesting that the evolution of endothermy was associated with a fundamental change in the tempo of range evolution in terrestrial vertebrates. These results are consistent with two previously hypothesized relationships between range size and metabolic rate: the thermal plasticity hypothesis, which suggests that high metabolic rate increases thermal tolerance, and the energy constraint hypothesis, which posits that due to the higher, sustained levels of energy requirements, individuals with high metabolic rates would necessitate to forage farther and to space themselves more broadly, which would result in lower population densities, larger home ranges and ultimately larger range sizes. On the other hand, there was substantial variation in rates of range size evolution among the studied taxa that cannot be explained by the evolution of endothermy alone.

Keywords Basal metabolic rate · Macroecology · Macroevolution · Diversification · Biogeography · Geographical distribution

Introduction

The geographical distribution of a species is arguably the single most important predictor of its evolutionary fate. Not surprisingly, the study of geographical ranges is at the center of several disciplines, including macroevolution (Eldredge & Gould, 1972; Gaston, 1998; Jablonski, 2008), biogeography (Stevens, 1989; Rosensweig, 1995), and invasion biology (Courchamp et al., 2017). Given this importance, it is rather surprising that relatively little has been achieved in terms of general principles of geographical range evolution. For instance, one of the few broad ideas for the evolution of range size—Rapoport's rule (i.e., the decrease in range size towards lower latitudes, see Stevens, 1989)—does not seem to be as general as originally thought (Gaston et al.,

1998). On the other hand, range size in general seems to be correlated with body size (Camacho et al., 2017; Pyron, 1999; Taylor & Gotelli, 1994), niche breadth (Olalla-Tárraga et al., 2019; Slatyer et al., 2013; Yu et al., 2017), mating system (Grossenbacher et al., 2015), and population density (Tales et al., 2004; but see Novosolov et al., 2017), yet the link between correlation and more mechanistic hypotheses is still lacking.

In the paper that marked the beginning of the discipline of macroecology, Brown and Maurer (1989; see also Brown, 1995). Brown et al. (1996) explored variation in mechanisms driving range limits to suggest that smaller ranges tend to be elongated north–south, whereas large ranges tend to be elongated east–west, but the evidence so far on this hypothesis has been mixed (Baselga et al., 2012; Castro-Insua et al., 2018; Pfrender et al., 1998; Schlachter, 2010). On the other hand, high-latitude geographical range limits in terrestrial vertebrates were recently shown to evolve 1.6 to 4 times faster than low-latitude limits (Pie & Meyer, 2017). Interestingly, Pie and Meyer (2017) also

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uncovered an intriguing pattern in which the latitudinal midpoint of mammals evolved nearly five times faster than in squamates. This pattern was confirmed by Rolland et al. (2018), who showed that climatic niche shifts are significantly faster in endotherms (birds and mammals) when compared to ectotherms (squamates and amphibians), as well as fewer latitudinal shifts in ectotherms. However, it is still unclear the extent to which this discrepancy is a direct outcome of differences in physiological tolerances, or whether they reflect indirect consequences of differential capacity for dispersal between ectotherms and endotherms, particularly in relation to the spatial dynamics of glacial expansion and contraction at higher latitudes over the past 100,000 years (Hewitt, 2004; Schmitt, 2007). Nevertheless, these differences could imply that the evolution of endothermy was associated with a marked change in the way geographical ranges evolve in vertebrates. Environmental temperatures have a much stronger impact on the metabolic activity of ectotherms in comparison with endotherms (Dillon et al., 2010; Araújo et al., 2013). However, the analyses in Pie and Meyer (2017) only focused on the rate of evolution of the latitudinal midpoint of species ranges, whereas the actual differences in the evolution of range sizes in ecto- and endotherms is still largely unknown.

