

Beyond latitude: Temperature, productivity, and thermal niche conservatism drive body size variation in Odonata

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28 **Abstract**

29 Latitudinal body size-clines are primarily discussed in the context of thermoregulation, *sensu*
30 Bergmann. However, body size patterns are ambiguous in ectotherms and this heterogeneity remains
31 poorly understood. We hypothesised that the contrasting effects of thermoregulation and resource
32 constraints obscure latitude–size relationships. Using data for 43% of all odonate species, we tested
33 whether body size increases with decreasing temperature and increasing productivity in
34 phylogenetically and spatially comparative analyses. We found strong but contrasting effects for
35 temperature between Anisoptera and Zygoptera and consistent positive effects for productivity that
36 explained 35%–57% of body size variation. We concluded that temperature, productivity, and
37 conservatism in size-based thermoregulation synergistically determine the distribution of ectotherms,
38 while the taxon-specific importance of these factors can lead to contrasting results and weak latitude–
39 size relationships. Our results reinforce the importance of body size as a determinant of species
40 distributions and responses to climate change.

INTRODUCTION

A mechanistic understanding of the variation in functional traits is crucial for understanding the drivers of species distribution (Lawton 1999; McGill *et al.* 2006; Pinkert & Zeuss 2018; White *et al.* 2007) and predicting biological responses to climate change (Buckley & Kingsolver 2012; MacLean & Beissinger 2017). Trait-based analyses have provided important insights into the mechanisms of community assembly, population dynamics, and range shifts, particularly for endotherms (Bruehlheide *et al.* 2018; de los Ríos *et al.* 2018; Estrada *et al.* 2016; Kraft *et al.* 2015). However, the thermal sensitivity of ectotherms differs fundamentally from that in endotherms (Atkinson & Sibly 1997). For example, insects rely on ambient temperature, not metabolically produced heat, to maintain optimal body temperature and support development, locomotion, and reproduction (Gillooly *et al.* 2001, 2002; Huey & Kingsolver 1989). This fundamental physiological difference can lead to biogeographical patterns in response to climate change that contrast those of endotherms (Atkinson & Sibly 1997; Buckley & Kingsolver 2012). Although the relationship between the ambient environment and phenotypic traits are well-documented through local scale and experimental studies (Atkinson & Sibly 1997; Lawton 1999; Whitman 2008), the extent to which they shape the distributions of ectotherms across larger spatial and taxonomic scales remains poorly understood.

Body size is associated with several physiological and ecological characteristics in animals, including metabolic rates, phenology, fecundity, and range size, with major consequences for species distribution and abundance (Gillooly *et al.* 2001, 2002; Honěk 1993; McCulloch *et al.* 2016; White *et al.* 2007; Whitman 2008). The body size of animals often increases along elevational or latitudinal gradients (Meiri & Dayan 2003). This pattern, *sensu lato* Bergmann's rule, is based on the principle that larger bodies have a smaller surface-to-volume ratio (greater capacity to retain body heat) than smaller bodies (Bergmann 1848). Therefore, larger species should have a thermoregulatory advantage in colder climates, while smaller species have a reduced risk of overheating in warmer climates. Bergmann's rule has been studied extensively in endotherms, but few studies have investigated geographical patterns in the body size of ectotherms. Among studies on insects, the majority of studies revealed no latitudinal cline in body size and the remaining studies report inconsistent results (Meiri & Dayan 2003; Shelomi 2012).

69 Resource availability is another important (Gillooly *et al.* 2001, 2002) but rarely considered
70 determinant of body size variation in animals (McNab 2010; Yom-Tov & Geffen 2006; Zeuss *et al.*
71 2017). The resource availability hypothesis states that a species' size is determined by energetic
72 requirements (Atkinson & Sibly 1997; Gillooly *et al.* 2001, 2002). Regions of higher resource
73 availability, for instance in the tropics, should thus support larger species than regions with lower
74 productivity—a latitudinal cline contrasting that of size-based thermoregulation. However, given the
75 lack of trait and distributional data, the importance of temperature and productivity in shaping global-
76 scale patterns in the body size of ectotherms remains largely unexplored. Because ectotherms
77 comprise >99.9% of all animal taxa (Atkinson & Sibly 1997), it is crucial for the conservation of overall
78 biodiversity, and the ecosystem services that they support (e.g. Kawahara *et al.* 2021), to elucidate
79 the mechanisms related to body size-clines.

80 This study provides a global analysis of the predictions of Bergmann's rule and the resource
81 availability hypothesis as they apply to ~43% of anisopteran (dragonflies) and zygopteran
82 (damselflies) species (Odonata; 69% of the genera; Figure S1). Our study design overcomes the
83 limitations of previous studies that reported body size variation resulting from idiosyncrasies of
84 temperate taxa or the investigated regions (Klok & Harrison 2013; Shelomi 2012) as well as trade-
85 offs between different mechanisms underlying a latitudinal gradient in body size (Ohlberger 2013;
86 Shelomi 2012; Zeuss *et al.* 2017). We hypothesised that body size would increase with (a) decreasing
87 temperature and (b) increasing productivity. If both thermoregulation and resource-driven growth
88 constraints shape this pattern, the overall latitudinal gradient in body size would be weaker than the
89 underlying environment–size relationships. We also assessed the relative importance of
90 thermoregulation and resource availability on the respective suborders of Odonata that have similar
91 ranges of body length but differ markedly in their body shape. Because Anisoptera are thick-bodied
92 and Zygoptera are slender, we hypothesised that anisopteran species would have a greater thermal
93 capacity, which should be reflected by stronger temperature-size clines in Anisoptera compared to
94 Zygoptera.

