

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

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## Abstract

**Aim:** So far, latitudinal body size clines have been discussed primarily in the context of thermoregulation, *sensu* Bergmann. However, body size patterns are ambiguous in ectotherms, and this heterogeneity remains poorly understood. We tested whether Bergmann's rule and the resource availability rule, which states that energetic requirements determine species body size, apply to damselflies and dragonflies (Odonata). Furthermore, we hypothesized that the contrasting effects of thermoregulation and resource availability (e.g., productivity) can obscure the overall gradient in body size variation.

**Location:** Global.

**Time period:** Contemporary.

**Major taxa studied:** Odonata.

**Methods:** Using data for 43% of all odonate species described so far, we tested our hypotheses in phylogenetically and spatially comparative analyses at assemblage and species levels. For the distribution data, we integrated expert range maps and ecoregional ranges based on all available occurrence records. To distinguish between long-term and evolutionarily recent responses of environmental drivers in body size, we constructed a phylogenetically informed classification of all odonate species and decomposed the body size into its phylogenetic and specific components for our subset of species.

**Results:** We documented a weak positive relationship between body length and latitude but found strong and contrasting effects for temperature between dragonflies and damselflies and consistent positive effects for productivity that explained 35–57% of body size variation. Moreover, we showed a strong phylogenetic signal in size-based thermoregulation that shaped the distribution of dragonflies, but not of damselflies.

**Main conclusions:** We concluded that temperature, productivity and conservatism in size-based thermoregulation synergistically determine the distribution of ectotherms, while the taxon-specific importance of these factors can lead to contrasting and weak latitude-size relationships. Our results reinforce the importance of body size as a determinant of species distributions and responses to climate change.

## KEY WORDS

Bergmann's rule, body size, comparative analysis, ecogeographical rule, ectotherm, niche conservatism, Odonata, resource availability, thermoregulation, trait–environment relationship

## 1 | INTRODUCTION

A mechanistic understanding of the variation in functional traits is crucial for understanding the drivers of species' distributions (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 (Bruelheide et al., 2018; de los Ríos et al., 2018; Estrada et al., 2016; Kraft et al., 2015; Rocha-Ortega et al., 2022). However, the thermal sensitivity of ectotherms differs fundamentally from that of endotherms (Atkinson & Sibly, 1997). For example, insects rely mostly 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 with those of endotherms (Atkinson & Sibly, 1997; Buckley & Kingsolver, 2012; Pinkert, Clausnitzer, et al., 2022). Although the relationships 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, dispersal ability, phenology, fecundity and range size, with major consequences for species' distributions and abundance (Gillooly et al., 2001, 2002; Honěk, 1993; McCulloch et al., 2016; Stevens et al., 2012; White et al., 2007; Whitman, 2008). The body size of endothermic 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, 1847). Therefore, larger animal species should have a thermoregulatory advantage in colder climates. Bergmann's rule is widely supported for endotherms, but geographical patterns in the body size of ectotherms remain ambiguous. Among studies on insects, the majority of studies have revealed no latitudinal cline in body size, and the remaining studies report inconsistent results (Meiri & Dayan, 2003; Shelomi, 2012).

Resource availability is another important (Gillooly et al., 2001, 2002) but rarely considered determinant of body size variation in animals (McNab, 2010; Yom-Tov & Geffen, 2006; Zeuss et al., 2017). The resource availability (eNPP) rule states that the size of a species is determined by energetic requirements (*sensu* Atkinson &

Sibly, 1997; Gillooly et al., 2001, 2002; Huston & Wolverton, 2011). Regions of higher resource availability, for instance in the tropics, should thus support larger species than regions with lower productivity; a latitudinal cline contrasting that of size-based thermoregulation. However, given the lack of trait and distributional data, the importance of temperature and productivity for shaping global-scale patterns in the body size of ectotherms remains largely unexplored. Given that ectotherms comprise >99.9% of all animal taxa (Atkinson & Sibly, 1997), it is crucial for the conservation of overall biodiversity and the ecosystem services that they support (e.g., Kawahara et al., 2021) to elucidate the environment-trait interactions that underpin species responses to climate change (Pinkert, Clausnitzer, et al., 2022).

