

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

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## Abstract

Latitudinal body size-clines are primarily discussed in the context of thermoregulation, *sensu* Bergmann. However, body size patterns are ambiguous in ectotherms and this heterogeneity remains poorly understood. We hypothesised that the contrasting effects of thermoregulation and resource constraints obscure latitude–size relationships. Using data for 43% of all odonate species, we tested whether body size increases with decreasing temperature and increasing productivity in phylogenetically and spatially comparative analyses. We found strong but contrasting effects for temperature between Anisoptera and Zygoptera and consistent positive effects for productivity that explained 35%–57% of body size variation. 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 results and weak latitude–size relationships. Our results reinforce the importance of body size as a determinant of species distributions and responses to climate change.

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

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12

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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.

## 41 INTRODUCTION

42 A mechanistic understanding of the variation in functional traits is crucial for understanding the drivers  
43 of species distribution (Lawton 1999; McGill *et al.* 2006; Pinkert & Zeuss 2018; White *et al.* 2007) and  
44 predicting biological responses to climate change (Buckley & Kingsolver 2012; MacLean & Beissinger  
45 2017). Trait-based analyses have provided important insights into the mechanisms of community  
46 assembly, population dynamics, and range shifts, particularly for endotherms (Bruehlheide *et al.* 2018;  
47 de los Ríos *et al.* 2018; Estrada *et al.* 2016; Kraft *et al.* 2015). However, the thermal sensitivity of  
48 ectotherms differs fundamentally from that in endotherms (Atkinson & Sibly 1997). For example,  
49 insects rely on ambient temperature, not metabolically produced heat, to maintain optimal body  
50 temperature and support development, locomotion, and reproduction (Gillooly *et al.* 2001, 2002; Huey  
51 & Kingsolver 1989). This fundamental physiological difference can lead to biogeographical patterns  
52 in response to climate change that contrast those of endotherms (Atkinson & Sibly 1997; Buckley &  
53 Kingsolver 2012). Although the relationship between the ambient environment and phenotypic traits  
54 are well-documented through local scale and experimental studies (Atkinson & Sibly 1997; Lawton  
55 1999; Whitman 2008), the extent to which they shape the distributions of ectotherms across larger  
56 spatial and taxonomic scales remains poorly understood.

57         Body size is associated with several physiological and ecological characteristics in animals,  
58 including metabolic rates, phenology, fecundity, and range size, with major consequences for species  
59 distribution and abundance (Gillooly *et al.* 2001, 2002; Honěk 1993; McCulloch *et al.* 2016; White *et al.*  
60 *et al.* 2007; Whitman 2008). The body size of animals often increases along elevational or latitudinal  
61 gradients (Meiri & Dayan 2003). This pattern, *sensu lato* Bergmann's rule, is based on the principle  
62 that larger bodies have a smaller surface-to-volume ratio (greater capacity to retain body heat) than  
63 smaller bodies (Bergmann 1848). Therefore, larger species should have a thermoregulatory  
64 advantage in colder climates, while smaller species have a reduced risk of overheating in warmer  
65 climates. Bergmann's rule has been studied extensively in endotherms, but few studies have  
66 investigated geographical patterns in the body size of ectotherms. Among studies on insects, the  
67 majority of studies revealed no latitudinal cline in body size and the remaining studies report  
68 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

