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# **Ice age, current climate, habitat availability, and the diversity of European dragonflies and damselflies**

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# 1 Ice age, current climate, habitat availability, and the diversity of European 2 dragonflies and damselflies

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## 8 **Abstract**

9 Several studies show that species richness patterns are determined by current climate and Pleistocene  
10 climatic oscillations. Additionally, habitat availability is an important driver of current species  
11 diversity, especially in aquatic ecosystems where lentic (standing water) and lotic (running water)  
12 habitats play distinct roles in species composition and richness. Odonates, an order of aquatic insects,  
13 exhibit distinct adaptive traits in response to climate and to lentic and lotic habitats. In this work, we  
14 study the species richness patterns of European odonates and the influence of past climate, current  
15 climate, and habitat availability. The study covers 124 species distributed across Europe (excluding  
16 Russia and all European islands except Great Britain and Ireland), divided into three groups: Odonata,  
17 lentic species, and lotic species. We analyzed their diversity in Northern and Southern Europe,  
18 divided according to the 0°C Isotherm of the Last Glacial Maximum (21,000 years ago), using data  
19 on current and Last Glacial Maximum climate (temperature and precipitation), as well as on habitat  
20 data from land cover and hydrology GIS maps. Our results suggest that the species richness patterns  
21 of dragonflies and damselflies are largely determined by the water-energy balance, with temperature  
22 influencing the decline in richness towards the south and precipitation determining the decline  
23 towards the north. Past climate oscillations affect species richness in southern and northern Europe.  
24 Habitat availability also influences odonate diversity, though to a lesser extent, with a positive  
25 correlation between lotic habitat availability and lotic species richness. In contrast, lentic species  
26 show a negative correlation with the availability of lentic habitats.

## 27 **Highlights**

- 28 • We evaluate whether the variation of dragonfly species richness across Europe is  
29 determined by current climate, the climatic conditions during the last ice age, and the  
30 availability of freshwater habitats.
- 31 • Dragonfly species richness is higher in Central Europe and decreases both northwards and  
32 southwards from there. These variations are primarily determined by current and past  
33 climate, and to a lesser extent by habitat availability.
- 34 • Temperature determines the southward decrease in species richness, while the northward  
35 decrease is so by precipitation.
- 36 • Ice age climate has a greater influence than current climate throughout Europe, while in  
37 southern Europe current climate has a greater influence, particularly for species related to  
38 standing water habitats.
- 39 • Species richness is higher in areas with more rivers and water courses, while the relationship  
40 with the availability of standing water habitats is more nuanced.

41  
42 **Keywords:** contemporary climate, distribution, freshwater animals, glaciations, habitat, history,  
43 odonata, species richness.

## 44 45 **Introduction**

46 The current geographic patterns of diversity have been studied in ecology and biogeography for more  
47 than a century. Hypotheses based on current climate have strong empirical support for a range of taxa.  
48 Among these, the water–energy hypothesis outstands (O’Brien 1998). This hypothesis states that the  
49 main factors shaping diversity gradients change with latitude. At lower latitudes where energy input  
50 is abundant, such as tropical, subtropical, and warm temperate zones, species diversity is mainly  
51 constrained by water availability. Conversely, at higher latitudes, such as polar and boreal zones,

52 environmental energy is the most limiting factor for species diversity (Hawkins et al. 2003, 2005;  
53 Keil et al. 2008). Therefore, this hypothesis predicts a peak of species richness at mid latitudes,  
54 because of the change in the relative importance of energy and water inputs (Hortal et al. 2011;  
55 Calatayud et al. 2016). This hypothesis has been found to be informative for several taxa in the  
56 European continent, including butterflies (Hawkins et al. 2003), amphibians (Rodríguez et al. 2005;  
57 Whittaker et al. 2007), mammals and plants (Whittaker et al. 2007).

58  
59 Despite the importance of current climate in shaping contemporary diversity patterns, historical  
60 climate has been also shown to play an important role. Evidence sustains that current diversity  
61 patterns in the northern hemisphere also hold the geographical signal left by Pleistocene cold  
62 climates. Indeed, a signature of the Last Glacial Maximum (herein LGM; 21,000 yr BP) on current  
63 diversity patterns has been found in trees (Svenning and Skov 2007b), amphibians and reptiles  
64 (Araújo et al. 2008), mammals (Santos et al. 2020), and different groups of beetles (Hortal et al. 2011,  
65 Calatayud et al. 2016). These studies show a sharp decrease in species diversity towards northern  
66 Europe, which has been suggested to be in part a consequence of the faunal loss experimented during  
67 glacial ages, together with the limitations of most organisms to recolonize it. Therefore, it is  
68 understood that northern assemblages consist of species with high dispersal ability, which enabled  
69 them to recolonize the previously glaciated areas of northern Europe. As a result, the past climate  
70 signal should be weaker in groups that disperse better (Svenning and Skov 2007a, 2007b; Svenning  
71 et al. 2008).

72  
73 Besides large-scale climate gradients and historical climate events, factors such as habitat availability  
74 are also important determinants of current species' diversity (MacArthur, 1964). Habitat availability  
75 can act as a driver of species richness, as higher habitat availability supports larger populations, which  
76 promotes the persistence of more species. Empirical evidence for habitat availability influence on  
77 species diversity has been corroborated for terrestrial taxa including butterflies (Storch et al. 2003),

78 birds (Storch et al. 2003) and *Carabus* beetles (Calatayud et al. 2016). In aquatic ecosystems, habitat  
79 is known to play a crucial role in the life of freshwater organisms due to the relationships between  
80 habitat stability, dispersal capacity, and species distribution patterns (Hof et al. 2008). Aquatic  
81 habitats are divided into lentic (standing water) and lotic habitats (running water), which differ in  
82 their environmental and spatiotemporal configurations (Hof et al. 2006; Dehling et al. 2010). Lentic  
83 habitats are more unpredictable on an evolutionary time scale than lotic habitats (Hof et al. 2008),  
84 which has implications for the evolutionary traits and distribution patterns of aquatic organisms that  
85 depend on these habitats (Hof et al. 2006, 2008). An example of this is that lentic species tend to have  
86 a higher dispersal ability than lotic species (Hof et al. 2006). Consequently, it would be logical to  
87 consider habitat availability as a good predictor of the distribution of aquatic organisms. However,  
88 Dehling et al. (2010) found that habitat availability was a poor indicator of freshwater species  
89 diversity.