Given their relatively small number of species for an insect order, but extensive documentation of species ranges and body size data in literature, odonates provide an ideal study system for investigations of trait–environment relationships (Pinkert, Clausnitzer, et al., 2022; Rocha-Ortega et al., 2022). By mobilizing and integrating these data, we provide a global analysis of the predictions of Bergmann's rule and the resource availability rule for ~43% of the anisopteran (dragonfly) and zygopteran (damselfly) species (Odonata; 69% of the genera; Supporting Information Figure S1). Our study design overcomes the previous limitations of a research focus on body size variations in temperate taxa and regions (Klok & Harrison, 2013; Shelomi, 2012) and the simplification of potential drivers of body size to studies of latitudinal gradients (Ohlberger, 2013; Shelomi, 2012; Zeuss et al., 2017). We hypothesized that body size would increase with (1) decreasing temperature and (2) increasing productivity. If both thermoregulation and resource-driven growth constraints shape this pattern, the overall latitudinal gradient in body size would be weaker than the underlying environment–size relationships. We also assessed the relative importance of thermoregulation and resource availability for the respective suborders of Odonata that differ markedly in their body shape. Given that Anisoptera are thick-bodied and Zygoptera are slender, we hypothesized that anisopteran species would have a greater thermal capacity, which should be reflected by stronger temperature–size clines in Anisoptera compared with Zygoptera.

We show that body length in Odonata increases only weakly with increasing latitude. However, this overall pattern stems from strong, 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. Thus, a greater thermoregulatory capacity seems to have promoted the distribution and diversification of select Anisoptera lineages, while most odonate lineages retained their original tropical niche.

## 2 | METHODS

### 2.1 | Body size

We compiled body size data from measurements of museum specimens and from the literature for 2802 odonate species world-wide. For the main analyses, we used only data of body length for adult male individuals but mobilized other proxies of body size, if available, for imputation of the body length and supplementary analysis of differences in body shape between Anisoptera and Zygoptera. Specifically, we measured the body and hindwing length (excluding terminal appendages) from images of 724 individuals of African odonates provided by the Naturalis Biodiversity Center (RHNM) and 487 specimens of African species from the Senckenberg Natural History Museum (SNHM). 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. The body area and body length data from image-based measurements of 1146 individuals were used to test for the difference in the body shape of both suborders. An additional 3612 length measurements were extracted from species descriptions provided in 19 literature and two internet sources (Supporting Information Table S1). Owing to sexual dimorphism, we did not use females in our study if measurements from the literature differentiated between sexes. If sources reported descriptive body size statistics, we collected the minimum and maximum values to aid the integration of data across sources. For 305 individuals, we predicted the body length from the provided hindwing length with a linear mixed-effects model that included a random slope for genus nested in family and suborder ( $n = 810$ , conditional  $R^2 = .92$ ). Finally, the 5128 individual measurement values (1909 singletons, including those where only average values were provided) of 2802 species were aggregated to average values of body length (“body size” hereafter) per species. In our dataset, 719 species have a temperate-centred distribution and 1753 species a tropic-centred distribution (temperate latitude,  $>23.27^\circ$ ; tropical latitude,  $<23.27^\circ$ ).

### 2.2 | Distribution data

We combined two types of distributional information: expert range maps and ranges derived from intersections of occurrence records with the terrestrial ecoregions of the world. We downloaded expert range maps from IUCN.org (IUCN, 2021) and digitized range maps that cover the entire ranges of European odonates from Boudot

and Kalkman (2015). The data were taxonomically harmonized and intersected with grid cells of c.  $100\text{km} \times 100\text{km}$  [military grid reference system (mgrs)]. However, many of the IUCN range maps were incomplete or were delineated by political borders instead of factual species ranges (Hughes et al., 2021). Except for the range maps from the study by Boudot and Kalkman (2015), we used ecoregional ranges to extend and complete the dataset characterizing the distribution (Pinkert, Sica, et al., 2022; Rocha-Ortega et al., 2020).

To generate ecoregional ranges, spatially cleaned and taxonomically harmonized occurrence records were taken from the study by Sandall et al. (2022; originally downloaded from GBIF.org, 8 July 2021, DOI: <https://doi.org/10.15468/dl.tc7q68>), which were based on data from the Global Biodiversity Information Facility (GBIF) and the African Dragonflies and Damselflies Online database (<http://addo.adu.org.za/>). The cleaning of the data included taxonomic harmonization of species names with the most up-to-date taxonomy (Paulson et al., 2021) and the removal of duplicate entries based on coordinates, records from marine areas, common coordinate placeholders and spatial outliers, in addition to records close to GBIF institutions and country centres. Using the country-level checklist of Sandall et al. (2022), records  $>1000\text{km}$  away from a country of known occurrence were removed from the dataset, except when the number of outlier records per country for a species was equal to or greater than the number of countries from these records. For more details on the cleaning methods, see Pinkert, Barve, et al. (2022), and for details on how many species and records were removed during the cleaning process, see Sandall et al. (2022). Subsequently, occurrence records intersecting with expert maps were removed. The remaining records were intersected with a layer of the global terrestrial ecoregions (Dinerstein et al., 2017; downloaded from OneEarth.org, n.d.). These ecoregional ranges were then intersected with our equal-area grid. We used ecoregions as a broader definition of species ranges because 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 (Pinkert, Sica, et al., 2022). Finally, we pooled the gridded expert and ecoregional species ranges and removed duplicate cell-species combinations and cells with  $>50\%$  water (i.e., with  $>50\%$  of the values being not available in the mean annual temperature layer). The final distribution dataset included 5233 (83%) of all 6322 currently accepted Odonata species (Sandall et al., 2022), covering 2802 species with associated body size data.