95 Our results show only a weak positive relationship between body length and latitude in Odonata
96 that stems from strong, but contrasting, effects of temperature and productivity on body size and

differences in the relative importance of both drivers between lineages. Moreover, we demonstrate that a substantial phylogenetic signal in size-based thermoregulation shaped the distribution of the thicker-bodied Anisoptera, but not that of the slender-bodied Zygoptera, suggesting that a greater thermoregulatory capacity promoted the distribution and diversification of select Anisoptera lineages, while most odonate lineages retained their original tropical niche. With these results we provide the first global-scale support for Bergmann's rule, the resource availability hypothesis, and thermal niche conservatism in insects, and we highlight that the interplay of different constraints to size is likely of broad ecological and evolutionary significance in ectotherms.

METHODS

Body size

We compiled body size data from measurements of museum specimens and from the literature for 2,803 odonate species worldwide. As proxies of body size, we measured the body and hindwing length (excluding appendices) from images of 724 individuals of African odonates provided by the Naturalis Biodiversity Center (RHNM, Leiden, The Netherlands) and 487 specimens of African species from the Senckenberg Natural History Museum (SNHM, Frankfurt, Germany). For the images of African species from the Naturalis Biodiversity Center, European species from Dijkstra and Lewington (2006), and North American species from Needham *et al.* (2000), we calculated the body length, hindwing length, and body area as previously described (Pinkert *et al.* 2017; Zeuss *et al.* 2017) using the R-package 'png' (Urbanek 2013). In short, the number of pixels of the body from the head to the distal end of the abdomen, that of the hindwing from its base to the tip, and the number of all pixels of the body were calculated. The pixel estimates were transformed to metric units through the product of the scale (provided or measured on the images) and image resolution; 3,612 additional length measurements were extracted from 19 literature and 2 internet sources (Table S1). To account for variation related to sexual dimorphism, we did not use females in this study if measurements from literature differentiated between sexes. If sources reported descriptive body size statistics, we used the minimum and maximum values instead of means to aid the integration of data across sources. For 305 individuals, we predicted the body length from the provided hindwing length with a linear

125 mixed effect model that included a random slope for genus nested in family and suborder ($n = 810$,
126 conditional $R^2 = 0.92$). Finally, the 5,128 individual measurements of 2,803 species were aggregated
127 to average values of body length ('body size' hereafter) per species.

129 **Distribution data**

130 We combined two types of distributional information: expert range maps and ranges derived from
131 intersections of occurrence records with the terrestrial ecoregions of the world. We downloaded expert
132 range maps from IUCN.org (IUCN 2021) and digitised range maps that cover the entire ranges of
133 European odonates from Boudot and Kalkman (2015). The data were taxonomically harmonised and
134 intersected with a grid of approximately 100 km × 100 km cells (military grid reference system [mgrs]).
135 However, many of the IUCN range maps were incomplete or were delineated by political borders
136 instead of factual species ranges (Hughes *et al.* 2021). Except for the range maps from Boudot and
137 Kalkman (2015), we used ecoregional ranges to extend and complete the distribution dataset.

138 To generate ecoregional ranges, spatially cleaned and taxonomically harmonised occurrence
139 records were taken from Sandall *et al.* (2022), which were based on data from the Global Biodiversity
140 Information Facility (GBIF) and the African Dragonflies and Damselflies Online database
141 (<http://addo.adu.org.za/>). The cleaning of the data included taxonomic harmonisation of species
142 names with the most up to date taxonomy (Paulson *et al.* 2021) as well as the removal of duplicated
143 entries based on coordinates, records from marine areas, common coordinate placeholders, spatial
144 outliers, as well as records close to GBIF institutions and country centres. Using a country-level
145 checklist of Sandall *et al.* (2022), records more than 1000 km away from a country of known
146 occurrence were removed from the dataset and only species locations supported by a relatively high
147 number of records were kept. For more details on the cleaning methods, see Pinkert *et al.* (2022),
148 and for details on how many species and records were removed during the cleaning process, see
149 Sandall *et al.* (2022). Subsequently, occurrence records intersecting with expert maps were removed.
150 The remaining records were intersected with a layer of the global terrestrial ecoregions (Dinerstein *et al.*
151 *et al.* 2017; downloaded from OneEarth.org). These ecoregional ranges were then intersected with our
152 equal-area grid. We used ecoregions as a broader definition of species ranges as they were

developed based on ecological characteristics and expert knowledge, and therefore provide an advantage over traditional methods, such as alpha-hulls, convex hulls, or simple equidistant buffers around occurrence records. Finally, we pooled the gridded expert and ecoregional species ranges and removed duplicated cell–species combinations as well as cells with >50% water (i.e. with >50% of the values being 'NA' in the mean annual temperature layer). The final distribution dataset included 5,233 (83%) of 6,322 odonate species.

Environmental data

Based on the predictions of Bergmann's rule and the resource availability hypothesis, we used two variables associated with geographic patterns of temperature (mean annual temperature and elevation) along with the enhanced vegetation index (EVI) as a proxy for productivity. The data were downloaded from the CHELSA (Karger *et al.* 2017, 2018; chelsa.org, current condition records) and EarthEnv (Amatulli *et al.* 2018) databases. The EVI layer was cropped to the extent of the climate variables (1 km × 1 km). For species-level analysis, the environmental data were extracted and aggregated to average values across the species ranges. Corresponding functions are provided in the R-package 'raster' (Hijmans *et al.* 2016).

