FRONTIERS OF BIOGEOGRAPHY
The scientific journal of The International Biogeography Society

Frontiers of Biogeography 18, 2025, e136933 | DOI 10.21425/fob.18.136933

RESEARCH ARTICLE

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

Mónica Gómez-Vadillo[1,2], Joaquín Calatayud[3,4], Fernanda Alves-Martins[5,6], Cristina Ronquillo[1], Joaquín Hortal[1]

1 *Department of Biogeography & Global Change, Museo Nacional de Ciencias Naturales (MNCN-CSIC), Madrid, Spain*
2 *PhD Program in Ecology, Universidad Autónoma de Madrid, Madrid, Spain*
3 *Department of Biology and Geology, Physics and Inorganic Chemistry, Rey Juan Carlos University, Madrid, Spain*
4 *Global Change Research Institute, Rey Juan Carlos University, Madrid, Spain*
5 *CIBIO-InBIO, Research Centre in Biodiversity and Genetic Resources, University of Porto, Campus de Vairão, 4485-661 Vairão, Portugal*
6 *BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, Vairão, Portugal*

Corresponding author: Mónica Gómez-Vadillo (monica.gomez@mncn.csic.es)

Editor Susanne Fritz
Received 12 September 2024 ♦ **Accepted** 6 June 2025 ♦ **Published** 25 June 2025

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 and 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: all odonates, lentic species, and lotic species. Notably, lentic species total 70% of the studied Odonata species, thus influencing overall species richness patterns. We analyzed their diversity in Northern and Southern Europe, divided according to the 0 °C 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 north and precipitation determining the decline towards the south. Past climate oscillations affect species richness in southern and northern Europe. Habitat availability also influences odonate diversity to a lesser extent, with a positive correlation between lotic species richness and their habitat availability. In contrast, lentic species richness showed 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 northward decrease in species richness, while the southward decrease is so by precipitation.
- The last ice age climate had a greater influence than current climate in northern 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

Copyright *Mónica Gómez-Vadillo et al.* This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

PENSOFT

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 stands out (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; Allen et al. 2007; Keil et al. 2008). This has been attributed to a functional relationship between species richness and temperature, which is then shaped up by other limiting factors such as water availability or number of freezing days (Segovia 2023). 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 premise has been found to be informative for several taxa in the European continent, including butterflies (Hawkins et al. 2003; Stefanescu et al. 2011), 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. Biodiversity patterns have been hypothesized to arise from both equilibrium mechanisms – where species richness is driven by contemporary environmental conditions, and non-equilibrium processes – where historical events, such as glaciations, have left long-lasting imprints on species distribution patterns. Both kinds of drivers have been repeatedly found to interact in the northern hemisphere, where Pleistocene cold climates have left a strong signal in current diversity patterns. Indeed, an important signal of the 0 °C isotherm at 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 coinciding with the 0 °C LGM isotherm, which has been suggested to be in part a consequence of the faunal loss experienced 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, other equilibrium 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 (Fahrig 2013), albeit this may be affected by habitat fragmentation (Hanski 2015). This is particularly true for habitat specialists (see, e.g., Stefanescu et al. 2011), although larger habitat areas can support higher species richness even if some habitat types have small sizes (see Hortal et al. 2009, 2013). Empirical evidence for habitat availability influence on species diversity has been corroborated for terrestrial taxa including butterflies (Storch et al. 2003), birds (Storch et al. 2003) and *Carabus* beetles (Calatayud et al. 2016). In aquatic ecosystems, habitat is known to play a crucial role in the life of freshwater organisms due to the relationships between habitat stability, dispersal capacity, and species distribution patterns (Ribera and Vogler 2000; Ribera et al. 2001; Ribera et al. 2003; Hof et al. 2008). Aquatic habitats are divided into lentic (standing water) and lotic (running water) habitats, which differ in their environmental and spatiotemporal configurations (Ribera and Vogler 2000; Hof et al. 2006; Dehling et al. 2010). Lentic habitats are more unpredictable in the long term than lotic habitats (Ribera and Vogler 2000; Hof et al. 2008). This has implications for the evolutionary traits and distribution patterns of aquatic organisms that depend on these habitats, such as the higher dispersal ability of lentic species than lotic species (Ribera and Vogler 2000; Ribera et al. 2001; Hof et al. 2006, 2008). Consequently, it would be logical to consider habitat availability as a good predictor of the distribution of aquatic organisms. However, Dehling et al. (2010) found that habitat availability was a poor indicator of freshwater species diversity.