90  
91 One such freshwater taxon is Odonata, which includes the suborders Anisoptera (dragonflies) and  
92 Zygoptera (damselflies). A strong association of Odonata distribution with climate has been  
93 demonstrated in several studies (see Hassall 2008; 2015 for a review), coinciding largely to the  
94 contemporary world climatic zones (Kalkman et al. 2008; Beatty et al. 2022). The highest diversity  
95 is found in the tropics, while species richness in the Palaearctic region is relatively low (Kalkman et  
96 al. 2008; Alves-Martins et al. 2019). Within Europe, Odonata species richness is highest in the  
97 western and central regions and decreases towards both the colder conditions of Northern Europe and  
98 the drier environments of the south of the continent (Keil et al. 2008). The northern latitudes of Europe  
99 have a larger proportion of anisopterans (Askew 2004; Boudot and Kalkman 2015) and lentic species,  
100 which are assumed to have higher dispersal abilities (Hof et al. 2006). Conversely, in the southern  
101 latitudes there is a predominance of zygopterans (Askew 2004; Boudot and Kalkman 2015) and lotic  
102 species (Heiser and Schmitt 2010). Pinkert et al. (2018) found a strong signal of LGM in the  
103 contemporary diversity patterns in Europe and argued that differences in composition between

104 northern and southern assemblages are the result of the stronger dispersal ability of lentic species,  
105 which were able to recolonize the previously glaciated areas of northern Europe after LGM.

106

107 Besides the prominent role that historical (Pinkert et al. 2018) and current climate (Termaat et al.  
108 2019) have on the distribution of extant European odonates, the intensification of habitat  
109 transformations over the past few centuries have had a profound impact on the current patterns of  
110 European biodiversity (Santos et al. 2020). As odonates are freshwater insects, they depend on either  
111 lentic or lotic habitats for breeding, egg deposition and larval survival (Corbet, 1999), so habitat  
112 availability is expected to influence their extant distribution and diversity patterns. Although  
113 European Odonata have been hypothesized to respond to current climate (Keil et al., 2008) and  
114 historical climatic oscillations (Pinkert et al. 2018), the complementary role of past climate, current  
115 climate and habitat availability has not been tested yet.

116

117 In this study we aim to disentangle the signatures of habitat availability, past climate and current  
118 climate on the diversity patterns of European Odonata. First, we evaluated the influence of current  
119 climate, past climate changes, and the availability of habitat on these patterns by three complementary  
120 (i.e. non-exclusive) hypotheses: H1 proposes that odonate richness is driven by the current climate's  
121 water-energy balance. If this holds true, we predict (P1) shifts in the drivers of species richness  
122 gradient both southward and northward. Odonate assemblages in the drier southern Europe are  
123 expected to be primarily limited by water availability, whereas northern assemblages in colder  
124 climates will be limited primarily by energy inputs. H2 proposes that past climate influence Odonata  
125 species richness. If confirmed, we predict that (P2.1) the relationship between species richness and  
126 past climate oscillations will be different between the northern region, most exposed to glaciations,  
127 and the southern less exposed areas. Therefore, (P2.2) species richness will be lower in the north of  
128 the 0°C LGM isotherm than in the south. Furthermore, we expect (P2.3) that the differences in  
129 richness will be more pronounced for lotic species, which are worse dispersers, compared to lentic

130 species. H3 proposes that species richness depends on habitat availability. If this holds true, we expect  
 131 that (P3.1) species richness will increase in areas where habitat availability is higher, but also that  
 132 such increase is habitat dependent. Thus, we predict (P3.2) higher lotic species richness in regions  
 133 with more river streams and (P3.3) increased lentic species richness in areas with more ponds and  
 134 lakes.

135

## 136 **Methods**

### 137 *Data on species distributions*

138 We extracted the distribution of European odonates species based on the information available in  
 139 three specialised publications on Odonata: a monograph (Askew 2004), a field guide (Dijkstra and  
 140 Lewington 2006), and an atlas of distribution and conservation status (Boudot and Kalkman 2015).  
 141 This information was complemented with the distribution records available on the Global  
 142 Biodiversity Information Facility (GBIF, 2020, <https://www.gbif.org/>).

143

144 The field guide (Dijkstra and Lewington 2006) provided the distribution maps of 145 species present  
 145 that were used as background information. These maps were scanned and georeferenced using QGIS  
 146 3.4.15-Madeira software (QGIS.org 2020). Then, they were overlaid on a grid of 50 km cells, based  
 147 on the European ETRS89-LAEA (<https://www.eea.europa.eu/data-and-maps/data/eea-reference-grids-2>).

148 We added also those species that are listed with a non-overlapping close relative distribution:  
 149 *Ceriagrion georgifreyi* (Schmidt, 1953), *Coenagrion intermedium* (Lohmann, 1990), *Boyeria*  
 150 *cretensis* (Peters, 1991), *Gomphus lucasii* (Selys in Lucas, 1849) and *Gomphus ubadschii* (Schmidt,  
 151 1953). The resultant grid was visually compared with the distributions presented in Askew (2004)  
 152 and the Atlas of Boudot & Kalkman (2015) to complete the species presences manually in QGIS,  
 153 giving priority to the most up-to-date reference. Those species present in the field guide that do not  
 154 appear in the atlas were removed (see Supplementary Appendix S1). In addition, two species that  
 155 were only present in the atlas were included in the database: *Ischnura intermedia* (Dumont, 1974)

156 and *Anax junius* (Drury, 1773). With these modifications, our preliminary European Odonata  
157 shapefile/map compilation consisted of 138 species.