### 2.3 | Environmental data

Based on the predictions of Bergmann's rule and the resource availability rule, we used two variables associated with geographical 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](http://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., 2022).

## 2.4 | 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 tree based on the most recent taxonomic data and phylogenetic inferences of internal nodes (Supporting Information 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 the study by Letsch et al. (2016). We treated the monotypic genus *Epiophlebia* (family Epiophlebiidae, suborder Anisozygoptera) as Anisoptera because it is morphologically distinct from (similar fore- and hindwings) but phylogenetically closely related to Anisoptera (Bybee et al., 2021). 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 for all species using the function "multi2di", and branch length was calculated using Grafen's method (Grafen, 1989). Corresponding functions are provided in the R package "ape" (Paradis et al., 2004). For the final analyses, we pruned the tree to include only species with corresponding body length data.

Pagel's  $\lambda$  (Pagel, 1999), calculated for the body size of species of the two suborders separately with the function "phylosig" of the R package "phytools" (Revell, 2017), was .98 in Anisoptera and .99 in Zygoptera. Because of this very strong phylogenetic signal in the body size of odonates, we partitioned the total variance of average species body size into a phylogenetic component and a specific component, using Lynch's comparative method (Lynch, 1991) in the R package "ape" (Paradis et al., 2004). The different aspects of body size variation in species-level and assemblage-level analyses (i.e., averaged across species co-occurring within a 100 km × 100 km grid cell) are hereafter called "raw" (unpartitioned), "P component" and "S component", respectively. The P component, which explained 42% of the (raw) body size variation in Anisoptera and 39% in Zygoptera, represents the variation in body size predicted by the phylogenetic relationships between species. The S component represents residuals from these predictions, hence the species-specific deviation from the phylogenetically predicted part. The P component can be interpreted as the outcome of long-term evolutionary processes, whereas the S component indicates recent adaptations and includes plastic variation (Lynch, 1991).

## 2.5 | Spatial autocorrelation

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

Spatial autocorrelation in the residuals of linear regression models is a ubiquitous feature of macroecological patterns (Dormann et al., 2007). This non-independence of neighbouring grid cells can lead to an overestimation of the degrees of freedom, hence to false parameter estimates and model inference. From correlograms constructed using the R package "ncf", we observed significant spatial autocorrelation between the residuals of the linear regression models of body size (raw, P component and S component) and environmental predictors (Supporting Information Figure S4). We therefore 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.

## 2.6 | Statistical analysis

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

To elucidate the mechanisms of body size variation in Anisoptera and Zygoptera, we conducted analyses at both the species and assemblage levels. 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 and for its P and S components for both approaches.

Species-level responses were analysed using multiple regressions, with interaction terms of environmental factors and with family as a predictor to account for idiosyncrasies of the families. 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 environment-trait

**TABLE 1** Assemblage-level multiple regressions between  $\log_{10}$ -transformed body length (a proxy for body size) and environmental variables with a spatial dependency weight (spatial autoregressive model, SAR).

