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

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Abstract

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

Highlights

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

Keywords: contemporary climate, distribution, freshwater animals, glaciations, habitat, history, odonata, species richness.

Introduction

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

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

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

Besides large-scale climate gradients and historical climate events, factors such as habitat availability are also important determinants of current species' diversity (MacArthur, 1964). Habitat availability can act as a driver of species richness, as higher habitat availability supports larger populations, which promotes the persistence of more species. Empirical evidence for habitat availability influence on 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

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

Methods

Data on species distributions

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

The field guide (Dijkstra and Lewington 2006) provided the distribution maps of 145 species present that were used as background information. These maps were scanned and georeferenced using QGIS 3.4.15-Madeira software (QGIS.org 2020). Then, they were overlaid on a grid of 50 km cells, based on the European ETRS89-LAEA (https://www.eea.europa.eu/data-and-maps/data/eea-reference-grids-2). We added also those species that are listed with a non-overlapping close relative distribution: *Ceriagrion georgifreyi* (Schmidt, 1953), *Coenagrion intermedium* (Lohmann, 1990), *Boyeria cretensis* (Peters, 1991), *Gomphus lucasii* (Selys in Lucas, 1849) *and Gomphus ubadschii* (Schmidt, 1953). The resultant grid was visually compared with the distributions presented in Askew (2004) and the Atlas of Boudot & Kalkman (2015) to complete the species presences manually in QGIS, giving priority to the most up-to-date reference. Those species present in the field guide that do not appear in the atlas were removed (see Supplementary Appendix S1). In addition, two species that were only present in the atlas were included in the database: *Ischnura intermedia* (Dumont, 1974)

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

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

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

refer to historical climate variability. In this context, *"vart."* represents temperature variation, and "*varp*." represents precipitation variation. These measures indicate the deviation in temperature and precipitation from the Last Glacial Maximum (LGM) to current conditions. A lower climate variability value indicates a more stable climate over time.

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

Statistical analyses

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

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

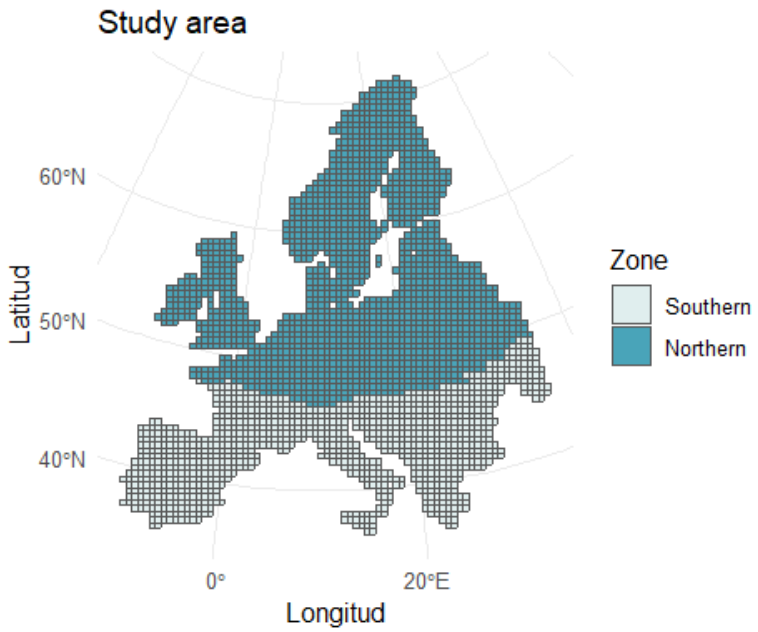

Figure 1. Map of the study area, showing the division of northern and southern Europe according to the 0ºC isotherm at the Last Glacial Maximum.

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

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

Results

Species richness patterns

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

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

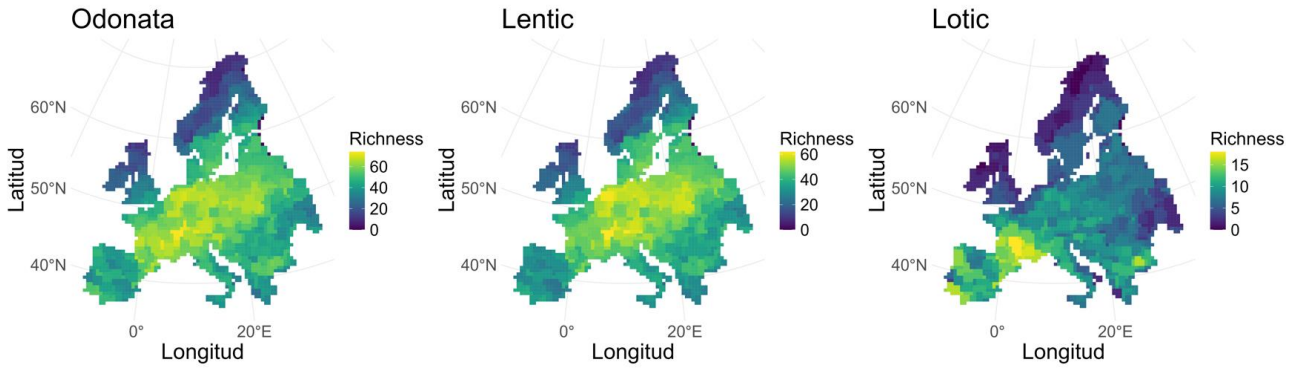

Figure 2. Geographic patterns of species richness per 50x50 km grid cell in Europe for the different groups analyzed in this work: all Odonata, lentic species, and lotic species.