There are several potential ways in which endothermy could affect the evolution of range sizes. First, the internal temperature buffering conferred by endothermy could allow for species to be less constrained physiologically (Agosta et al., 2013). For instance, climate plays a more important role to explain the distribution of terrestrial ectotherms in relation to their endothermic counterparts in the Iberian Peninsula (Aragón et al., 2010; see also Buckley et al., 2012). Indeed, the high metabolic rates of endotherms might constrain individuals to forage farther and space themselves more widely to meet their energetic demands, leading to low population densities, larger home ranges, and thus larger species distributions to maintain minimum viable population sizes to avoid extinction (Agosta et al., 2013). However, the link between thermoregulation and animal spacing is still limited (Tamburello et al., 2015; but see Todd & Kowakowski, 2021). As a consequence of these mechanisms, endotherms might be able to attain broader limits in their ranges, as well as improve their dispersal capacities, leading to relatively larger range sizes. Likewise, given that endotherm species could more likely take advantage of ecological opportunities without being held back by more strict physiological constraints, they might as a consequence experience faster rates of geographical range evolution. This could be reflected both in terms of changes in geographical range sizes, as well as more straightforward changes in the position of their distributions as species occupy different geographical regions. To the best of our knowledge, none

of these hypotheses have been explicitly addressed before, particularly using large-scale datasets.

The goal of our study was to integrate four large-scale datasets of terrestrial vertebrates (mammals, birds, squamates, and anurans) to test three hypotheses regarding the impact of endothermy on geographical ranges. In particular, we predict that endotherms should have (1) larger geographical ranges; (2) faster rates of range size evolution and (3) faster changes in the latitudinal position of the centroid of geographical ranges.

Materials and Methods

Phylogenetic relationships among the studied taxa were obtained for amphibians (Jetz & Pyron, 2018), birds (Jetz et al., 2012; Ericson backbone trees), mammals (Upham et al., 2019; birth–death node-dated trees), and squamates (Tonini et al., 2016) from VertLife.org (<http://vertlife.org/phylosubsets/>). Instead of including all of the species in those clades, we focused on subclades that were more ecologically homogeneous to facilitate the interpretation of the obtained estimates, as well as on the particular species for which both phylogenetic and distribution data were available. The combined dataset included 19,256 species distributed across mammals [Carnivora (N = 216), Cetartiodactyla (N = 138), Chiroptera (N = 1123), Diprotodontia (N = 138), Primates (N = 376)], Squamates [Anguimorpha (N = 153), Gekkota (N = 1065), Iguania (N = 1080), Lacertoidea (N = 494), Scincoidea (N = 1044), Serpentes (N = 1931)], Amphibia [Anura (N = 4975), Caudata (N = 534), Gymnophiona (N = 148)], and Aves [Charadriiformes (N = 321), Columbiformes (N = 264), Passeriformes (N = 4604), Piciformes (N = 331), Psittaciformes (N = 321)]. Geographical distributions were obtained from shapefiles available on The IUCN Red List of Threatened Species database Version 2018-2 (IUCN, 2018). Shapefiles were mapped on a cylindrical equal-area projection and the area and the centroid coordinates of the geographical distribution were obtained for each species using QGIS 3.8.3 (QGIS Development Team, 2020) and geosphere 1.5-7 (Hijmans, 2019), respectively. We omitted all introduced and uncertain ranges.

We began analyses by exploring the distribution of range sizes across different clades using histograms of their log₁₀-transformed areas. We then estimated rates of evolution of range sizes and latitudinal midpoints as the σ^2 parameter of a Brownian motion model of evolution using the fitcontinuous function in GEIGER 2.0.7 (Pennell et al., 2014). In order to account for phylogenetic uncertainty, we repeated estimates for 1000 alternative topologies and report the mean, standard deviation and ranges of each set of estimates. We recognize that the Brownian motion might necessarily not be the best-fit model across all taxa and topologies. However, we chose