Suborder	Dependent variable	Predictor	Estimate	SE	z-value	p-value	R <sup>2</sup>
Overall	Average body size	MAT	$-4.52 \times 10^{-2}$	$\pm 5.20 \times 10^{-4}$	-87.10	<.001	
		EVI	$1.62 \times 10^{-2}$	$\pm 3.72 \times 10^{-4}$	43.42	<.001	
		Elev	$-1.11 \times 10^{-2}$	$\pm 2.66 \times 10^{-4}$	-42.13	<.001	
Anisoptera	Average body size	MAT	$-5.84 \times 10^0$	$\pm 5.85 \times 10^{-2}$	-99.82	<.001	
		EVI	$9.13 \times 10^{-1}$	$\pm 4.31 \times 10^{-2}$	21.20	<.001	.51
		Elev	$-1.51 \times 10^0$	$\pm 3.03 \times 10^{-2}$	-49.90	<.001	
	P component	MAT	$-4.06 \times 10^0$	$\pm 3.42 \times 10^{-2}$	-118.71	<.001	
		EVI	$-1.92 \times 10^{-1}$	$\pm 2.74 \times 10^{-2}$	-7.01	<.001	
		Elev	$-1.12 \times 10^0$	$\pm 1.91 \times 10^{-2}$	-58.70	<.001	
	S component	MAT	$-1.06 \times 10^0$	$\pm 3.25 \times 10^{-2}$	-32.50	<.001	
		EVI	$8.03 \times 10^{-1}$	$\pm 2.17 \times 10^{-2}$	36.92	<.001	.28
		Elev	$-3.27 \times 10^{-1}$	$\pm 1.47 \times 10^{-2}$	-22.22	<.001	
Zygoptera	Average body size	MAT	$6.21 \times 10^{-1}$	$\pm 3.10 \times 10^{-2}$	20.01	<.001	
		EVI	$1.78 \times 10^0$	$\pm 3.01 \times 10^{-2}$	58.92	<.001	
		Elev	$8.50 \times 10^{-1}$	$\pm 1.99 \times 10^{-2}$	42.75	<.001	.35
	P component	MAT	$2.50 \times 10^{-1}$	$\pm 3.47 \times 10^{-2}$	7.19	<.001	
		EVI	$1.57 \times 10^0$	$\pm 2.39 \times 10^{-2}$	65.61	<.001	
		Elev	$8.09 \times 10^{-1}$	$\pm 1.72 \times 10^{-2}$	46.79	<.001	
	S component	MAT	$-5.90 \times 10^{-3}$	$\pm 2.34 \times 10^{-1}$	-0.25	.8011	
		EVI	$2.95 \times 10^{-1}$	$\pm 1.33 \times 10^{-2}$	22.09	<.001	
		Elev	$-3.69 \times 10^{-2}$	$\pm 9.40 \times 10^{-3}$	-3.92	<.001	

Note: The dataset (2652 species and 17,605 assemblages) was divided into Anisoptera (1182 species and 17,476 assemblages) and Zygoptera (1470 species and 15,650 assemblages) to account for differences in body shape. The phylogenetic (P) component is the phylogenetically predicted part of body length variation, and the specific (S) component represents its deviation. For results of ordinary least squares models, see the Supporting Information (Table S3).

Abbreviations: Elev, elevation; EVI, annual enhanced vegetation index (productivity); MAT, mean annual temperature; pseudo- $R^2$ ,  $R^2$  values based on maximum likelihood (Nagelkerke).

relationships that might result from pseudo-replications of taxa and regions. To avoid basing our conclusions on confounding taxonomic and spatial factors, we focused 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.

In species-level analyses, families with <10 species (i.e., 25 of 46 families) were excluded, leaving 1470 anisopteran species and 1182 zygoteran species. In assemblage-level analyses, grid cells with fewer than five species were excluded to avoid the effect of low sample size on average estimation (Pinkert et al., 2017; Supporting Information Figure S5), leaving 1550 anisopteran species and 1252 zygoteran species. To improve the robustness of our results, we removed regions from our dataset where body size was available for <25% of the species, in addition to smaller islands (Supporting Information 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% (2652) and 69% of odonate species and genera (274 Anisoptera and 200

Zygoteran), respectively. All analyses and data processing were conducted using the software R (R Core Team, 2022).

## 3 | RESULTS

### 3.1 | Descriptive results

The body length of all odonate species ranged from 17 to 129 mm. Anisoptera had an average body size of 51 mm, ranging between 19 (*Celithemis martha*) and 118 mm (*Anax tristis*). Zygoptera had an average body size of 41 mm, ranging between 17 (*Africocypha varicolor*) and 129 mm (*Mecistogaster amalia*). Anisoptera had longer bodies than Zygoptera on average ( $r = -.36, F = .59, p < .001$ ). Analysis of a subset of species showed a steeper increase in the body area of Anisoptera with increasing body length compared with Zygoptera (Anisoptera slope  $\pm$  SE,  $4.18 \times 10^{-1} \pm 1.08 \times 10^{-2}$ ; Zygoptera slope  $\pm$  SE,  $2.77 \times 10^{-1} \pm 8.71 \times 10^{-3}$ ;  $R^2 = .72, p < .001$  for both,  $n = 1146$  individual measurements; Supporting Information Figure S6). Using Pagel's  $\lambda$ , we observed a strong phylogenetic signal for body length of odonate

species and for mean temperature, elevation and productivity across species ranges ( $\lambda = .97, .98, .84$  and  $.97$ , respectively).