Phylogenetic autocorrelation

Phylogenetic bias in the analysis of subsets of species challenges the statistical assumption that all data points are independent. To account for this phylogenetic autocorrelation and in the absence of a complete global phylogeny for Odonata, we constructed a super-tree based on the most recent taxonomic data and phylogenetic inferences of internal nodes (Figure S2). Family-level relationships were resolved based on inferences from Bybee *et al.* (2021) and the relationships between the genera of Anisoptera were resolved based on information from Letsch *et al.* (2016). We added species to the respective genera in the tree and randomly resolved the intra-genus relationships using the R-package 'phytools' (Revell 2017). Multifurcations in the tree were randomly resolved using the function 'multi2di' and branch length was calculated using Grafen's method (Grafen 1989). Corresponding

180 functions are provided in the R-package 'ape' (Paradis *et al.* 2004). Only species with corresponding
181 body length data were included in the tree.

182 Pagels lambda (λ , Pagel 1999)—calculated with the function 'phylosig' of the R-package
183 'phytools' (Revell 2017)—was 0.98 in Anisoptera and 0.99 in Zygoptera, confirming a strong
184 phylogenetic signal for body size in Odonata. Therefore, we partitioned the total variance of average
185 species body size into a phylogenetic and specific component, using Lynch's comparative method
186 (Lynch 1991) in the R-package 'ape' (Paradis *et al.* 2004). The different aspects of body size variation
187 in assemblage-level analyses (i.e. of species co-occurring within a 100 km × 100 km grid cell) are
188 hereafter called 'raw' (unpartitioned), 'P component', and 'S component', respectively. The P
189 component, which explained 42% of the (raw) body size variation in Anisoptera and 39% in Zygoptera,
190 represents the variation in body size predicted by the phylogenetic relationships between species.
191 The S component represents residuals from these predictions and hence the species-specific
192 deviation from the phylogenetically predicted part. The P component can be interpreted as the
193 outcome of long-term evolutionary processes, whereas the S component indicates recent adaptations
194 and includes plastic variation (Lynch 1991).

195

196 **Spatial autocorrelation**

197 We tested the importance of environmental factors in explaining the spatial variation in body size at
198 the assemblage-level using two types of linear regression models. In the first type of models, we
199 considered the average body size of each assemblage as the dependent variable and environmental
200 variables as predictors in ordinary least-squares regressions (Figure S3, Table S2). In the second
201 type of models, we accounted for spatial autocorrelation in the residuals of these regressions using
202 spatial autoregressive error models (Table 1).

203 Spatial autocorrelation in the residuals of linear regression models is an ubiquitous feature of
204 macroecological patterns (Dormann *et al.* 2007). This non-independence of neighbouring grid cells
205 can lead to an overestimation of the degrees of freedom and hence to false parameter estimates and
206 model inference. From correlograms constructed using the R-package 'ncf', we observed significant
207 spatial autocorrelation between the residuals of the linear regression models of body size (raw, P

component, and S component) and environmental predictors (Figure S4); we repeated all analyses using spatial autoregressive models (SARs) in the R-package 'spdep' (Bivand *et al.* 2017; Table 1). In these models, we fitted a spatial dependency weight using the model-specific point of spatial independence (i.e. the distances in the correlograms at which Moran's I reaches zero) as the upper boundary in a Euclidean distance matrix.

Statistical analysis

To elucidate the mechanisms of body size variation in Anisoptera and Zygoptera, we conducted analyses at both the species and assemblage level. To determine the relative importance of environmental drivers for long-term versus evolutionarily recent responses in body size, we fitted separate models for the variation in raw body size as well as for its P and S component. Taxon-specific responses were analysed using multiple regressions with interaction-terms of environmental factors and family as predictor. A general limitation of species-level analyses is that they oversimplify environmental variation within a species' range (e.g. Olalla-Tárraga *et al.* 2010). Therefore, we also analysed biogeographical patterns in body size at the assemblage level. Phylogenetic and spatial autocorrelation structures of co-occurring species were considered to reduce the potential impact of spurious trait–environment relationships that may result from pseudo-replications of taxa and regions. To avoid basing our conclusions on confounding taxonomic and spatial factors, we based our discussions of the evolutionary importance of body size on species-level analyses and our discussions of the environmental drivers of biogeographical patterns on assemblage-level analyses.

Frequency distributions of all model residuals were visually assessed for normality. Only body length needed to be \log_{10} -transformed. Environmental variables were z-scaled to facilitate comparison across models and predictors. As linear measurements do not account for the difference in the body shape of Anisoptera and Zygoptera (Zeuss *et al.* 2017), we did not only analyse size–environment relationships collectively for all species, but also separately for the two suborders. In species-level analyses, families with less than 10 species were excluded.

In assemblage-level analyses, grid cells with less than five species were excluded to avoid the effect of low sample size on average estimation (Pinkert *et al.* 2017; Figure S5). To improve the

robustness of our results, we removed regions from our dataset where body size was available for <25% of the species as well as smaller islands (Figure S1). Note that only small regions in central Amazonia and the southern Andes had a species coverage <50% (global coverage was >75%). The exclusion criteria reduced the number of species in our assemblage-level analyses to 43% (2,625) and 69% of odonate species and genera (274 Anisoptera and 200 Zygoptera), respectively. All analyses and data processing were conducted using the software R (R Core Team 2021).