to consistently use it throughout the analyses for two main reasons. First, none of the commonly used models (BM, EB, OU, etc.) is likely to provide a good absolute fit to our data, particularly in the case of fairly large phylogenies. To properly account for variation in tempo and mode across taxa and topologies, one would not only need to assess model adequacy in each case (e.g., Pennell et al., 2015), but also to account for eventual heterogeneity in evolutionary regimes. Carrying out such endeavor at the scale of our study datasets would be unfeasible. However, our goal is not to model precisely range evolution, but rather to provide a reasonable approximation of their rates, and for this purpose BM seems to us a good first approximation. Second, different models have particular sets of parameters, and the rate estimates would not necessarily be directly comparable across different models. Differences between clades were interpreted based on the obtained confidence intervals. We preferred this approach rather than using a composite tree for all taxa and using an approach such as that of O'Meara et al. (2006) because it would preclude us to account for phylogenetic uncertainty. However, the differences between clades in their estimated rates are so substantial to the point that our conclusions would remain unaltered.

Results

The distribution of range sizes for each clade revealed consistently larger ranges in endotherms than in ectotherms (Fig. 1). For instance, while median range sizes varied between 4257 km² (Gekkota) and 50,085 km² (Serpentes) in squamates and between 1153 km² (Gymnophiona) and 4337 km² (Anura) in amphibians, they varied between 63,322 km² (Primates) and 1,590,497 km² (Carnivora) and between 115,736 km² (Columbiformes) and 4,644,783 km² (Charadriiformes) in birds (Table S1). Moreover, an even more striking difference in range distributions involved the relative frequency of small ranges: although there was some level of left skew in all taxa, ranges below 10,000 km² were considerably rare in endotherms. On the other hand, the right tail of endotherm distributions appears to be strongly affected by available area, given that a near truncation is found among endotherms with large ranges when they approach the size of continents (Fig. 1).

In general, endotherms also tended to show the highest rates of range size evolution (Table 1). For instance, the six lowest rates were found in ectotherms, whereas all but two of the 11 highest rates were found in endotherms. The main exception was found in Serpentes, which also have the largest range sizes among ectotherms (Fig. 1). However, this difference in rates might have been constrained in terms of the lower bound to viable range sizes for endotherms on the left and the size of continents on the right, as indicated above.

Interestingly, the rate of evolution in the latitudinal mid-point was even more dramatic: nine of the highest rates were found among endotherms, whereas eight of the lowest rates were found in ectotherms. The only exception (again) was Serpentes, which showed higher rates than Diprotodontia.

Discussion

Our results suggest an important difference in the tempo of range evolution in tetrapods between endotherms and ectotherms. In particular, we confirmed all of our tested predictions, namely that endotherms show (1) larger geographical ranges; (2) faster rates of range size evolution and (3) faster changes in the geographical position of their ranges. To the best of our knowledge, none of these three hypotheses had been tested before, although some of our results are consistent with previous evidence, such as the lower frequency of latitudinal shifts in ectotherms (Rolland et al., 2018). The most obvious explanation for this difference involves metabolism: endothermic vertebrates might require at least an order of magnitude more energy than ectotherms (Buckley et al., 2012; Pough, 1980). For instance, field metabolic rate (FMR) estimates of the western fence lizard *Sceloporus occidentalis* were approximately 3 to 4% that of a bird or mammal of equal size (Bennet & Nagy, 1977). Moreover, FMRs are either stable or decrease slightly with temperature for endotherms, whereas they generally increase for ectotherms, thus leading to opposing latitudinal gradients of expected FMR (Buckley et al., 2012). These trends translate into distinct geographical variation in their metabolic budgets. For instance, ectotherms at high latitudes are limited by the available periods in which foraging activity would lead to an energetic surplus, as the warm summer months might not be sufficient to allow for persistence throughout the rest of the year, despite their relatively low metabolic demands (Buckley et al., 2012).