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

105

## 106 **METHODS**

### 107 **Body size**

108 We compiled body size data from measurements of museum specimens and from the literature for  
109 2,803 odonate species worldwide. As proxies of body size, we measured the body and hindwing  
110 length (excluding appendices) from images of 724 individuals of African odonates provided by the  
111 Naturalis Biodiversity Center (RHNM, Leiden, The Netherlands) and 487 specimens of African species  
112 from the Senckenberg Natural History Museum (SNHM, Frankfurt, Germany). For the images of  
113 African species from the Naturalis Biodiversity Center, European species from Dijkstra and Lewington  
114 (2006), and North American species from Needham *et al.* (2000), we calculated the body length,  
115 hindwing length, and body area as previously described (Pinkert *et al.* 2017; Zeuss *et al.* 2017) using  
116 the R-package 'png' (Urbanek 2013). In short, the number of pixels of the body from the head to the  
117 distal end of the abdomen, that of the hindwing from its base to the tip, and the number of all pixels of  
118 the body were calculated. The pixel estimates were transformed to metric units through the product  
119 of the scale (provided or measured on the images) and image resolution; 3,612 additional length  
120 measurements were extracted from 19 literature and 2 internet sources (Table S1). To account for  
121 variation related to sexual dimorphism, we did not use females in this study if measurements from  
122 literature differentiated between sexes. If sources reported descriptive body size statistics, we used  
123 the minimum and maximum values instead of means to aid the integration of data across sources.  
124 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.

128

### 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

153 developed based on ecological characteristics and expert knowledge, and therefore provide an  
154 advantage over traditional methods, such as alpha-hulls, convex hulls, or simple equidistant buffers  
155 around occurrence records. Finally, we pooled the gridded expert and ecoregional species ranges  
156 and removed duplicated cell–species combinations as well as cells with >50% water (i.e. with >50%  
157 of the values being 'NA' in the mean annual temperature layer). The final distribution dataset included  
158 5,233 (83%) of 6,322 odonate species.

159

### 160 **Environmental data**

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

169

### 170 **Phylogenetic autocorrelation**

171 Phylogenetic bias in the analysis of subsets of species challenges the statistical assumption that all  
172 data points are independent. To account for this phylogenetic autocorrelation and in the absence of a  
173 complete global phylogeny for Odonata, we constructed a super-tree based on the most recent  
174 taxonomic data and phylogenetic inferences of internal nodes (Figure S2). Family-level relationships  
175 were resolved based on inferences from Bybee *et al.* (2021) and the relationships between the genera  
176 of Anisoptera were resolved based on information from Letsch *et al.* (2016). We added species to the  
177 respective genera in the tree and randomly resolved the intra-genus relationships using the R-  
178 package 'phytools' (Revell 2017). Multifurcations in the tree were randomly resolved using the function  
179 '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 ( $\lambda$ , 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

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

213

## 214 **Statistical analysis**

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

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

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

236 robustness of our results, we removed regions from our dataset where body size was available for  
237 <25% of the species as well as smaller islands (Figure S1). Note that only small regions in central  
238 Amazonia and the southern Andes had a species coverage <50% (global coverage was >75%). The  
239 exclusion criteria reduced the number of species in our assemblage-level analyses to 43% (2,625)  
240 and 69% of odonate species and genera (274 Anisoptera and 200 Zygoptera), respectively. All  
241 analyses and data processing were conducted using the software R (R Core Team 2021).

242

## 243 RESULTS

244 The body length of all odonate species ranged from 17 mm to 129 mm. Anisoptera had an average  
245 body size of 51 mm, ranging between 19 mm (*Celithemis martha*) and 118 mm (*Anax tristis*).  
246 Zygoptera had an average body size of 41 mm, ranging between 17 mm (*Africocypha varicolor*) and  
247 129 mm (*Mecistogaster amalia*). Anisoptera had longer bodies than Zygoptera on average ( $r = -0.36$ ,  
248  $F = 0.59$ ,  $p < 0.001$ ). Analysis of a subset of species showed a steeper increase in the body area of  
249 Anisoptera with increasing body length compared to Zygoptera (Anisoptera slope  $\pm$  SE:  $4.18 \times 10^{-1} \pm$   
250  $1.08 \times 10^{-2}$ ; Zygoptera slope  $\pm$  SE:  $2.77 \times 10^{-1} \pm 8.71 \times 10^{-3}$ ;  $R^2 = 0.72$ ,  $p < 0.001$  for both,  $n = 1,146$   
251 individual measurements; Figure S6).