158

159 To obtain species occurrences from GBIF biodiversity data portal, we downloaded all the records  
160 located in the European continent that included information on coordinates, Odonata as Scientific  
161 name and with no geospatial problem. Then, these records were processed using basic filtering  
162 criteria, following the rationale outlined in Ronquillo et al. (2024). We eliminated fossil and  
163 introduced species, and records with coordinates that fall into the sea or in zoos. After cleaning, we  
164 kept information for 102 out of the 150 species initially downloaded. These records were added as  
165 presences in the corresponding grid cells and species of the main geodatabase. In addition, the  
166 distribution of the species in areas adjacent to Europe, such as North Africa and the Anatolian  
167 peninsula, was also included, encompassing the whole West Palearctic region. The so-obtained  
168 updated species distribution data were published as an open access map database (Gómez Vadillo et  
169 al. 2020).

170

171 To conduct this study, some modifications were made to the study area covered by the  
172 abovementioned database. To avoid the noise produced by the effects of isolation on richness  
173 patterns, all European islands were eliminated, except for Great Britain and Ireland, which  
174 biogeographically can be considered as a large peninsula due to their connection to the continent  
175 during much of the ice ages. North Africa and the Anatolian Peninsula were also removed to assess  
176 strictly European species. In addition, several grid cells adjacent to Russia were eliminated because  
177 they showed extremely low richness, likely due to digitisation inconsistencies. By making these  
178 modifications to the data, several species, whose distribution corresponded only to the removed areas,  
179 were eliminated (see Supplementary Appendix S1 for eliminated species). As a result, this study  
180 analyzed the 124 species present in Europe (including Great Britain and Ireland), out of the 138



181 species available in the dataset, and excluding Russia and all other islands (see Supplementary Tables  
182 S1 and S2 for a complete checklist).

183

#### 184 ***Study groups***

185 The database was subdivided into three main groups: Odonata, lentic species, and lotic species. The  
186 decision to focus on the groups of lentic and lotic species, instead of considering the high-level  
187 taxonomic classification of odonates (i.e., suborders Anisoptera and Zygoptera), was based on a  
188 preliminary analysis that evaluated the relevance of classifying all species according to their habitat  
189 type (lentic or lotic) rather than their suborder (see Supplementary Appendix S2 for more  
190 explanations and results). Species richness was calculated as the number of species present in each  
191 50x50 km cell of the European grid for these three different groups. Additionally, we calculated  
192 species richness for other subsets (richness of Anisoptera species, richness of Zygoptera species,  
193 combinations based on both suborder and habitat type such as Anisoptera-lentic species richness,  
194 Zygoptera-lentic species richness, etc.). However, because the species richness patterns showed  
195 stronger correlations within the same habitat type compared to the correlations based on suborders,  
196 our results focus solely on the first three groups (Additional information on the other subsets can be  
197 found in the Supplementary Appendix S2.1 and Fig. S2.1).

198

#### 199 ***Environmental and habitat data***

200 To assess the relationship between richness and water-energy balance and ensure comparability  
201 between the variables describing current and past climate, we used mean annual temperature and  
202 annual precipitation from the paleoclimatic model ECHAM3 (Braconnot et al. 2007) to describe  
203 current climate, and estimates of temperature and precipitation from the Last Glacial Maximum from  
204 the same paleoclimatic model to assess the effects of past climate. Following Hortal et al. (2011) and  
205 Calatayud et al. (2016), we calculated the historical variability of temperature and precipitation as the  
206 difference between current and LGM values. Hereafter, we will use the term 'climate variability' to

207 refer to historical climate variability. In this context, “*var<sub>t</sub>*.” represents temperature variation, and  
208 “*var<sub>p</sub>*.” represents precipitation variation. These measures indicate the deviation in temperature and  
209 precipitation from the Last Glacial Maximum (LGM) to current conditions. A lower climate  
210 variability value indicates a more stable climate over time.

211

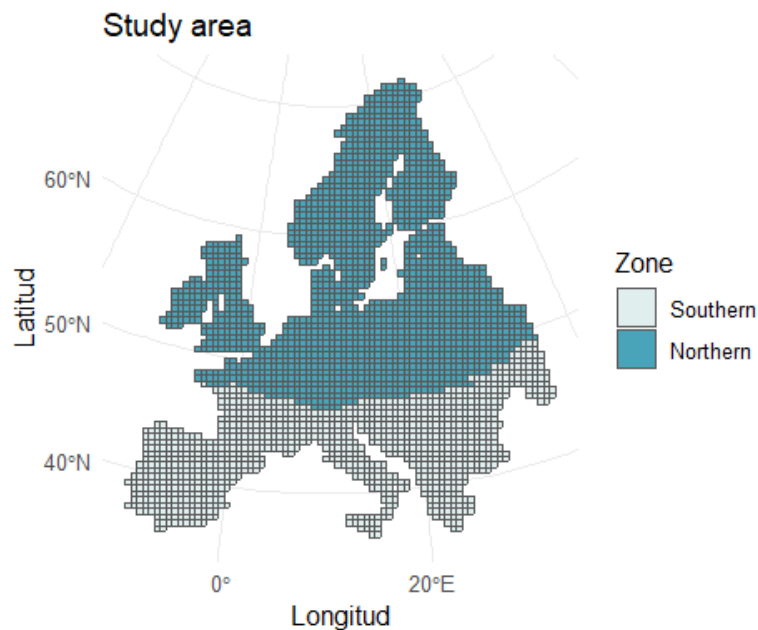
212 To calculate the availability of freshwater habitats, we used Corine Land Cover (CLC 2018,  
213 <https://land.copernicus.eu/pan-european/corine-land-cover/lcc-2012-2018>) and EuroGlobalMap  
214 dataset (EGM, <https://eurogeographics.org/>). From CLC 2018, which provides data in the raster  
215 format, we used water courses (code 511) for lotic habitats, and inland marshes (411), peat bogs (412)  
216 and water bodies (512) for lentic habitats. EGM provides hydrographic data in vectorial format, which  
217 allows describing linear features such as rivers and streams with a higher precision. Thus, from this  
218 database we have used watercourse (BH502) for lotic habitats, and Spring / Water Hole (BH170) for  
219 lentic habitats. To calculate the availability of lotic habitats for each 50x50 km grid cells, we  
220 estimated the total length of watercourses within each cell using QGIS. To calculate the availability  
221 of lentic habitats per 50x50 km grid cell, the lentic habitat layers were rasterized at 100 m resolution,  
222 and the number of pixels available in each grid cell was counted, returning the area of lentic habitats  
223 available for each grid cell.