Agosta et al. (2013) provide three hypotheses relating basal metabolic rate (BMR) and range size: (1) the thermal plasticity hypothesis: higher BMR would be associated with increased thermal tolerance, thus allowing for larger range sizes; (2) activity levels/dispersal hypothesis: higher BMR would increase activity levels and dispersal potential of species, leading to increases in potential range sizes and (3) energy constraint hypothesis: the elevated energy requirements associated with high BMR would constrain individuals to forage farther and space themselves more widely, leading to larger home ranges and ultimately larger geographical distributions. Agosta et al. (2013) also compiled a large dataset of BMR and range sizes for terrestrial mammals and found a positive relationship between range size and both BMR and mass-independent BMR. Although the hypotheses presented by Agosta et al. (2013) were

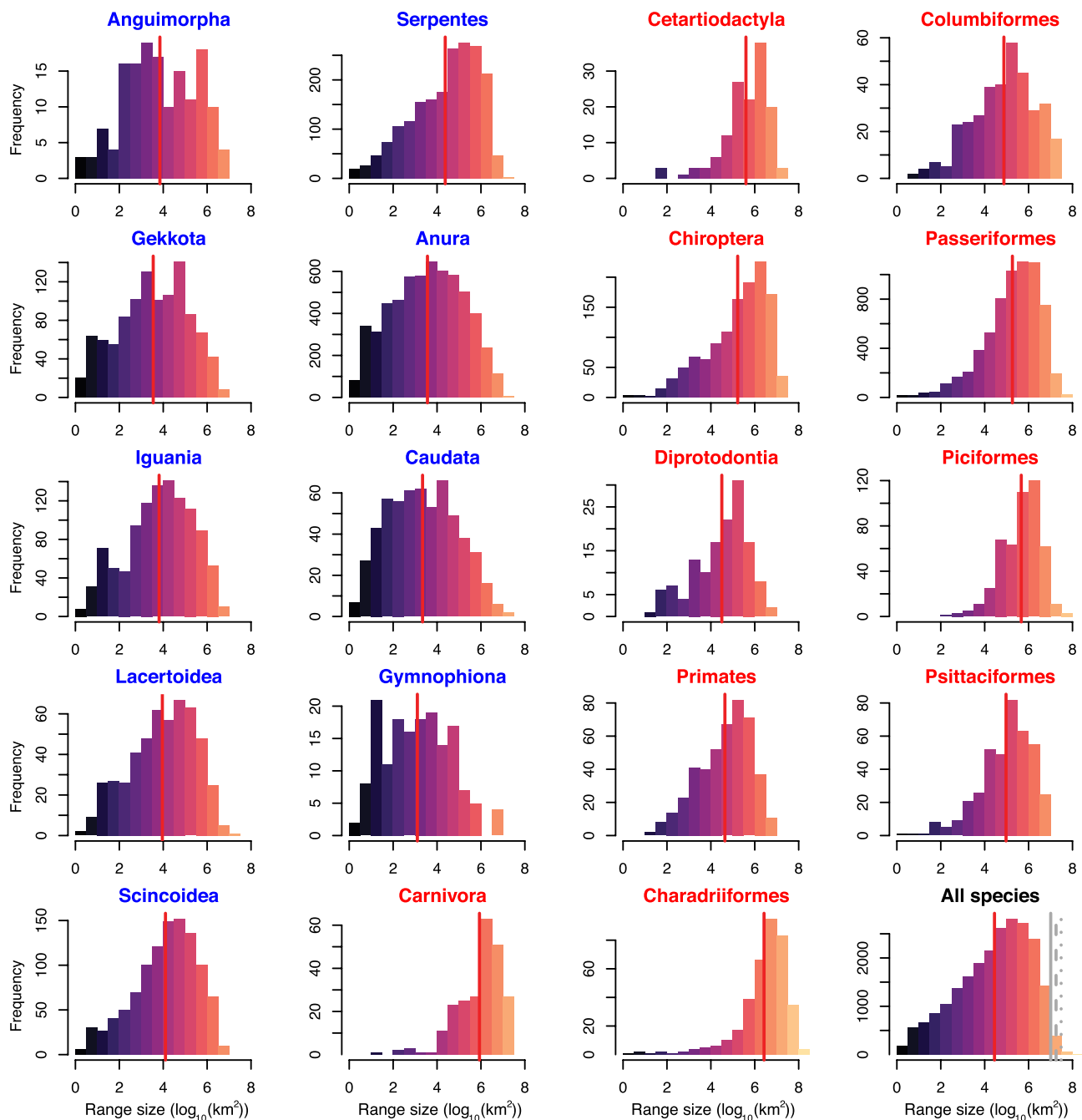


Fig. 1 Distribution of range sizes of the studied clades. Original data (in km^2) were \log_{10} -transformed. Ectotherm and endotherm taxon names are indicated in blue and red, respectively. Red vertical bars correspond to the means of each distribution. Colors are used

to facilitate the comparison across plots. Color palette was obtained using the viridis package (Garnier, 2018). For comparison, the solid, dashed, and dotted gray lines on the last plot indicate the areas of Europe, South America, and Africa, respectively (Color figure online)

formulated in the context of mammals, the same mechanisms should apply for ectotherms, and the data obtained in our study can be assessed, even if indirectly, in light of their three hypotheses. First, range sizes indeed tended to be larger in endotherms (Table 1), which is consistent with the thermal plasticity hypothesis. This is particularly apparent when comparing the largest ranges in each taxon which

often reach continental dimensions, as opposed to the considerably lower range sizes in ectotherms. Second, our data cannot directly test the activity level/dispersal hypothesis, given that we do not have independent data on activity/dispersal capacity of the studied taxa. However, it is important to note that the shapes of the range size distributions appear qualitatively consistent with this hypothesis as well. For