RESULTS

The body length of all odonate species ranged from 17 mm to 129 mm. Anisoptera had an average body size of 51 mm, ranging between 19 mm (*Celithemis martha*) and 118 mm (*Anax tristis*). Zygoptera had an average body size of 41 mm, ranging between 17 mm (*Africocypha varicolor*) and 129 mm (*Mecistogaster amalia*). Anisoptera had longer bodies than Zygoptera on average ($r = -0.36$, $F = 0.59$, $p < 0.001$). Analysis of a subset of species showed a steeper increase in the body area of Anisoptera with increasing body length compared to Zygoptera (Anisoptera slope \pm SE: $4.18 \times 10^{-1} \pm 1.08 \times 10^{-2}$; Zygoptera slope \pm SE: $2.77 \times 10^{-1} \pm 8.71 \times 10^{-3}$; $R^2 = 0.72$, $p < 0.001$ for both, $n = 1,146$ individual measurements; Figure S6).

Using Pagel's lambda model, we observed a strong phylogenetic signal for body size as well as mean temperature, elevation, and productivity across species' ranges ($\lambda = 0.97, 0.98, 0.84$, and 0.97 , respectively). In species-level analysis of the phylogenetically predicted part of body size variation (P component), the body size of anisopteran species was negatively affected by mean annual temperature and elevation ($R^2 = 0.02$; Table S2). The P component in zygopteran species was positively affected by mean annual temperature ($R^2 = 0.01$). At the family level, environmental variables collectively explained 44% of body size variation (Figure S7). Body size variation in 5 (1 Anisoptera, 4 Zygoptera) of 21 families was not influenced by environmental factors, but these families were represented by relatively few species. Except for two families, body size trends in the remaining families either followed the predictions of Bergmann or that of the resource availability hypothesis. We observed differences in body size responses between and within Anisoptera and Zygoptera. Anisoptera generally showed stronger and more consistent responses to temperature than Zygoptera.

Specifically, the body size of species from five anisopteran and two zygopteran families increased with either decreasing mean annual temperature or increasing elevation. Six families showed the opposite body size–temperature relationship. The body size of species from four anisopteran and one zygopteran family increased with increasing productivity, for which three families showed an opposing trend.

In the assemblage-level analyses, body length generally increased with increasing latitude, and latitude explained 12% of the body size variation (Figure 1, Table S4). In multiple regression models that included discrete environmental predictors instead of latitude, average assemblage body size increased with decreasing temperature, decreasing productivity, and increasing elevation (Table 1, Figure S3). These three environmental predictors explained 51% of the variation in body size. While the effect of productivity (EVI) was consistent in both Anisoptera and Zygoptera, the effect of temperature differed between the suborders. The body size of anisopteran assemblages increased with decreasing mean annual temperature and decreasing elevation. Conversely, the body size of zygopteran assemblages increased with increasing mean annual temperature and decreasing elevation.

Mean annual temperature was the most important environmental predictor in models of the raw and P component of body size in anisopteran assemblages (Table 1, Figure 2). Productivity was the most important environmental predictor in models of the S component in anisopteran assemblages and in all models for zygopteran assemblages. All variables collectively explained 57% and 35% (SAR) of the body size variation in anisopteran and zygopteran assemblages, respectively. Temperature and productivity explained more of the variation in the P component of body size variation in Anisoptera (SAR, R^2 : 68%), whereas the variation explained by these variables was similar for all models in Zygoptera (SAR: $35\% < R^2 < 38\%$). The multiple regression models showed weaker effects and explained less of the total variation than models accounting for spatial autocorrelation, but the direction and ranking of the effects of environmental variables were similar (Table S3). The species richness of both suborders decreased from the equator to the poles (Figure S1a), but the proportion of Anisoptera from the total number of species per assemblage increased with latitude (Figure 3).

DISCUSSION

Our global-scale analysis of body size variation in Anisoptera and Zygoptera provides unique insights into the importance of thermoregulation and resource constraints for insects. In line with Bergmann's rule and the resource availability hypothesis, we found that the body size generally increases with decreasing temperature and increasing productivity in Odonata. Previous smaller-scaled studies reported conflicting effects of environmental drivers in determining body size clines along elevational and latitudinal gradients (Horne *et al.* 2018, Klok & Harrison 2013; Shelomi 2012), which fuelled doubts about the general validity of mechanistic explanations to ecogeographical patterns in body size otherwise well-documented in endotherms. We demonstrate that the interplay of temperature and productivity renders conclusions misleading that are solely based on geographical body size clines. Simultaneous analyses of the effects of temperature and productivity that vary with latitude, highlighted that the importance of size-based thermoregulation in ectotherms is similar to that in endotherm taxa (Olson *et al.* 2009; Santini *et al.* 2018). Temperature–size relationships were much stronger than latitudinal size gradients and explained a much higher proportion of the variation in body size in Odonata. We found that the weak and partly divergent latitudinal size clines in tropical regions and divergent patterns between the two suborders resulted from the strong positive effects of resource availability.