224

### 225 *Statistical analyses*

226 To assess the effect of glaciations on richness, we divided the study area in Northern and Southern  
227 Europe, based on the 0°C isotherm at LGM: (see Hortal et al. 2011). To establish the Northern Europe  
228 region, we selected all grid cell with a temperature at the LGM below 0 °C, for Southern Europe those  
229 above 0 °C (Fig. 1). To test our prediction (P2.2) that species richness would be lower north of the  
230 0°C LGM isotherm compared to the south, we linked the regional and local richness within each  
231 study group (Odonata, lentic species and lotic species) in both regions. We performed a Mann-

232 Whitney U-test, a non-parametric alternative of the Student's t-test, to assess if there are significant  
 233 differences in local richness between Northern and Southern Europe.



234  
 235 **Figure 1.** Map of the study area, showing the division of northern and southern Europe according to the 0°C isotherm at  
 236 the Last Glacial Maximum.  
 237

238 We used Generalised Linear Models (GLMs) to explore the relationship between species richness,  
 239 past and current climate, and habitat availability. As species richness is a count data, we assumed a  
 240 Poisson distribution and a logarithmic link function. To assess whether the species richness  
 241 determinants change from one region to another, we performed statistical models for (1) whole  
 242 Europe, (2) Northern Europe and (3) Southern Europe. Subsequently, the independent variables were  
 243 standardized (scaled to 0 mean and 1 standard deviation) to allow comparison of their effects on  
 244 species richness pattern. We compared the slopes of the regression models and partitioned the  
 245 explained deviance between the current, past climate and habitat availability models (see Calatayud  
 246 *et al.*, 2019 for a similar approach). For the deviance partitioning, linear regressions were performed  
 247 for each of the climatic variables against the richness of the three groups and for each of the three  
 248 study regions. Statistical analyses were performed in RStudio (RStudio Team, 2023,  
 249 v2023.12.1+402) using the packages *stats* (R Core Team, 2023) for *glm* function, *base* (R Core Team,  
 250 2023), for *scale* function, *eulerr* (Larsson, 2023), *ggplot2* (Wickham *et al.*, 2023), *gridExtra* (Auguie,

251 2017) and *patchwork* (Pedersen, 2023) for graphics and maps. The deviance partitioning analyses  
252 were performed with the Spatial Analysis in Macroecology (SAM) software (Rangel et al. 2010).

## 253 **Results**

### 254 *Species richness patterns*

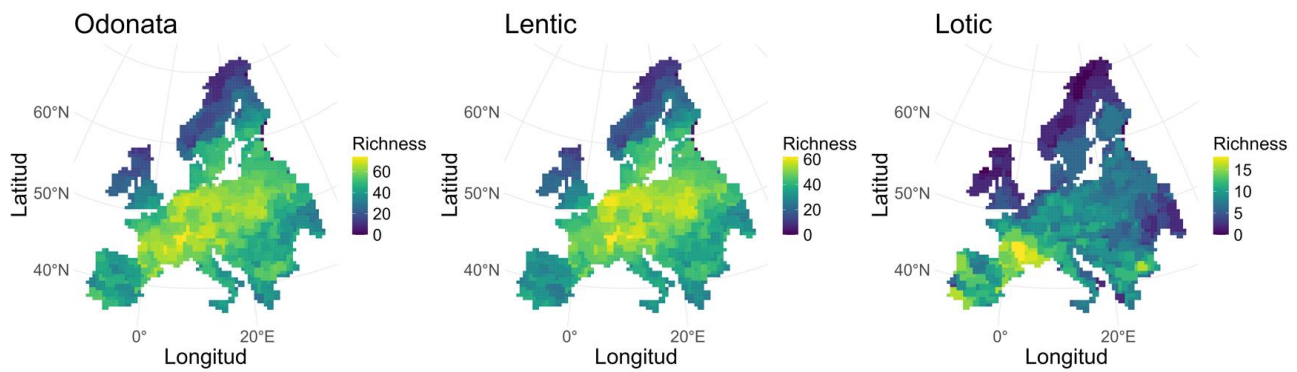
255 In general, Odonata species richness peaks in Central Europe, and decreases both northwards and  
256 southwards from Central Europe, with a more pronounced decline towards the north, confirming that  
257 there are shifts in the drivers of species richness gradient both southward and northward (P1). This  
258 distribution pattern resembles those observed by Hof et al. (2006), Kalkman et al. (2018) and  
259 Cancellario et al. (2022), although the areas of highest diversity in Cancellario et al. (2022) seem to  
260 be deviated towards the northwest, compared to our study and Kalkman et al. (2018). This difference  
261 may be due to the data used, since we consider a larger number of species, and compile data from a  
262 larger number of sources (see methods), thus providing a more comprehensive dataset.

263

264 As mentioned above, species richness is concentrated in Central Europe, notably in France, Germany,  
265 and the Alps, with the highest richness grid cell containing 74 species. Southern Norway, Sweden,  
266 and Finland maintain an average richness of around 50 species per grid cell, with sharp drops in only  
267 a few grid cells, reaching as low as 5-10 species per grid cell in the northernmost parts (Fig. 2). The  
268 richness patterns of lotic and lentic species are quite different from each other (Fig. 2). Lotic species  
269 (37 spp.) numbers are higher in southern France and northern Spain, mainly in the Massif Central and  
270 the Pyrenees (18 spp. in the richest grid), while lentic species (87 spp.) show the highest richness in  
271 Central Europe, particularly in the Alps and Germany (the richest grid cell holds 63 spp.).