### 3.2 | Species-level results

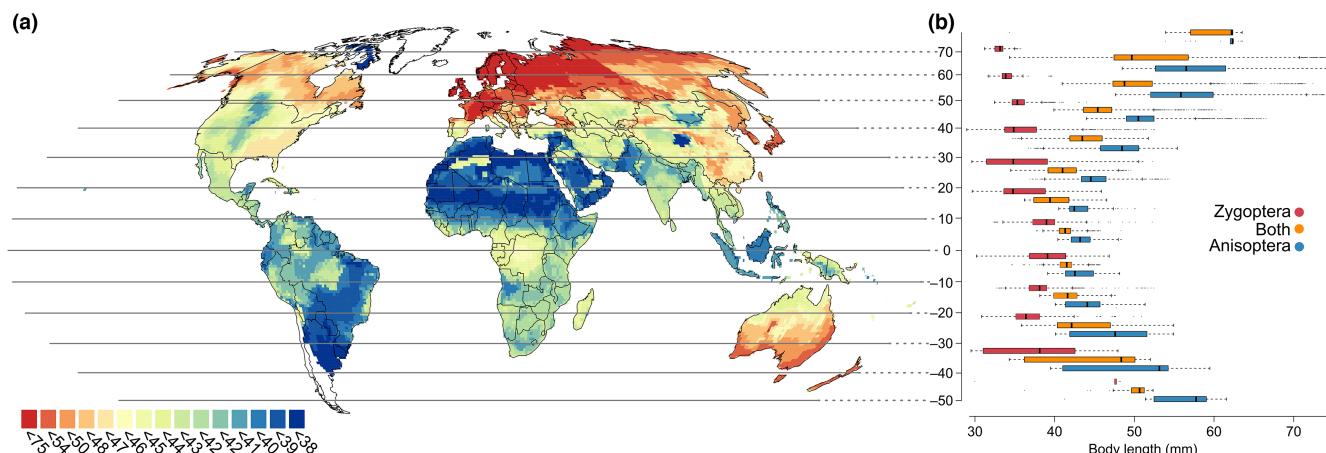
In species-level analysis of the phylogenetically predicted part of body size variation (P component), the body size of anisopteran species was negatively affected by mean annual temperature and elevation ( $R^2 = .02$ ; Supporting Information Table S2). The P component in zygopteran species was positively affected by mean annual temperature ( $R^2 = .01$ ). In the species-level analysis across odonate families, environmental variables collectively explained 44% of body size variation (Supporting Information 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 rule. 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. Three families showed an opposing trend.