252 Using Pagel's lambda model, we observed a strong phylogenetic signal for body size as well  
253 as mean temperature, elevation, and productivity across species' ranges ( $\lambda = 0.97, 0.98, 0.84$ , and  
254  $0.97$ , respectively). In species-level analysis of the phylogenetically predicted part of body size  
255 variation (P component), the body size of anisopteran species was negatively affected by mean  
256 annual temperature and elevation ( $R^2 = 0.02$ ; Table S2). The P component in zygopteran species was  
257 positively affected by mean annual temperature ( $R^2 = 0.01$ ). At the family level, environmental  
258 variables collectively explained 44% of body size variation (Figure S7). Body size variation in 5 (1  
259 Anisoptera, 4 Zygoptera) of 21 families was not influenced by environmental factors, but these families  
260 were represented by relatively few species. Except for two families, body size trends in the remaining  
261 families either followed the predictions of Bergmann or that of the resource availability hypothesis. We  
262 observed differences in body size responses between and within Anisoptera and Zygoptera.  
263 Anisoptera generally showed stronger and more consistent responses to temperature than Zygoptera.

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

269 In the assemblage-level analyses, body length generally increased with increasing latitude,  
270 and latitude explained 12% of the body size variation (Figure 1, Table S4). In multiple regression  
271 models that included discrete environmental predictors instead of latitude, average assemblage body  
272 size increased with decreasing temperature, decreasing productivity, and increasing elevation (Table  
273 1, Figure S3). These three environmental predictors explained 51% of the variation in body size. While  
274 the effect of productivity (EVI) was consistent in both Anisoptera and Zygoptera, the effect of  
275 temperature differed between the suborders. The body size of anisopteran assemblages increased  
276 with decreasing mean annual temperature and decreasing elevation. Conversely, the body size of  
277 zygopteran assemblages increased with increasing mean annual temperature and decreasing  
278 elevation.

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

291

## 292 **DISCUSSION**

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

309 Bergmann's rule is one of the oldest theories describing ecogeographical patterns in trait  
310 variation and, although originally formulated for endotherms, it has been frequently tested in  
311 ectotherms (Horne *et al.* 2018; Klok & Harrison 2013; Shelomi 2012). Contradictions to the original  
312 hypothesis in insects and other ectotherms were argued to result from sample biases towards  
313 temperate regions and taxa as well as the poor representation of environmental gradients underlying  
314 local latitudinal clines (Shelomi 2012). We showed that assemblages of Odonata in colder climates,  
315 including areas with a lower mean annual temperature and/or higher elevation, are generally  
316 composed of, on average, larger species (Table 1). Mean annual temperature was the most important  
317 predictor of the geographical pattern of body size variation and resulted in a moderately strong  
318 Bergmann-like latitudinal gradient. Consistent with evidence from experimental (Atkinson & Sibly  
319 1997; Brakefield & Willmer 1985) and local-scale studies (Heidrich *et al.* 2021; Pinkert *et al.* 2017;

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

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

345 Due to the lack of other pertinent size estimates accounting for the major differences in the  
346 body shape between Anisoptera and Zygoptera, we considered body length as a measure of size but  
347 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