272

273



274

275 **Figure 2.** Geographic patterns of species richness per 50x50 km grid cell in Europe for the different groups analyzed in  
 276 this work: all Odonata, lentic species, and lotic species.

277

278 ***Are regional and local assemblages richer in the south?***

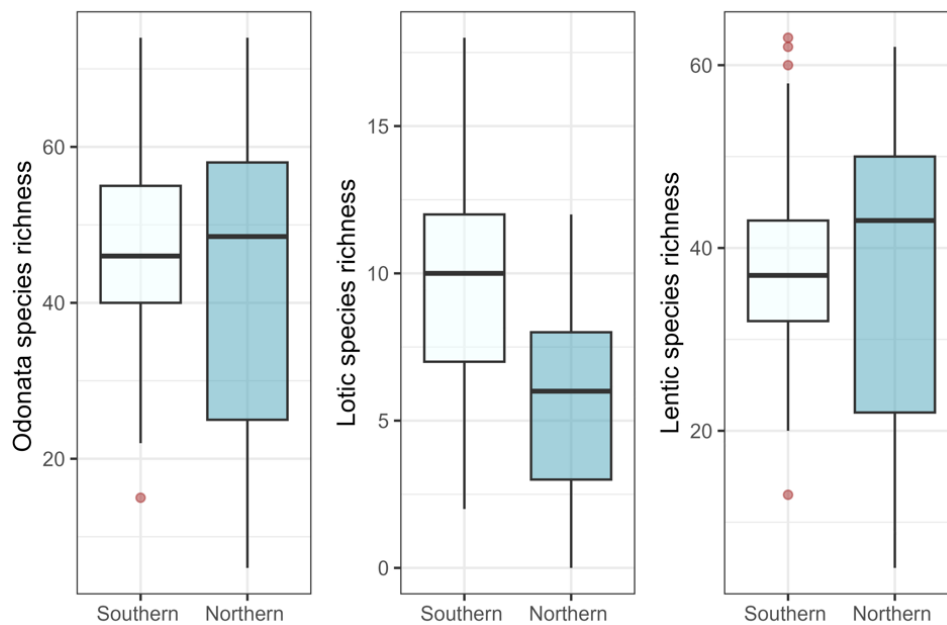
279 Local species richness differs significantly between northern and southern Europe for all Odonata, as  
 280 well as for lentic and for lotic species. The regional pool is consistently richer in the south than in the  
 281 north for all three groups (Fig. 3 and Table 1). Specifically, for lotic species, median local richness  
 282 was significantly higher in Southern Europe compared to Northern Europe. In contrast, both Odonata  
 283 and lentic species show significantly higher median local species richness in northern Europe (Table  
 284 1).

285

286 **Table 1.** Differences in species richness between Northern and Southern Europe. Mann-Whitney U-test results compare  
 287 species richness per grid cell. Also shown are the corresponding median values (see the box plot in Fig. 3) and the regional  
 288 species pool.  
 289

Group	P	U	Median richness		Regional pool	
			South	North	South	North
All Odonata	0.012	738606	46	48.5	119	92
Lotic species	< 0.001	1116192	10	6	37	19
Lentic species	< 0.001	635254	37	43	82	73

290



291

292

293

294

**Figure 3.** Box Plot showing the differences in species richness (Y-Axis) per grid cell between Northern and Southern Europe for the three study groups: all Odonata, lotic species, and lentic species.

295

***Relationships between richness, climate, climate stability, and habitat availability***

296

Current climate, past climate (measured as climate variation since LGM), and habitat availability

297

shape Odonata species richness patterns across Europe (Table 2 and Supplementary Appendix S3,

298

Fig. S3.1). Following the water-energy hypothesis, current climate is a key driver of Odonata

299

richness: as expected, temperature is most influential in northern Europe (0.215;  $p < 0.001$ ), while

300

precipitation dominates in the south (0.151;  $p < 0.001$ ). These results confirm that Odonata richness

301

is driven by the current climate's water-energy balance and show a distinct north-south gradient in

302

species richness (H1 and P1). Past climate also plays a role, with temperature variation (-0.190;  $p <$

303

0.001) and precipitation variation (-0.049;  $p < 0.001$ ) since the LGM significantly impacting northern

304

regions, though with a lesser effect in the south. This confirms that past climate affects Odonata

305

richness and that its impact varies between northern and southern regions (H2 and P2.1).

306

Additionally, habitat availability, including lentic (-0.040;  $p < 0.001$ ) and lotic (0.065;  $p < 0.001$ )

307

habitats, affects Odonata richness, particularly in the north, confirming that species richness is

308

influenced by habitat availability (H3).

309

310 When subdividing Odonata species into lotic and lentic species, we found consistent patterns  
311 explained primarily by the water-energy hypothesis and past climate (Table 2 and see Supplementary  
312 Appendix S3, Fig. S3.2). Variation in temperature since LGM (-0.226;  $p < 0.001$ ), current temperature  
313 (0.208;  $p < 0.001$ ), and precipitation (-0.141;  $p < 0.001$ ) play crucial roles in shaping the richness  
314 patterns of northern lotic species. In the south, the species richness patterns of lotic species are  
315 influenced by current precipitation patterns (0.431;  $p < 0.001$ ), oscillations in precipitation since the  
316 LGM (-0.348;  $p < 0.001$ ), and current temperature (0.205;  $p < 0.001$ ). It is noteworthy that the  
317 availability of lotic habitats also has a positive effect on the species richness patterns of northern lotic  
318 species (0.126;  $p < 0.001$ ). Similarly, the richness patterns of northern European lentic species are  
319 primarily driven by current temperature (0.212;  $p < 0.001$ ), variation in temperature since the LGM (-  
320 0.196;  $p < 0.001$ ), and current precipitation (-0.191;  $p < 0.001$ ). Southern European lentic species  
321 richness is driven by current precipitation (0.091;  $p < 0.001$ ), variation in temperature since the LGM  
322 (0.065;  $p < 0.001$ ), and temperature (0.056;  $p < 0.001$ ) (Table 2 and see Supplementary Appendix S3,  
323 Fig. S3.2). These results together highlight the strong influence of both past and current climate on  
324 European lotic and lentic odonates richness patterns.