Bergmann's rule is one of the oldest theories describing ecogeographical patterns in trait variation and, although originally formulated for endotherms, it has been frequently tested in ectotherms (Horne *et al.* 2018; Klok & Harrison 2013; Shelomi 2012). Contradictions to the original hypothesis in insects and other ectotherms were argued to result from sample biases towards temperate regions and taxa as well as the poor representation of environmental gradients underlying local latitudinal clines (Shelomi 2012). We showed that assemblages of Odonata in colder climates, including areas with a lower mean annual temperature and/or higher elevation, are generally composed of, on average, larger species (Table 1). Mean annual temperature was the most important predictor of the geographical pattern of body size variation and resulted in a moderately strong Bergmann-like latitudinal gradient. Consistent with evidence from experimental (Atkinson & Sibly 1997; Brakefield & Willmer 1985) and local-scale studies (Heidrich *et al.* 2021; Pinkert *et al.* 2017;

Schweiger & Beierkuhnlein 2016; Zeuss *et al.* 2017), our results support the ecological importance of size-based thermoregulation in ectotherms. However, the contrasting temperature-size clines observed for the two Odonata suborders as well as conflicting reports of elevational and latitudinal patterns (Heidrich *et al.* 2020; Horne *et al.* 2018; Shelomi 2012) indicate that a substantial part of body size variation is caused by additional mechanisms.

Our results indicate that both size-based thermoregulation and resource constraints on growth may have major impacts on the geographical patterns and evolution of body size in Odonata (Table 1). Although, the effects of resource availability on interspecific variation in animal body size are well-documented in experimental studies (Atkinson & Sibly 1997; Gillooly *et al.* 2001, 2002), far less attention has been given to its role at larger spatial scales. We exemplify that latitudinal gradients in body size are weakened or even neutralized by the effects of decreasing productivity from the equator to the poles (Table S4, Figure 2): While larger species seem to have a thermoregulatory advantage in colder regions, the higher availability of resources also favours larger species in tropical climates (e.g. Olson *et al.* 2009). In general, larger species require more energy for metabolism, and growth, but larger body size in ectotherms could also confer greater fecundity (Gillooly *et al.* 2001, 2002; Honěk 1993). Resource-based size constraints provide an alternative explanation for the converse-Bergmann patterns frequently documented in studies of elevational and latitudinal gradients in body size (Horne *et al.* 2018; Shelomi 2012) and idiosyncrasies found even for closely related taxa investigated in the same context (e.g. Brehm & Fiedler 2004; Heidrich *et al.* 2021). The consistent and strong effects of productivity that we documented for Odonata, a group of insect predators (Kalkman *et al.* 2008), further suggest that resource-based size constraints apply throughout the food web, from primary producers to consumers and predators (see also Ohlberger [2013] and Olson *et al.* [2009]). Our results emphasize the need to incorporate proxies for resource availability in models of body size variation in ectotherms, not only because of its role as confounding factor but also because of its fundamental importance in shaping geographical patterns in body size variation.

Due to the lack of other pertinent size estimates accounting for the major differences in the body shape between Anisoptera and Zygoptera, we considered body length as a measure of size but separately analysed data for the two suborders. An image-based analysis of 1,146 species confirmed

348 that, when accounting for body length, Anisoptera had larger bodies than Zygoptera, which has
349 important physiological consequences (Figure S6). As a larger body increases the potential for heat
350 absorption and heat retention, these results suggest that Anisoptera should have a greater thermal
351 capacity than Zygoptera. Our results reconcile previous findings of a critical threshold in body size
352 beyond which size-based thermoregulation is less effective (Clusella-Trullas *et al.* 2007; Schweiger &
353 Beierkuhnlein 2016). We propose that integrating both body shape and size into the analysis of
354 temperature–size responses may further resolve inconsistent experimental (Forster *et al.* 2012) and
355 macroecological results (Horne *et al.* 2018).

356 Our finding that thermoregulation shapes the geographical pattern of anisopteran but not
357 zygopteran assemblages also suggests that the slender-bodied Zygoptera rely on an alternative
358 thermoregulatory mechanism for heat gain. During the last decade, studies on a broad spectrum of
359 ectotherm taxa, including beetles, butterflies, moths, and odonates, provided strong and consistent
360 support for the role of colour-based heat gain (Heidrich *et al.* 2021; Pinkert & Zeuss 2018; Schweiger
361 & Beierkuhnlein 2016). These studies highlight that ectotherms are generally coloured darker in colder
362 and lighter in warmer regions as well as the interaction between lightness and size (Clusella-Trullas
363 *et al.* 2007; Schweiger & Beierkuhnlein 2016). Particularly, smaller species have been found to vary
364 more in their colour lightness than larger species. Our results suggest a greater importance of colour-
365 based versus size-based thermoregulation in the smaller and slenderer Zygoptera. However, a
366 rigorous test of this hypothesis would require a much greater coverage of data on species' body area
367 or body volume, which is currently unavailable. Thus, our results are encouraging for further
368 investigations of the interactions between and differences in the relative importance of size- and
369 colour-based thermoregulation across regions, scales, and taxa.

370 In addition to its importance in shaping their contemporary distribution, phylogenetically
371 comparative analyses and distributional anomalies also indicate that niche conservatism has greatly
372 influenced the distribution and diversification of Odonata. Although Odonata are globally distributed,
373 the greatest number of families and genera are found in tropical climates, where the group originated
374 (Bybee *et al.* 2021; Sandall *et al.* 2022). We found that the relatively few lineages in extreme climates
375 (both desert and permafrost regions) are almost exclusively anisopteran (Figure 3). In addition, we

demonstrated that the phylogenetically predicted proportion of body size variation was strongly driven by size-based thermoregulation in Anisoptera, but not in Zygoptera, and markedly more variance was explained by models of temperature in Anisoptera (Table 1, $R^2 = 0.68$ and 0.38 , respectively; Figure 3). In line with our previous finding that conservatism in adaptations to cold climates shapes the latitudinal decline of phylogenetic diversity in European odonate assemblages (Pinkert *et al.* 2018), we show that thermal preference carries a strong phylogenetic signal (λ in mean temperature = 0.98 , λ in mean elevation = 0.84). Together, our results suggest that a greater capacity for size-based thermoregulation facilitated the distributional success and diversification of Anisoptera, while most families retained their original tropical niche. Our study provides strong support for the long-standing hypothesis of thermal niche conservatism in Odonata (Tillyard 1916; Wiens *et al.* 2010) and exemplifies the evolutionary importance of size-based thermoregulation in insects.