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

387

## 388 **CONCLUSIONS**

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

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

415

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423

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602 **TABLES**

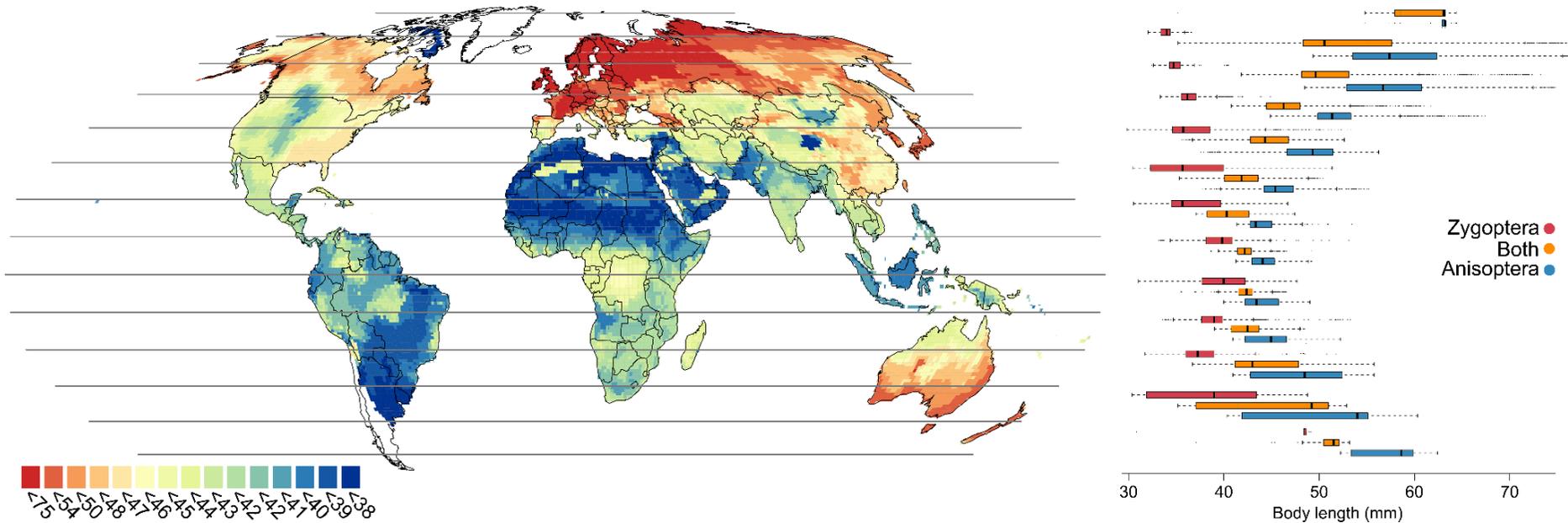
603 **TABLE 1** Assemblage-level multiple regressions between  $\log_{10}$ -transformed body length (a proxy for  
604 body size) and environmental variables with a spatial dependency weight (spatial autoregressive  
605 model, SAR). The dataset (2,652 species and 17,605 assemblages) was divided into 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	<i>p</i>	<i>R</i> <sup>2</sup>
Overall	Average body size	MAT	$-4.52 \times 10^{-2}$	$\pm 5.20 \times 10^{-4}$	-87.10	<0.001	
		EVI	$1.62 \times 10^{-2}$	$\pm 3.72 \times 10^{-4}$	43.42	<0.001	0.51
		Elev	$-1.11 \times 10^{-2}$	$\pm 2.66 \times 10^{-4}$	-42.13	<0.001	
Anisoptera	Average body size	MAT	$-5.84 \times 10^0$	$\pm 5.85 \times 10^{-2}$	-99.82	<0.001	
		EVI	$9.13 \times 10^{-1}$	$\pm 4.31 \times 10^{-2}$	21.20	<0.001	0.57
		Elev	$-1.51 \times 10^0$	$\pm 3.03 \times 10^{-2}$	-49.90	<0.001	
	P component	MAT	$-4.06 \times 10^0$	$\pm 3.42 \times 10^{-2}$	-118.71	<0.001	
		EVI	$-1.92 \times 10^{-1}$	$\pm 2.74 \times 10^{-2}$	-7.01	<0.001	0.68
		Elev	$-1.12 \times 10^0$	$\pm 1.91 \times 10^{-2}$	-58.70	<0.001	
		S component	MAT	$-1.06 \times 10^0$	$\pm 3.25 \times 10^{-2}$	-32.50	<0.001
Zygoptera	Average body size	EVI	$8.03 \times 10^{-1}$	$\pm 2.17 \times 10^{-2}$	36.92	<0.001	0.28
		Elev	$-3.27 \times 10^{-1}$	$\pm 1.47 \times 10^{-2}$	-22.22	<0.001	
		MAT	$6.21 \times 10^{-1}$	$\pm 3.10 \times 10^{-2}$	20.01	<0.001	
	P component	EVI	$1.78 \times 10^0$	$\pm 3.01 \times 10^{-2}$	58.92	<0.001	0.35
		Elev	$8.50 \times 10^{-1}$	$\pm 1.99 \times 10^{-2}$	42.75	<0.001	
Zygoptera	P component	MAT	$2.50 \times 10^{-1}$	$\pm 3.47 \times 10^{-2}$	7.19	<0.001	
		EVI	$1.57 \times 10^0$	$\pm 2.39 \times 10^{-2}$	65.61	<0.001	0.38
		Elev	$8.09 \times 10^{-1}$	$\pm 1.72 \times 10^{-2}$	46.79	<0.001	
	S component	MAT	$-5.90 \times 10^{-3}$	$\pm 2.34 \times 10^{-1}$	-0.25	0.8011	
		EVI	$2.95 \times 10^{-1}$	$\pm 1.33 \times 10^{-2}$	22.09	<0.001	0.36
		Elev	$-3.69 \times 10^{-2}$	$\pm 9.40 \times 10^{-3}$	-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).