Are regional and local assemblages richer in the south?

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

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

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

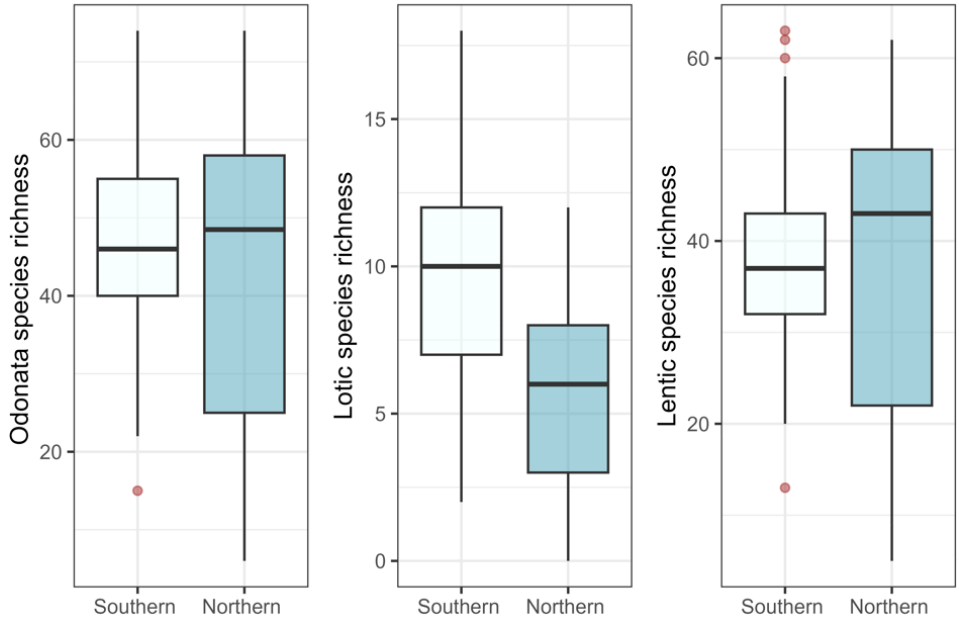

Figure 3. Box Plot showing the differences in species richness (Y-Axis) per grid cell between Northern and Southern Europe for the three study groups: all Odonata, lotic species, and lentic species.

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

Current climate, past climate (measured as climate variation since LGM), and habitat availability shape Odonata species richness patterns across Europe (Table 2 and Supplementary Appendix S3, Fig. S3.1). Following the water-energy hypothesis, current climate is a key driver of Odonata richness: as expected, temperature is most influential in northern Europe (0.215; $p < 0.001$), while precipitation dominates in the south (0.151; $p < 0.001$). These results confirm that Odonata richness is driven by the current climate's water-energy balance and show a distinct north-south gradient in species richness (H1 and P1). Past climate also plays a role, with temperature variation (-0.190; $p < 0.001$) and precipitation variation (-0.049; $p < 0.001$) since the LGM significantly impacting northern regions, though with a lesser effect in the south. This confirms that past climate affects Odonata richness and that its impact varies between northern and southern regions (H2 and P2.1). Additionally, habitat availability, including lentic (-0.040; $p < 0.001$) and lotic (0.065; $p < 0.001$) habitats, affects Odonata richness, particularly in the north, confirming that species richness is influenced by habitat availability (H3).

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

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

		North		South	
	Variable	**S.C.**	**p-value**	**S.C.**	**p-value**
Odonata	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^2	0.593		0.347	
Lotic species	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^2	0.442		0.227	
Lentic species	Variation in temperature	-0.196	< 0.001	0.065	< 0.001
	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^2	0.589		0.456	