### 3.3 | Assemblage-level results

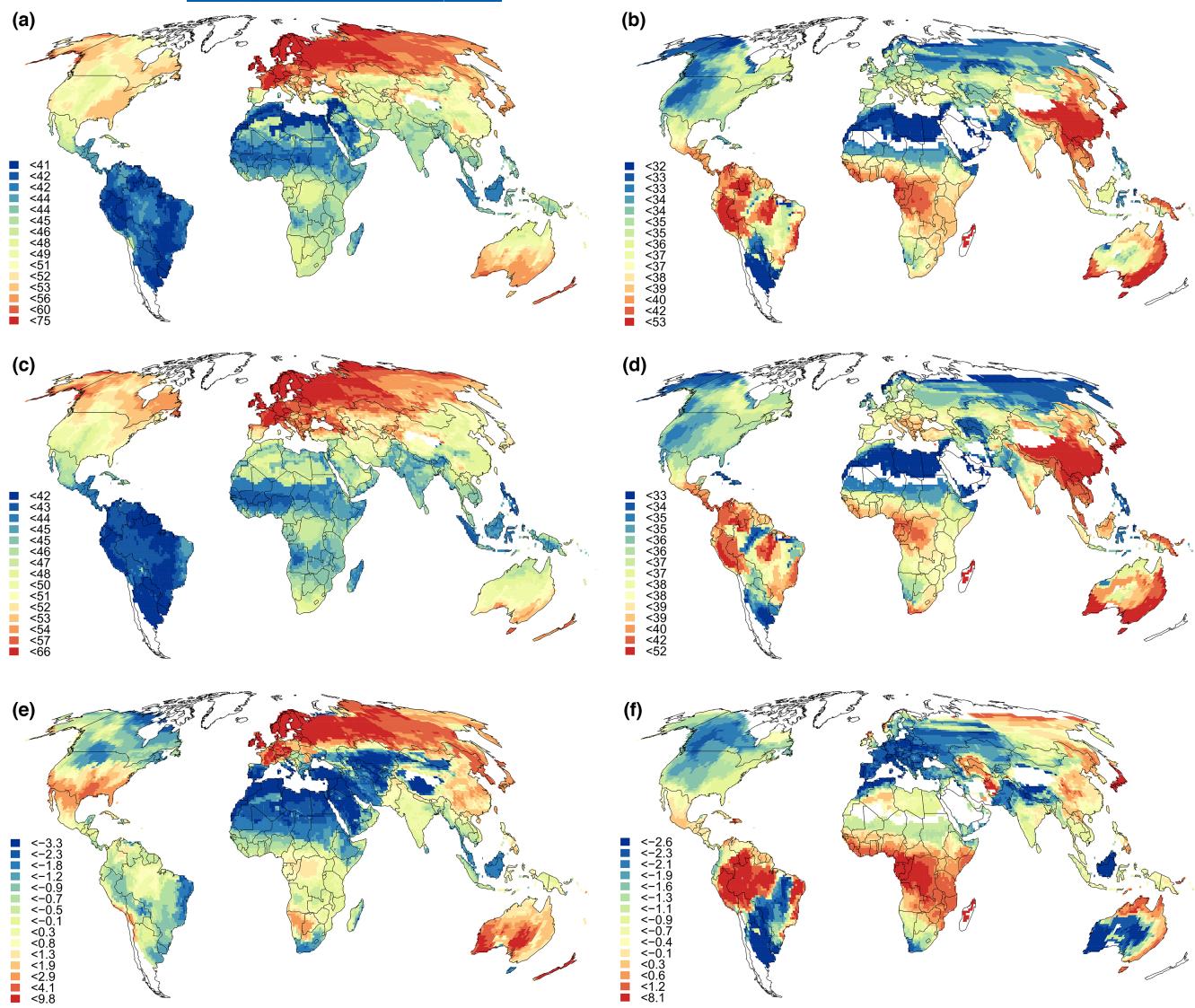
In the assemblage-level analyses, body length generally increased with increasing latitude, and latitude explained 12% of the body size

variation (Figure 1; Supporting Information Table S4). In multiple regression models for all Odonata that included environmental predictors instead of latitude, the body size of assemblages increased with decreasing temperature, increasing productivity and decreasing elevation (Table 1). These three environmental predictors explained 51% of the variation in body size. The effect of productivity (EVI) in multiple regression models was consistent in both Anisoptera and Zygoptera, but 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 increasing elevation. Except for the decrease in body size with increasing productivity in Anisoptera trends were similar but weaker in single compared with multiple regressions (Supporting Information Figure S3).

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 (Supporting Information Table S3). The species richness of both suborders decreased from the equator to the poles (Supporting Information Figure S1a), but the proportion of Anisoptera from the total number of species per assemblage increased with latitude (Figure 3).



**FIGURE 1** (a) The map shows the spatial variation in body length (a proxy for body size) of odonate assemblages (17,605 grid cells of  $100\text{ km} \times 100\text{ km}$ , representing body length values of 2652 species). The map is shown in Mollweide projection, and colour scale intervals follow an equal-frequency classification, ranging from blue (short) to red (long). (b) Horizontal boxplots show the body size range of assemblages across latitudinal bands ( $10^\circ$  intervals). Blue boxplots show the body length of Anisoptera (dragonflies), red boxplots that of Zygoptera (damselflies), and orange boxplots that of both suborders together.