Table 1 Median rates of evolution of range size and latitudinal position in terrestrial vertebrates and their corresponding 95% quantiles considering estimates across 1000 alternative topologies

Taxa	Range size		Latitudinal position	
	Median	95% quantiles	Median	95% quantiles
Mammalia				
Carnivora	0.65	0.39–1.85	154.35	98.41–394.26
Cetartiodactyla	0.63	0.42–1.53	73.58	57.10–140.61
Chiroptera	1.34	0.97–2.19	124.96	88.93–197.84
Diprotodontia	0.80	0.45–2.20	22.95	13.34–76.77
Primates	0.78	0.53–1.50	37.03	26.72–68.60
Aves				
Charadriiformes	0.58	0.35–6.33	236.12	152.87–2144.43
Columbiformes	0.75	0.36–7.34	99.12	51.08–760.02
Passariiformes	0.98	0.64–4.44	106.76	69.40–421.41
Piciformes	0.43	0.21–3.36	93.03	46.28–829.55
Psittaciformes	0.61	0.33–3.80	54.37	29.14–342.82
Squamata				
Anguimorpha	0.37	0.21–1.02	7.17	4.12–33.58
Gekkota	0.23	0.17–0.36	6.57	4.28–12.66
Iguania	0.56	0.41–1.09	14.61	8.80–35.85
Lacertoidea	0.29	0.19–0.53	10.25	6.09–27.01
Scincoidea	0.30	0.22–0.59	7.92	5.10–17.70
Serpentes	0.71	0.48–1.53	24.66	17.73–44.31
Amphibia				
Anura	0.60	0.38–3.96	14.87	9.31–95.25
Caudata	0.29	0.19–1.84	2.73	1.61–18.83
Gymnophiona	0.18	0.08–1.27	4.50	2.08–28.16

Rates are measured in units of $\log_{10}(\text{km}^2)^2/\text{My}$ and $\log(\text{degrees})^2/\text{My}$, respectively

instance, taxa that are notoriously good dispersers, such as Charadriiformes and Chiroptera tend to have more right-skewed distributions in relation to other taxa with relatively lower dispersal capacity, such as Psittaciformes and Diprotodontia (Fig. 1). However, this interpretation is necessarily tentative, given that we have not analyzed independent data on dispersal capacity and metabolic rates, nor whether higher metabolic rates would be a cause or a consequence of higher dispersal capacity. Finally, there is clear evidence for the energy constraint hypothesis, as small ranges are exceedingly rare in endotherms in relation to ectotherms (Fig. 1).