CONCLUSIONS

Our study on body size variation in Odonata provides the first global-scale analysis of size-based thermoregulation, resource-based size constraints, and thermal niche conservatism for any insect taxon. We showed that temperature and productivity explained a substantial proportion of body size variation (51%) in Odonata and that the varying importance of these drivers can lead to contrasting and weak latitude–size relationships among taxa. Our results reconcile the ambiguous findings of physiological experiments and macroecological studies on body size variation in ectotherms, but they also call for caution on interpretation based on geographical clines alone. The strong similarities in the documented effects of temperature and resource availability between endotherms and ectotherms as well as the evolutionary significance of size-based thermoregulation in Odonata reinforce the importance of ecophysiological mechanisms of body size variation across animal taxa. In the face of climate change, size–environment relationships and phylogenetic conservatism underline the predictive importance of body size for a broad range of biological responses. For instance, larger species of Anisoptera are expected to shift their ranges towards higher latitudes and altitudes; but, because many are at the geographical limits of their distribution, increasing temperatures are likely to impact local abundance and threaten these species with extinction (Estrada *et al.* 2016). Hence, our

results support the hypothesis that the average body size of ectotherms will decrease with global warming. Moreover, the contrasting effects of changes in productivity and differences in the relative importance of temperature and productivity among lineages will likely affect community composition and ecosystem function. Incorporating phylogenetic information and trait–environment interactions is therefore crucial to inform and improve forecasts of species responses to climate change. Our study represents important progress towards mechanistic predictions of spatiotemporal changes in body size. Given the relative lack of body size data—the most fundamental trait data—even for a well-studied insect taxon, we recognise that future studies should employ further trait information from the treasure trove of resources that natural history collections and literature provide. Finally, the coverage map presented in this study can be used to inform future research efforts of regions where body size data are lacking.

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602 **TABLES**

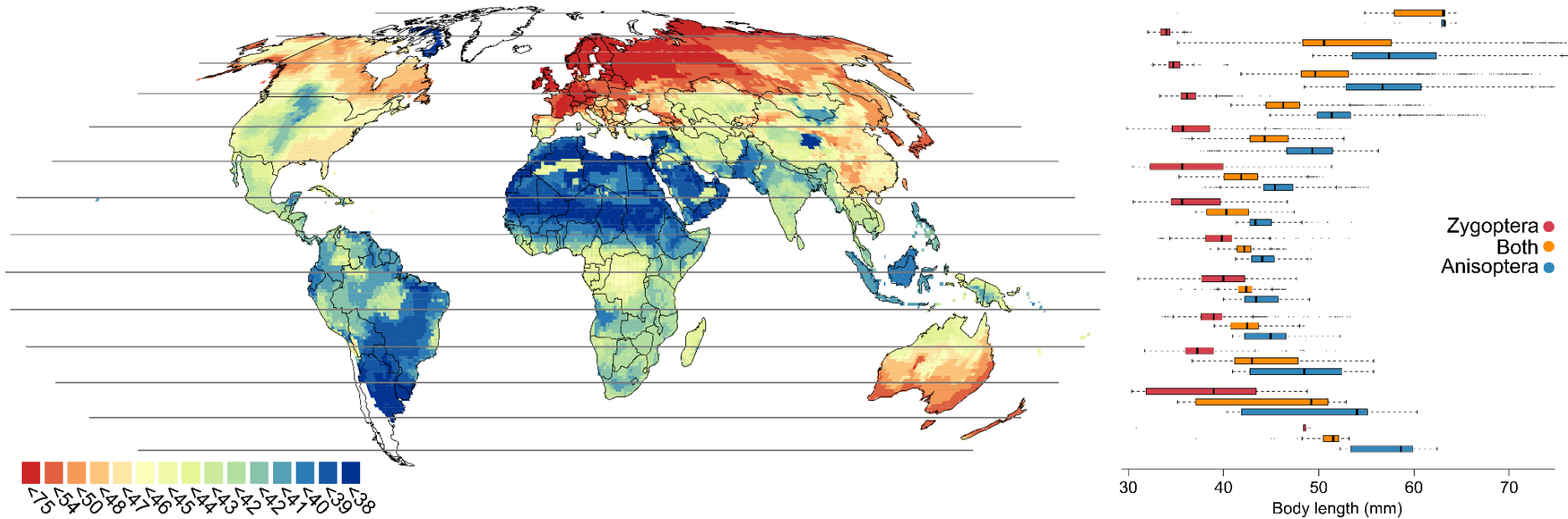
603 **TABLE 1** Assemblage-level multiple regressions between log₁₀-transformed body length (a proxy for
604 body size) and environmental variables with a spatial dependency weight (spatial autoregressive
605 model, SAR). The dataset (2,652 species and 17,605 assemblages) was divided into Anisoptera
606 (1,182 species and 17,476 assemblages) and Zygoptera (1,470 species and 15,650 assemblages) to
607 account for differences in body shape. The phylogenetic (P) component is the phylogenetically
608 predicted part of body length variation, and the specific (S) component represents its deviation. See
609 Table S3 for results of ordinary least squares models.