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

of the stronger dispersal ability of lentic species, which were able to recolonize the previously glaciated areas of northern Europe after LGM.

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

In this study we aim to disentangle the signatures of habitat availability, past climate and current climate on the diversity patterns of European Odonata. First, we evaluated the influence of current climate, past climate changes, and the availability of habitat on these patterns by three complementary (i.e. non-exclusive) hypotheses: H1 proposes that odonate richness is driven by the current climate's water-energy balance. If this holds true, we predict (P1) shifts in the drivers of species richness gradient both southward and northward. Odonate assemblages in the drier southern Europe are expected to be primarily limited by water availability, whereas northern assemblages in colder climates will be limited primarily by energy inputs. H2 proposes that past climate influences Odonata species richness. If confirmed, we predict that (P2.1) the relationship between species richness and past climate oscillations will be different between the northern region, most exposed to glaciations, and the southern less exposed areas. Therefore, (P2.2) species richness will be lower in the north of the 0 °C LGM isotherm than in the south. Furthermore, we expect (P2.3) that the differences in 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 specialized 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 occurrence 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 (European Environment Agency 2018). In addition to the species mapped in the field guide, we also included species whose distribution was not mapped but rather indicated by Dijkstra and Lewington (2006) as being a close relative of one of a mapped species with a non-overlapping distribution range in Europe. These species present small distributions in the studied area, but were considered in this study because they represent taxonomically and biogeographically relevant occurrences that complement our dataset. Specifically, we added: *Ceriagrion georgifreyi* (Schmidt, 1953) (from Southern Balkans), *Coenagrion intermedium* (Lohmann, 1990) (from Crete), *Boyeria cretensis* (Peters, 1991) (from Crete), *Gomphus lucasii* (Selys in Lucas, 1849) (from the Maghreb region) and *Gomphus ubadschii* (Schmidt, 1953) (distributed along southern Turkey and Levant in eastern Mediterranean). The resultant grid was visually compared with the distributions presented in Askew (2004) and the Atlas of Boudot and 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 Suppl. material 2). 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 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 in the darwinCore field 'Scientific name' and with no geospatial issues. 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. GBIF records were filtered to include only those dated between 2000 and 2010 to match the temporal resolution of the primary sources and climate datasets, and to avoid bias from recent colonization events. 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 Suppl. material 2). As a result, this study analyzed the 124 species out of the 138 species available in the dataset (see Suppl. materials 1, 5 for a complete checklist).

Study groups

The database was subdivided into three main groups: all odonates, lentic species, and lotic species. The decision to focus on the groups of lentic and lotic species, instead of considering the high-level taxonomic classification of odonates (i.e., suborders Anisoptera and Zygoptera), was based on a preliminary analysis that evaluated the relevance of classifying all species according to their habitat type (lentic or lotic) rather than their suborder (see Suppl. material 3). This ecological distinction between habitat types was also emphasized in earlier studies (Ribera and Vogler 2000; Ribera et al. 2001). Here it is worth noting that lentic species account for 87 species, that is 70% of all studied European Odonata, compared with 37 lotic specialists. Species richness was calculated as the number of species present in each 50 km × 50 km cell of the European grid for these three different groups (all odonates, Lentic and Lotic species). Additionally, we calculated species richness for other subsets (richness of Anisoptera species, richness of Zygoptera species, combinations based on both suborders and habitat type such as Anisoptera-lentic species richness, Zygoptera-lentic species richness, as Anisoptera-lotic species richness and Zygoptera-lotic species richness). However, species richness patterns showed stronger correlations within the same habitat type than based on suborders, hence our results focus solely on the first three groups (other subsets can be found in the Suppl. material 3).

Environmental and habitat data

To assess the relationship between richness and water-energy balance and ensure comparability between the variables describing current and past climate, we used mean annual temperature and annual precipitation from the paleoclimatic model ECHAM3 (Braconnot et al. 2007) to describe current climate and estimates of temperature and precipitation from the Last Glacial Maximum from the same paleoclimatic model to assess the effects of past climate. Following Hortal et al. (2011) and Calatayud et al. (2016), we calculated the historical variability of temperature and precipitation as the 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.