It is important to emphasize that several sources of bias might influence the inferences obtained in the present study. First, range sizes might be influenced by taxonomic decisions regarding species delimitation, which often are difficult to ascertain. This might be particularly important in face of the risk of taxonomic inflation (Isaac et al., 2004), under which differentiated populations of a single species might erroneously be elevated to the species level. Likewise,

a set of cryptic species might be mistakenly recognized as a single, broadly distributed species. However, it is important to note that, if these factors indeed are influencing our results, they are more likely to occur in endotherms than in ectotherms, given that more emphasis has been placed on mammal and bird taxonomy than possibly any other animal taxon. The split of a broadly distributed species into smaller ranges would underestimate the true average range size for a given clade, thus rendering the differences in range size between ecto- and endotherms to be conservative. Perhaps more importantly, it is crucial to recognize the relatively low power of including only two endotherm and two ectotherm clades (Rolland et al., 2018). This limitation is not unique to our study, but is rather common to rare but important evolutionary events. However, the fact that many of the patterns uncovered in the present study are consistent across several clades that are so different ecologically and geographically suggests that the causal relationship between ecto- and endothermy and the dynamics of their range evolution is plausible.

Although endothermy/ectothermy are commonly thought of as discrete phenomena, it is important to note that there is variation in the level of thermoregulation in those groups. For instance, there is variability among mammal lineages in the degree of variability in their body temperature, as well as the capacity to lower metabolic demands, such as by entering torpor or by accommodating higher ambient temperatures (Angilletta et al., 2010; Levesque et al., 2016). Moreover, many ectotherm groups are able to thermoregulate through behavior (Huey, 1982). Such variation might provide a useful way to assess whether the patterns identified in the present study extend to differences in temperature regulation within endotherms, as well as whether they are able to explain the marked differences in rates of range size evolution within ecto and endotherms. One particularly intriguing such case involves snakes, which share many of the patterns of range size evolution of endotherms, such as large ranges and fast rates of evolution (Fig. 1, Table 1). The causes for this pattern are difficult to ascertain, but it is intriguing to note that snakes tend to show unusually high rates of climatic niche evolution among squamates (Pie et al., 2017). Interestingly, this pattern is not shared among all snakes, with *Colubroidea* showing a more typical ectotherm range size distribution, whereas viperids and particularly elapids show a marked decrease in the frequency of small ranges characteristic of many endotherm range distributions (Fig. S1). In addition to exploring patterns within the studied clades, another potentially revealing area of future research might involve assessing the extent to which the geographical patterns identified here also extend to altitudinal ranges of montane species. It is important to note that the physiological differences between endotherms and ectotherms are unlikely to be the only source of variation in geographical

ranges among the studied taxa. Rather, factors such as body size, trophic level and biotic interactions are likely to play an important role in driving interspecific differences in rates of geographical range evolution. However, currently available phylogenetic comparative methods are still limited with respect to allowing for simultaneous tests for multiple correlates of evolutionary rates, but this area seems like a particularly interesting area for further investigation.

Together with body size, range size is a strong predictor of anthropogenic extinction risk (Newsome et al., 2020). We hope that our results might contribute to a more mechanistic understanding of range size evolution, as well as to predict the impacts of global climate change on the future distribution of terrestrial vertebrates. In particular, the relatively lower rate of geographical range evolution in ectotherms suggests that they are more vulnerable to the impacts of climate change, particularly in the tropics where ectotherms tend to be closer to their optimal temperatures (e.g. Deutsch et al., 2008; Dillon et al., 2010; Nowakowski et al., 2018).

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s11692-021-09537-x>.

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Author Contributions MRP designed the study; RD and FSC collected the data; MRP, RD, and FSC analyzed the data; MRP led the writing.

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Data Availability All analyses were based on publicly available data.

Code Availability There was no custom code. All used functions and packages are indicated in the text.

Declarations

Conflict of interest The authors have no conflict of interest to declare.

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