Suborder	Dependent variable	Predictor	Estimate	SE	z-value	p	R ²
Overall	Average body size	MAT	-4.52×10 ⁻²	±5.20×10 ⁻⁴	-87.10	<0.001	0.51
		EVI	1.62×10 ⁻²	±3.72×10 ⁻⁴	43.42	<0.001	
		Elev	-1.11×10 ⁻²	±2.66×10 ⁻⁴	-42.13	<0.001	
Anisoptera	Average body size	MAT	-5.84×10 ⁰	±5.85×10 ⁻²	-99.82	<0.001	0.57
		EVI	9.13×10 ⁻¹	±4.31×10 ⁻²	21.20	<0.001	
		Elev	-1.51×10 ⁰	±3.03×10 ⁻²	-49.90	<0.001	
	P component	MAT	-4.06×10 ⁰	±3.42×10 ⁻²	-118.71	<0.001	0.68
		EVI	-1.92×10 ⁻¹	±2.74×10 ⁻²	-7.01	<0.001	
		Elev	-1.12×10 ⁰	±1.91×10 ⁻²	-58.70	<0.001	
	S component	MAT	-1.06×10 ⁰	±3.25×10 ⁻²	-32.50	<0.001	0.28
		EVI	8.03×10 ⁻¹	±2.17×10 ⁻²	36.92	<0.001	
		Elev	-3.27×10 ⁻¹	±1.47×10 ⁻²	-22.22	<0.001	
Zygoptera	Average body size	MAT	6.21×10 ⁻¹	±3.10×10 ⁻²	20.01	<0.001	0.35
		EVI	1.78×10 ⁰	±3.01×10 ⁻²	58.92	<0.001	
		Elev	8.50×10 ⁻¹	±1.99×10 ⁻²	42.75	<0.001	
	P component	MAT	2.50×10 ⁻¹	±3.47×10 ⁻²	7.19	<0.001	0.38
		EVI	1.57×10 ⁰	±2.39×10 ⁻²	65.61	<0.001	
		Elev	8.09×10 ⁻¹	±1.72×10 ⁻²	46.79	<0.001	
	S component	MAT	-5.90×10 ⁻³	±2.34×10 ⁻¹	-0.25	0.8011	0.36
		EVI	2.95×10 ⁻¹	±1.33×10 ⁻²	22.09	<0.001	
		Elev	-3.69×10 ⁻²	±9.40×10 ⁻³	-3.92	<0.001	

610 MAT = mean annual temperature; EVI = annual enhanced vegetation index (productivity); Elev = elevation. pseudo- R^2 =
611 R^2 values based on maximum likelihood (Nagelkerke).

612 **FIGURES**

613



614

615 **FIGURE 1** The map in the left panel shows the spatial variation in body length (a proxy for body size) of odonate assemblages (17,605 grid cells of 100
 616 km × 100 km representing body length values of 2,652 species). The map is shown in Mollweide projection and colour scale intervals follow an equal-
 617 frequency classification, ranging from blue (short) to red (long). Boxplots in the right panel show the body size range of assemblages across latitudinal
 618 bands (10° intervals). Blue boxplots show the body length of Anisoptera (dragonflies), red boxplots that of Zygoptera (damselflies), and orange boxplots
 619 that of both suborders together.