325

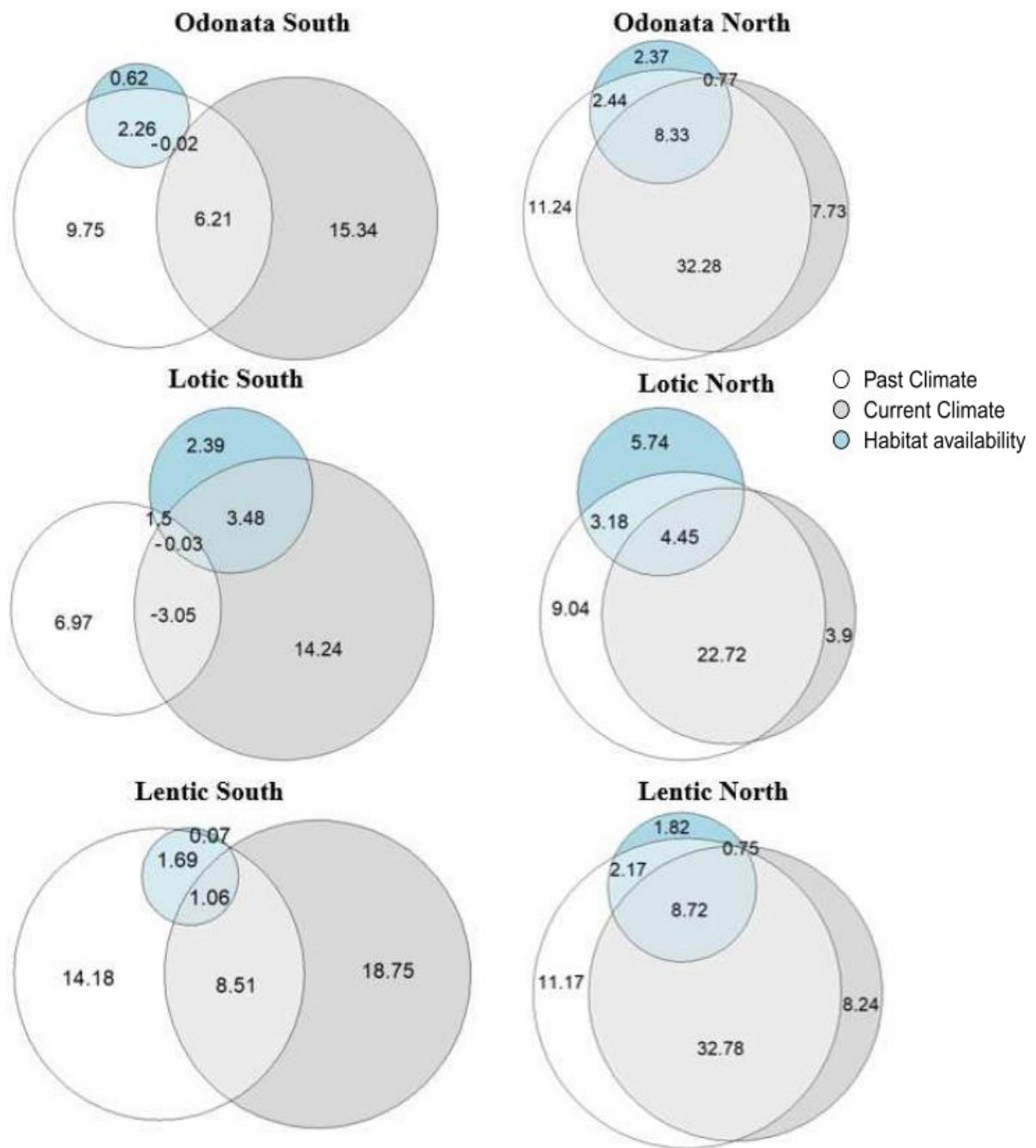
326 **Table 2.** Results of the GLMs assessing the relationships between species richness, variation in climate from LGM, current  
 327 climate and habitat availability for all Odonata, and Lotic and Lentic across Europe. The p-value, S.C. (Standardized  
 328 Coefficient estimated by the model) and the explained deviance (pseud-R<sup>2</sup>) for each model are shown.

	Variable	North		South	
		S.C.	p-value	S.C.	p-value
<b>Odonata</b>	Variation in temperature	-0.190	< 0.001	0.017	0.044
	Variation in precipitation.	0.049	< 0.001	-0.090	< 0.001
	Temperature	0.215	< 0.001	-0.008	0.220
	Precipitation	-0.169	< 0.001	0.151	< 0.001
	Availability of lentic habitat	-0.040	< 0.001	-0.014	0.006
	Availability of lotic habitat	0.065	< 0.001	0.014	0.010
	Pseudo R <sup>2</sup>	0.593		0.347	
<b>Lotic species</b>	Variation in temperature	-0.226	< 0.001	-0.185	< 0.001
	Variation in precipitation.	0.027	0.186	-0.348	< 0.001
	Temperature	0.208	< 0.001	0.205	< 0.001
	Precipitation	-0.141	< 0.001	0.431	< 0.001
	Availability of lentic habitat	0.126	< 0.001	0.053	< 0.001
	Pseudo R <sup>2</sup>	0.442		0.227	
	<b>Lentic species</b>	Variation in temperature	-0.196	< 0.001	0.065
Variation in precipitation.		0.059	< 0.001	-0.036	0.018
Temperature		0.212	< 0.001	-0.056	< 0.001
Precipitation		-0.191	< 0.001	0.091	< 0.001
Availability of lentic habitat		-0.021	< 0.001	-0.003	0.546
Pseudo R <sup>2</sup>		0.589		0.456	

329  
 330 ***Partitioning of explained deviances***

331 Our results highlight the primary roles of past and current climates the current Odonata richness in  
 332 Europe. Deviance partitioning shows that in the south, current climate predominantly determines  
 333 species richness for the three studied groups (Odonata, lotic, lentic), although past climate also  
 334 significantly contributes to the extant richness patterns (Fig. 4). In the north, there is a high overlap  
 335 between the effects of past and current climates on species richness for three groups; however, past  
 336 climate has a slightly greater isolated impact compared to current climate. Deviance partitioning also  
 337 indicates a greater contribution of habitat availability to the patterns of lotic species richness in the  
 338 three study areas (Europe, Northern and Southern Europe) (Fig. 4).