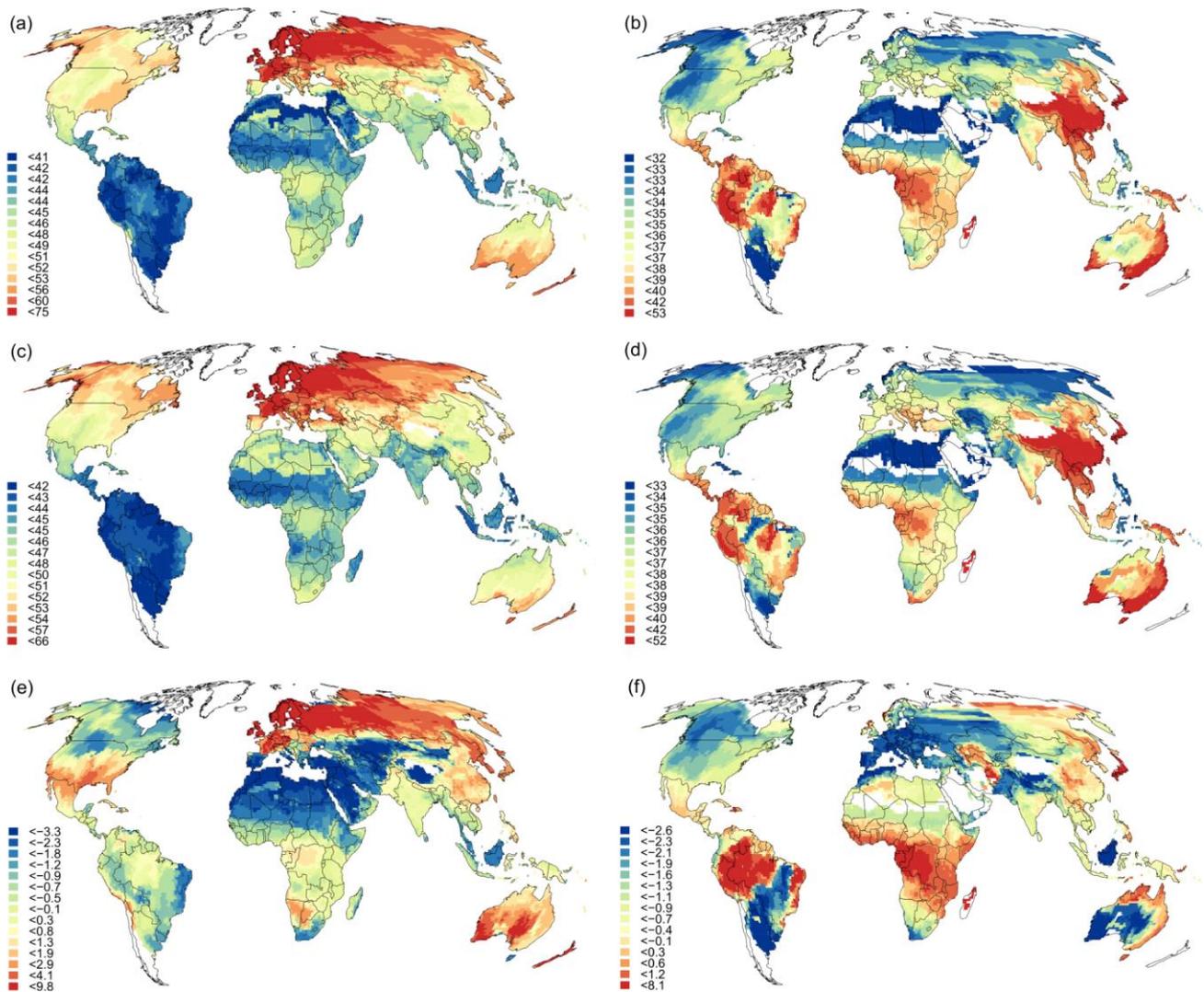
612 FIGURES

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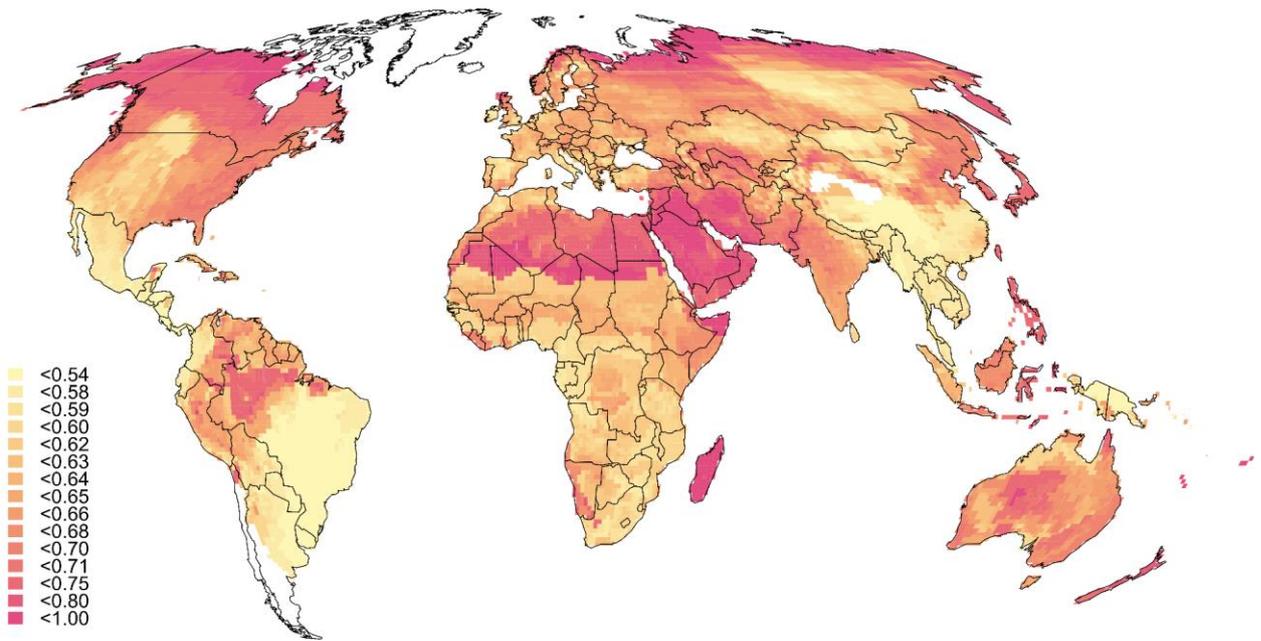
614

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.



620

621 **FIGURE 2** Spatial variation in body length (mm) of (a,c,e) anisopteran assemblages (17,476 grid cells  
 622 representing 1,182 species), (b,d,f) zygopteran assemblages (15,650 grid cells representing 1,470  
 623 species). From top to bottom, the maps represent the (a,b) average, (c,d) phylogenetic, and (e,f)  
 624 specific components of body size variation. Maps are shown in a Mollweide projection. Colour scale  
 625 intervals follow an equal-frequency classification, ranging from blue (short) to red (long). The  
 626 phylogenetic (P) component is the phylogenetically predicted part of body length variation, and the  
 627 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.