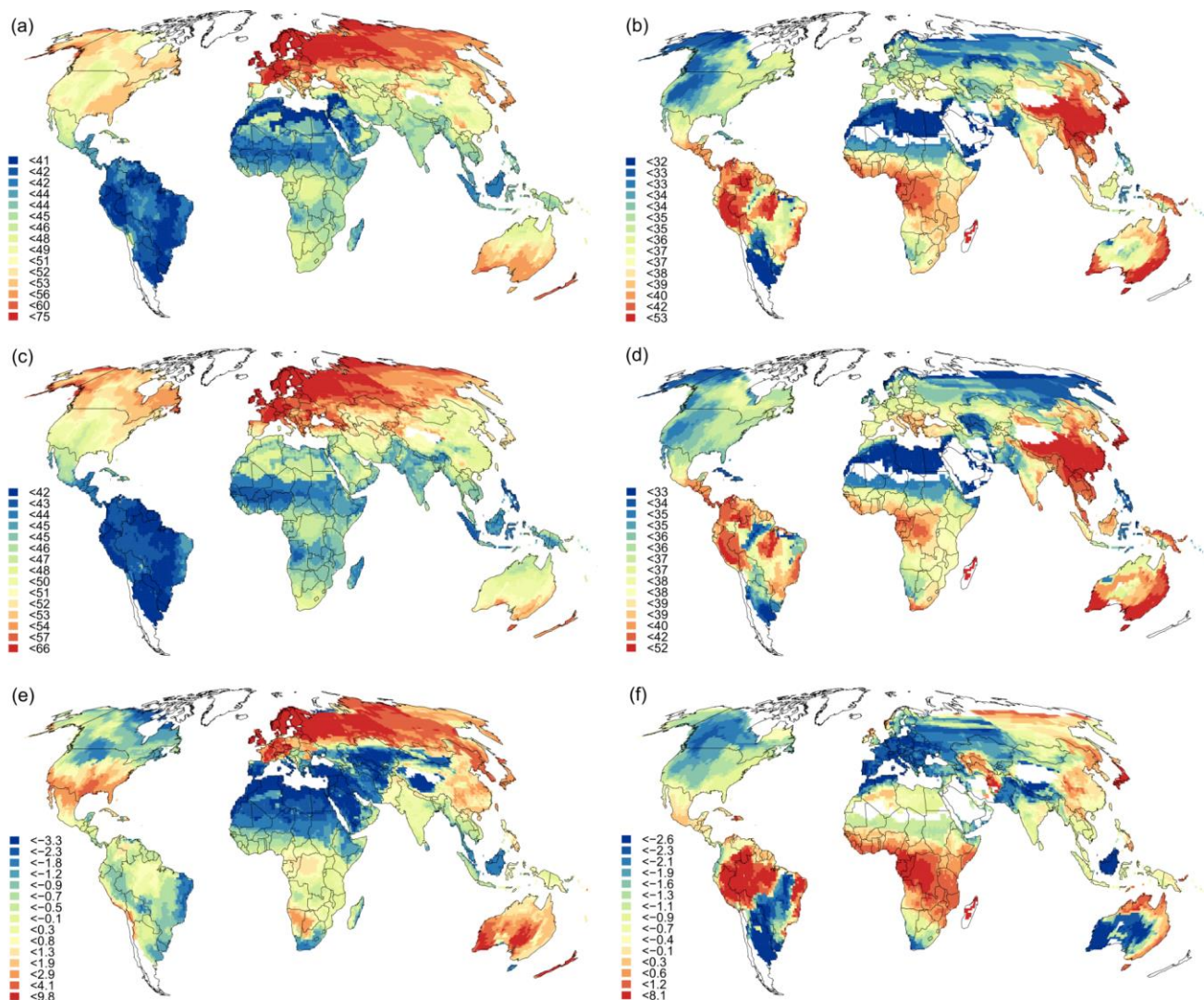
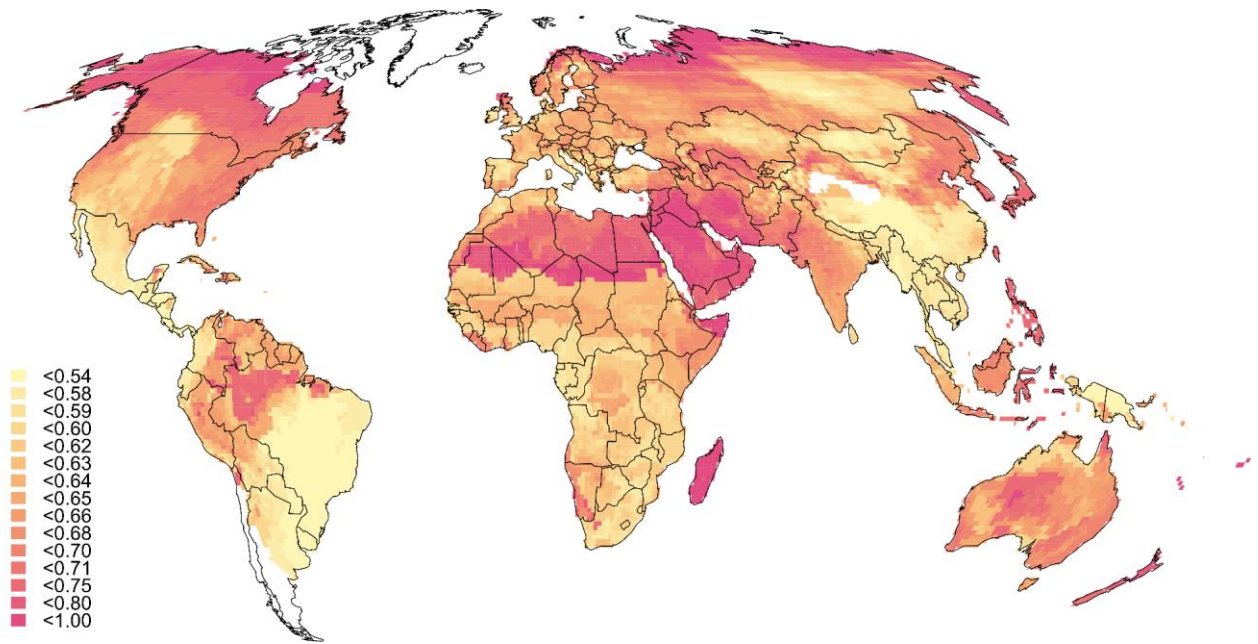


FIGURE 2 Spatial variation in body length (mm) of (a,c,e) anisopteran assemblages (17,476 grid cells representing 1,182 species), (b,d,f) zygopteran assemblages (15,650 grid cells representing 1,470 species). From top to bottom, the maps represent the (a,b) average, (c,d) phylogenetic, and (e,f) specific components of body size variation. Maps are shown in a Mollweide projection. Colour scale intervals follow an equal-frequency classification, ranging from blue (short) to red (long). The phylogenetic (P) component is the phylogenetically predicted part of body length variation, and the specific (S) component represents its deviation.



628

629 **FIGURE 3** Spatial variation in the proportion of anisopteran species to the total number of odonate
 630 species included in the analysis. Assemblages represent the distributions of 1,182 anisopteran and
 631 1,470 zygopteran species, respectively. Colour scale intervals follow an equal-frequency classification
 632 (quantiles), with beige/yellow indicating more zygopteran than anisopteran species and pink/red
 633 indicating the opposite. The dataset comprises 17,605 grid cells of 100 km × 100 km (Mollweide
 634 projection). Note that the main data source for Amazonia did not include Zygoptera, hence the high
 635 proportion of Anisoptera. Sources for all other regions included both suborders.