339

340 **Figure 4.** Venn diagrams depicting the results of the deviance partitioning analyses, expressed as percentages of explained  
 341 deviance of each independent and joint fraction of the predictors for the three study groups (Odonata, lotic, lentic) in two  
 342 study areas (Northern and Southern Europe).  
 343

344 **Discussion**

345 Our results show that current climate, past climate and, to a lesser extent, habitat availability  
 346 determine the distribution of European odonates. As these predictors are proxies of macroecological  
 347 and macroevolutionary processes that are related to each other, they cannot be considered in isolation  
 348 (Vogler & Ribera, 2003). Nonetheless, we find support for Hawkins' et al. (2003) conjecture that

349 energy will be the main constraint on species richness in cold regions such as northern Europe, while  
350 water will be the main predictor of species richness in warmer regions (H1). GLM results show that  
351 Odonata in general, as well as lotic and lentic species in particular, are governed by current climate.  
352 Regardless of habitat type, energy is the main limiting factor for species richness in the north, while  
353 in the south the limiting factor is water availability. These results also agree with the results obtained  
354 by Keil et al. (2008), where the pattern of Odonata richness in Europe and North Africa is studied in  
355 detail.

356

357 We also obtain evidence that in both southern and northern Europe there is a clear effect of past  
358 climate, being higher for the north than for the south, as found in Odonate (Pinkert et al. (2018) and  
359 other insect groups (e.g., Hortal et al. 2011; Calatayud et al. 2016). It is also worth noting the  
360 importance of climatic variability of temperature in the north of the 0°C isotherm of the LGM. For  
361 each group of study this variable has standardized regression coefficients equal to or greater than 0.2  
362 with a negative sign, indicating a drastic reduction of species numbers in the areas that were under  
363 the most extreme conditions during LGM. Cancellario *et al.* (2022) also observed that there is lower  
364 species richness in areas that are less climatically stable, and higher species richness in the more  
365 climatically stable areas. These results confirm our H2, that the past climate influences Odonata  
366 species richness gradients. Our prediction P2.1 is also fulfilled: the relationship between species  
367 richness and climate variability will be different between the northern region, most exposed to  
368 glaciations, and the southern less exposed areas. The effect of the past climate on the species richness  
369 must be due to the extensive ice sheets that covered the north, resulting in an impoverished fauna and  
370 flora (Calatayud *et al.* 2019; Hortal et al. 2011; Kalkman et al. 2018). In addition, most European  
371 mountain ranges have an east-west orientation, which may have prevented the movement of species  
372 during climatic oscillations in the LGM (Hof et al. 2006).

373

374 Strikingly, deviance partitioning results show that in northern Europe, past climate explains  
375 comparatively more than current climate, for the three groups of species. This suggests that the lower  
376 species richness in northern Europe could be, at least in part, due to the long period of time that this  
377 area was under extreme glacial climatic conditions, which were paired with local extinction processes  
378 during the Pleistocene glaciations (Hof et al. 2006; Hortal et al. 2011; Kalkman et al. 2018). This  
379 contrasts with southern Europe, where current climate alone explains a larger part of the deviation  
380 for both lentic species and all Odonata species together. This is likely a result of this region not being  
381 so exposed to climatic oscillations and, moreover, being the area where climatic refugia were located  
382 (Kalkman et al. 2018; see Morales-Barbero et al. 2018). Interestingly, although habitat availability  
383 has a minor effect compared to current climate and climate variability, the effect on lotic species is  
384 relevant regardless of region.

385

386 There are large differences in the distribution patterns shown by lentic and lotic species, a result  
387 previously found by other studies (Hof et al., 2006, 2008; Kalkman et al. 2018). Habitat is a  
388 determinant in the evolution of many ecological traits, so that species adapted to different habitats  
389 may show different geographic patterns of diversity (Hof et al. 2006). Lotic species have a more  
390 southern distribution, with the focus of richness centered in the south of France and the north of Spain,  
391 mainly in the Massif Central and the Pyrenees. Whereas lentic species are found mainly in central  
392 and western Europe. These differences may be due to the spatio-temporal characteristics of both  
393 habitat types. For example, since lentic habitat are more unpredictable (Hof et al. 2006), the species  
394 adapted to this type of habitat tend to have a greater dispersal capacity compared to those adapted to  
395 lotic ecosystems. Such better dispersal capacity, perhaps together with a greater availability of lentic  
396 habitat in the north, could have allowed lentic species to have a more northern distribution (Hof et al.  
397 2006; Dehling et al. 2010). In contrast, lotic species, having a lower dispersal capacity, have not been  
398 able to extend their distribution patterns northwards after the glaciations. These observations confirm  
399 our P2.3 that the differences in richness would be more pronounced for lotic species, which are worse

400 dispersers, compared to lentic species. Indeed, our results show that lotic species exhibit a more  
401 pronounced decrease in richness towards the north compared to lentic species, supporting the idea  
402 that dispersal limitations in lotic species have constrained their northward range expansion.  
403 Moreover, it should not be forgotten that dragonflies reach their highest diversity in warmer regions  
404 (Kalkman et al. 2018; Alves-Martins et al. 2024). In general, species richness at a regional level is  
405 highest in southern Europe for the three groups of species we studied. Although the median is higher  
406 in the north, the total species diversity of Odonata and lentic species is higher in southern Europe.  
407 This may be because species that are distributed farther north tend to have larger distribution ranges.  
408 The spatio-temporally unpredictable dynamics of lentic habitats promote that the species inhabiting  
409 these ecosystems have a greater dispersal capacity and tend to have larger range sizes (Hof et al.  
410 2006).