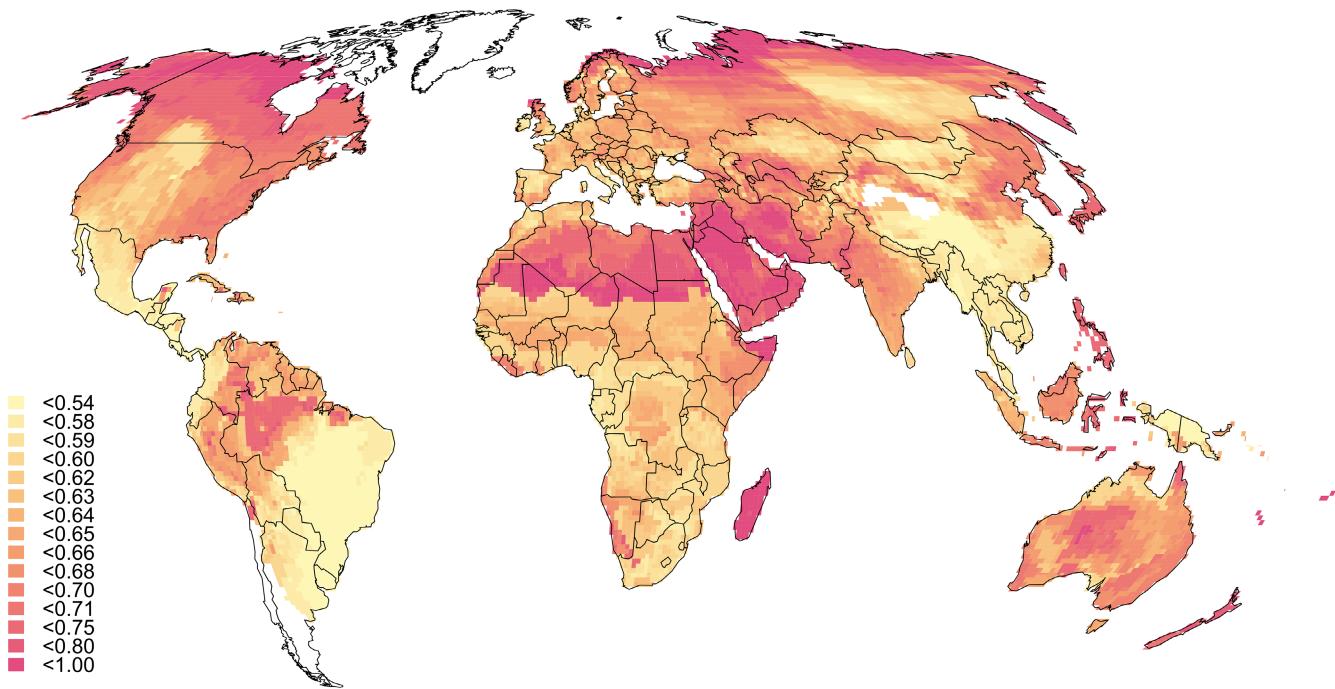


**FIGURE 2** Spatial variation in body length (in millimetres) of (a,c,e) anisopteran assemblages (17,476 grid cells representing 1182 species), and (b,d,f) zygopteran assemblages (15,650 grid cells representing 1470 species). From top to bottom, the maps represent the (a,b) average, (c,d) phylogenetic, 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.

## 4 | DISCUSSION

Our results provide the first global-scale support for the resource availability rule and for thermal niche conservatism in insects. We demonstrate that the interplay of different constraints to size is likely to be of broad ecological and evolutionary significance in ectotherms. In addition, we show that although overall odonates show a Bergmann-like body size pattern, major differences in the temperature-size relationship between the two suborders of Odonata are associated with differences in the body shape and the increasing proportion of dragonflies (Anisoptera) with increasing latitude. In line with Bergmann's rule and the resource availability rule, we find that body size generally increases with decreasing temperature and increasing productivity across odonates. Previous studies on smaller spatial scales 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). These results fuelled doubts about the general validity of mechanistic explanations for ecogeographical patterns in body size otherwise well documented in endotherms. We demonstrate here that the interplay of temperature and productivity renders conclusions misleading that are based solely 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 endotherms (Olson et al., 2009; Santini et al., 2018). Temperature-size relationships are much stronger than latitudinal size gradients and explain a much higher proportion of the variation in body size in odonates. We find that the weak and partly divergent latitudinal size clines in tropical regions and divergent patterns



**FIGURE 3** Spatial variation in the proportion of anisopteran species to the total number of odonate species included in the analysis. Assemblages represent the distributions of 1182 anisopteran and 1470 zygopteran species. Colour scale intervals follow an equal-frequency classification (quantiles), with beige/yellow indicating lower proportions of anisopteran species and pink/red indicating higher proportions. The dataset comprises 17,605 grid cells of 100 km × 100 km (Mollweide projection). Note that the main data source for Amazonia did not include Zygoptera, hence the high proportion of Anisoptera. Sources for all other regions included both suborders.

between the two suborders results from the strong positive effects of resource availability.

Bergmann's rule is one of the oldest theories describing eco-geographical patterns in trait variation and, although formulated originally for endotherms, it has been tested frequently 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 and from the poor representation of environmental gradients underlying local latitudinal clines (Shelomi, 2012). We show that assemblages of odonates 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 is the most important predictor of the geographical pattern of body size variation and results in a moderately strong Bergmann-like latitudinal gradient. Consistent with evidence from experiments (Atkinson & Sibly, 1997; Brakefield & Willmer, 1985) and studies across local or continental scales (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 suborders of odonates, in addition to conflicting reports of elevational and latitudinal patterns (Heidrich et al., 2021; Horne et al., 2018; Shelomi, 2012), indicate that a substantial part of body size variation is caused by additional processes.