Partitioning of explained deviances

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

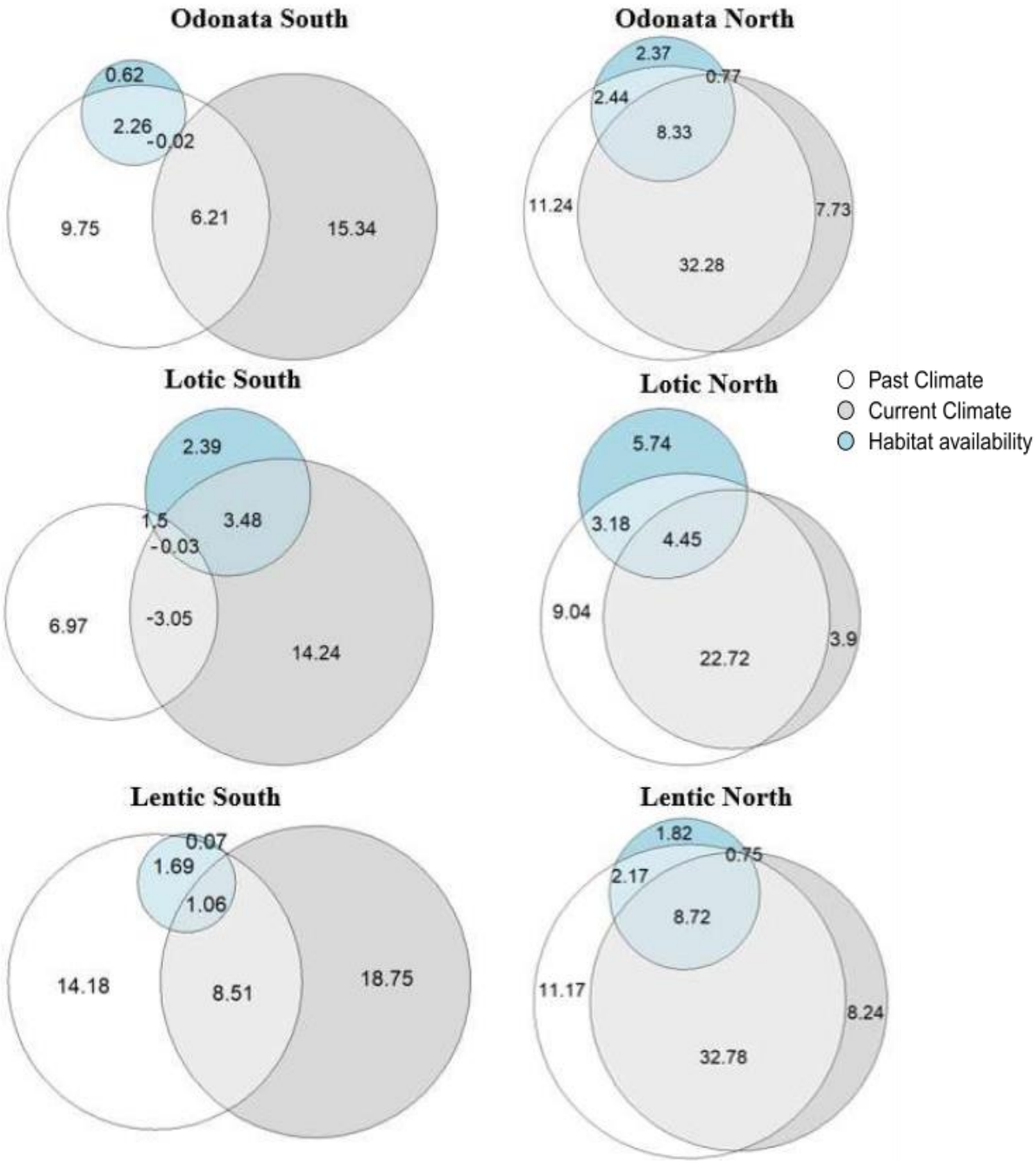

Figure 4. Venn diagrams depicting the results of the deviance partitioning analyses, expressed as percentages of explained deviance of each independent and joint fraction of the predictors for the three study groups (Odonata, lotic, lentic) in two study areas (Northern and Southern Europe).

Discussion

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

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

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

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

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

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

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

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

Conclusions

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

Our study highlights significant differences in the distribution patterns of lentic and lotic species. Habitat plays a crucial role in the evolution of species' biological traits, leading to distinct geographic patterns of diversity. Lotic species are primarily concentrated in southern Europe, while lentic species are more prevalent in central and western Europe (see also Hof et al. 2006; Kalkman et al. 2018). The lower temporal stability of lentic habitats has led to greater dispersal capacities in lentic species, facilitating their broader northern distribution. Furthermore, the availability of lotic habitats is positively correlated with species richness, while lentic habitat availability shows a more nuanced relationship. Alike Dehling et al. (2010), these results highlight the need to consider multiple factors, including habitat availability, dispersal capacity, and climatic history, when predicting species richness and distribution patterns of European odonates. Future research should continue to explore these dynamics, particularly to understand why the northward expansion of lotic species is limited, and whether European lotic environments indeed support more specialist species. This is crucial to provide a more comprehensive understanding of European dragonfly and damselfly diversity. Future studies should also: (1) analyse how habitat fragmentation influences the evolution of dispersal traits 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. R Code and cleaned dataset used for the analyses are available in
497 https://github.com/mgomezv26/European_odonate_species_richness_2024
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