411

412 Both current and past climate have distinct effects on lotic and lentic species richness in both northern  
413 and southern Europe. Current climate has a greater effect in the south, while past climate has a greater  
414 influence northward. However, for the southern lotic species, the effect of current climate is much  
415 more relevant. These results are consistent with the adaptive differences of the species to the two  
416 habitat types. Since lentic species disperse better than lotic species, they would have been able to  
417 recolonize the areas affected by the ice sheet during the Pleistocene. Consequently, the extant  
418 assemblages partially reflect these historical distributions. In contrast, the greater climate stability of  
419 southern Europe may have provided opportunities for specialization (Kalkman et al. 2018). This idea  
420 is corroborated for tropical species according to McCauley (2007) and Harabiš & Dolný (2011). If  
421 this holds for temperate environments, it could also explain why species adapted to lotic ecosystems  
422 do not disperse northward (see Fig. 2): being habitat specialists, they would need steppingstones in  
423 intermediate areas to move.

424

425 Besides that, Odonata species richness presents a positive relationship with lotic habitat availability,  
426 and a negative relationship with lentic habitat availability. Indeed, lotic species richness shows a  
427 positive and highly significant relationship with habitat availability, both in southern and northern  
428 Europe, indicating that an increase in lotic habitat availability is associated with an increase in lotic  
429 species richness. These results support the idea that species richness depends on habitat availability,  
430 a concept well-documented in studies of various terrestrial taxa. For instance, empirical evidence has  
431 shown that habitat availability influences species diversity in butterflies (Storch et al. 2003), birds  
432 (Storch et al. 2003), and *Carabus* beetles (Calatayud et al. 2016). In line with these findings, our  
433 study confirms predictions P3.1 and P3.2: we found that Odonata species richness increases in areas  
434 where habitat availability is higher, and that lotic species richness is positively correlated with the  
435 amount of river streams. This is consistent with the idea that greater habitat availability supports  
436 higher species richness. In contrast, in southern Europe the observed relationship between these  
437 variables is not significant, failing to confirm our prediction P3.6 that lentic species richness is  
438 expected to be higher in areas with more ponds and lakes. This may be related to the different  
439 dispersal capacities of the two groups; lentic species are characterized by a greater dispersal capacity  
440 and life cycles less dependent on permanent waters, in response to the lower spatial and temporal  
441 persistence of lentic habitats (Grewe et al. 2013). Having a greater dispersal capacity, they exhibit  
442 broader species distributions, less dependent on habitat availability. In contrast, lotic species have a  
443 lower dispersal capacity, making them more dependent on habitat availability (Hof et al. 2006).  
444 Nevertheless, based on our results and the study by Dehling *et al.* (2010), we can conclude that relying  
445 solely on habitat availability as a predictor of species richness is not advisable, as European odonate  
446 species are significantly more affected by past climate conditions, and current climate than by habitat  
447 availability.

448

## 449 **Conclusions**

450 Our results illustrate that the distribution of Odonata is primarily determined by the effects of current  
451 climate and climatic changes of the past, and in a lesser extent by habitat availability. We can  
452 conclude that the distribution of European odonate species richness, regardless of habitat types, seems  
453 to be determined by the water–energy balance. The temperature determines the southward decline of  
454 richness, while the northward decline in the number of species is determined by precipitation. On the  
455 other hand, there is a clear effect of past climate oscillations on current dragonfly and damselfly  
456 species richness in both southern and northern Europe (Hortal et al. 2011; Calatayud et al. 2016;  
457 Pinkert et al. 2018). Throughout the whole of Europe, and in northern Europe in particular, past  
458 climate influences more than current climate, for the three groups of species, while in southern Europe  
459 current climate alone has a greater influence for both lentic species and all Odonata species together.

460

461 Our study highlights significant differences in the distribution patterns of lentic and lotic species.  
462 Habitat plays a crucial role in the evolution of species' biological traits, leading to distinct geographic  
463 patterns of diversity. Lotic species are primarily concentrated in southern Europe, while lentic species  
464 are more prevalent in central and western Europe (see also Hof et al. 2006; Kalkman et al. 2018). The  
465 lower temporal stability of lentic habitats has led to greater dispersal capacities in lentic species,  
466 facilitating their broader northern distribution. Furthermore, the availability of lotic habitats is  
467 positively correlated with species richness, while lentic habitat availability shows a more nuanced  
468 relationship. Alike Dehling et al. (2010), these results highlight the need to consider multiple factors,  
469 including habitat availability, dispersal capacity, and climatic history, when predicting species  
470 richness and distribution patterns of European odonates. Future research should continue to explore  
471 these dynamics, particularly to understand why the northward expansion of lotic species is limited,  
472 and whether European lotic environments indeed support more specialist species. This is crucial to  
473 provide a more comprehensive understanding of European dragonfly and damselfly diversity. Future  
474 studies should also: (1) analyse how habitat fragmentation influences the evolution of dispersal traits  
475 and the adaptation of species to different types of aquatic habitats; (2) study the different dispersal

476 capabilities in natural versus human-altered habitats; and (3) explore how species interactions  
477 (competition, predation, mutualism) vary between lotic and lentic habitats and how these interactions  
478 influence dispersal and community structure.

479

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487

## 488 **Author Contributions**

489 MGV, JC, and JH designed research; MGV and CR gathered, processed and analyzed the data and  
490 wrote R code, with JC and FAM; FAM supervised and reviewed the information as an expert of the  
491 taxonomical group; MGV led the writing with contributions from all authors. All authors discussed  
492 the results and approved the last version of the manuscript.

493

## 494 **Data Accessibility**

495 Data for this work comes from open access databases available in digital.CSIC at  
496 [10.20350/digitalCSIC/12535](https://doi.org/10.20350/digitalCSIC/12535). R Code and cleaned dataset used for the analyses are available in  
497 [https://github.com/mgomezv26/European\\_odonate\\_species\\_richness\\_2024](https://github.com/mgomezv26/European_odonate_species_richness_2024)

498

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