Our results indicate that both size-based thermoregulation and resource constraints on growth 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 converse a Bergmann-like pattern due to the effects of decreasing productivity from the equator to the poles (Figure 2; Supporting Information Table S4): Larger species seem to have a thermoregulatory advantage in colder regions, whereas 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 latitudinal (and elevational) 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), also suggest that resource-based size constraints apply throughout the food web, from primary producers to consumers and predators (see also Ohlberger, 2013;

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.

Owing to the lack of other pertinent size estimates accounting for the major differences in body shape between Anisoptera and Zygoptera, we considered body length as a measure of size but analysed data separately for the two suborders. An image-based analysis of 1146 species confirmed that, when accounting for body length, Anisoptera had larger bodies than Zygoptera, which has important physiological consequences (Supporting Information Figure S6). Given that a larger body increases heat absorption and heat retention, these results suggest that Anisoptera should have a greater thermal capacity than Zygoptera (Castillo-Pérez et al., 2022). Our results reconcile previous findings of a critical threshold in body size, beyond which size-based thermoregulation is less effective (Clusella-Trullas et al., 2007; Schweiger & Beierkuhnlein, 2016). We propose that integrating both body shape and size into the analysis of temperature–size responses might help to resolve inconsistent experimental (Forster et al., 2012) and macroecological results (Horne et al., 2018).

Our finding that thermoregulation shapes the geographical pattern of anisopteran but not zygopteran assemblages also suggests that the slender-bodied Zygoptera rely on an alternative thermoregulatory mechanism for heat gain. During the last decade, studies on a broad spectrum of ectotherm taxa, including beetles, butterflies, moths and odonates, have provided strong and consistent support for the role of colour-based heat gain (Heidrich et al., 2021; Pinkert & Zeuss, 2018; Schweiger & Beierkuhnlein, 2016). These studies highlight that ectotherms are generally darker coloured in colder and lighter coloured in warmer regions (Clusella-Trullas et al., 2007; Schweiger & Beierkuhnlein, 2016). Also the colour lightness and body size of species has been found to interact, with smaller species varying more in their colour lightness than larger species. Our results suggest a greater importance of colour-based versus size-based thermoregulation in the smaller and more slender Zygoptera. However, a rigorous test of this hypothesis would require a much greater coverage of data on species body area or body volume and colour lightness, which is currently unavailable. We therefore encourage further investigations of the interactions between and differences in the relative importance of size- and colour-based thermoregulation across regions, scales and taxa.

In addition to its importance in shaping their contemporary distribution, phylogenetically comparative analyses and distributional anomalies also indicate that niche conservatism has greatly influenced the distribution and diversification of odonates. Although Odonata are globally distributed, the greatest number of families and genera are found in tropical climates, where the group originated (Bybee et al., 2021; Sandall et al., 2022). We found that the relatively few lineages in extreme climates (both desert and arctic regions) are almost exclusively anisopteran (Figure 3). In addition, we demonstrated that the phylogenetically predicted component 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;  $R^2 = .68$  and  $.38$ , 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 ( $\lambda$  in mean temperature =  $.98$ ,  $\lambda$  in mean elevation =  $.84$ ). 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.

## 5 | 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 have shown that temperature and productivity explain 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 interpretations based on geographical clines alone. The strong similarities in the documented effects of temperature and resource availability between endotherms and ectotherms, in addition to 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, strong environment-size 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 elevations, but because many are at the geographical limits of their distribution, increasing temperatures are likely to negatively 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 be likely to affect community composition and ecosystem function. Incorporating phylogenetic information and environment-trait interactions is therefore crucial to inform and improve forecasts of species responses to climate change. Our study represents important progress towards mechanistic predictions of spatio-temporal 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 recognize that future studies should use further trait information from the treasure trove of resources that natural history collections and literature provides. Where such efforts would most effectively complement existing data for odonates can be seen in the coverage map presented in this study.

## AUTHOR CONTRIBUTIONS

L.A.M. compiled the data and led the analyses. S.P. designed the study. S.P. assisted in analysing the data and led the writing of the manuscript with input from L.A.M., R.B. and C.H. All authors contributed substantially to revisions.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data that support our main findings is available via DOI: <https://doi.org/10.5061/dryad.hmgqnkmg>.

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## BIOSKETCH

**Laura Anna Mähn** is an ecologist and biogeographer with a broad interest in large-scale functional ecology, evolutionary biology and conservation prioritization in insects. Her work focuses on global patterns of trait variation in insects.

## SUPPORTING INFORMATION

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

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