To calculate de availability of freshwater habitats, we used Corine Land Cover (CLC 2018) and EuroGlobalMap dataset (EGM, year) (EuroGeographics 2021). We used water courses (code 511) for lotic habitats, and inland marshes (411), peat bogs (412) and water bodies (512) for lentic habitats from CLC. Besides, we used watercourse (BH502) for lotic habitats, and Spring/Water Hole (BH170) for lentic habitats from EGM. To calculate the availability of lotic habitats for each 50 km × 50 km grid cells, we estimated the total length of watercourses within each cell using QGIS. Then, lentic habitats layers were rasterized at 100 m resolution. We counted the number of 100 m × 100 m pixels of lentic habitat within each grid cell, using the zonal statistics tool available in QGIS. Finally, the area of lentic habitats available in each grid cell was calculated by multiplying the number of lentic habitat pixels by the area of each pixel (0.01 km²), providing the total area of lentic habitats within each 50 km × 50 km 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 0 °C isotherm at LGM. As commented above, this line identifies two separate responses of biodiversity to glaciations in Europe (see Hortal et al. 2011). To establish the Northern Europe region, we selected all grid cells with a temperature at the LGM below 0 °C, for Southern Europe those above 0 °C (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 (all odonates, 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.

We used Generalised Linear Models (GLMs) to explore the relationship between species richness, past and current climate, and habitat availability. As species richness values represent 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) Northern Europe and (2) Southern Europe. Subsequently, the independent variables were standardized

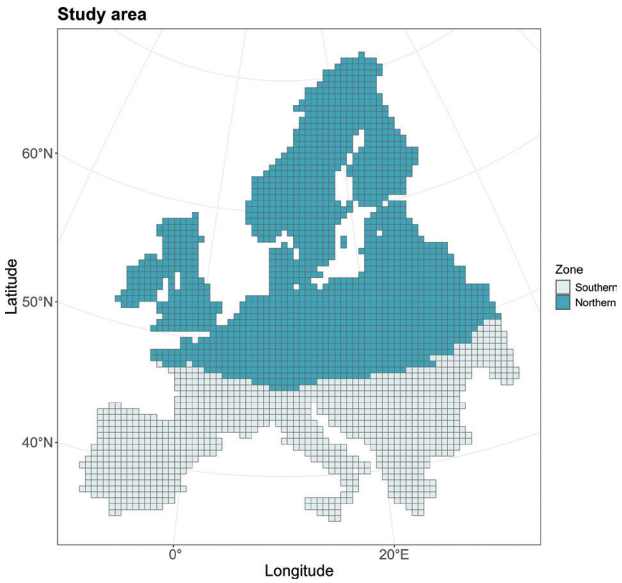

Figure 1. Map of the study area, showing the division of northern and southern Europe according to the 0 °C isotherm at the Last Glacial Maximum.

(scaled to 0 mean and 1 standard deviation) to allow comparison of their effects on species richness pattern. To account for spatial autocorrelation, we included spatial filters derived from Principal Coordinates of Neighbourhood Matrices (PCNM; Dray et al. 2006). We first computed a spatial distance matrix and generated eigenvectors representing different spatial structures, selecting a subset of them based on their ability to minimize residual spatial autocorrelation. We assessed spatial autocorrelation in the residuals using Moran's I index (Moran 1948) and selected spatial filters iteratively until autocorrelation was reduced to an acceptable level, defined by a p-value greater than 0.05 for Moran's I and a relative reduction of Moran's I (mud) below 0.1, indicating that adding further filters would not significantly improve spatial independence.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 each group and for each of the two study regions. Statistical analyses were performed in RStudio (RStudio Team 2024, v2023.12.1+402) using the packages stats (R Core Team 2023) to fit generalized linear models (GLMs), base (R Core Team 2023) for basic functions, letsR (Vilela and Villalobos 2015) for Moran's I test, ape (Paradis and Schliep 2019) for calculating Principal Coordinates of Neighbourhood Matrices (PCNM), vegan (Oksanen et al. 2024) for scaling functions, eulerr (Larsson 2023) for Venn diagrams, and 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 is highest in Central Europe, particularly in France, Germany, and the Alps, with the richest grid cell containing 74 species. Species richness decreases both northward and southward from there, with a more pronounced decline towards the north, where areas such as southern Norway, Sweden, and Finland maintain an average of around 50 species per grid cell. However, sharp declines are observed in a few northern most grid cells, where species richness can drop to as low as 5–10 species (Fig. 2). These patterns confirm that there are shifts in the drivers of species richness gradient both southward and northward (P1). The species richness patterns of lotic and lentic species are quite different from each other (Fig. 2). Lotic species numbers are higher in southern France and northern Spain, mainly in the Massif Central and the Pyrenees (18 spp. in the richest grid cell), while the more diverse lentic species show the highest richness in Central Europe, particularly in the Alps and Germany (the richest grid cell holds 63 spp.).

Are regional and local assemblages richer in the south?

Local species richness differs significantly between northern and southern Europe for all odonates, as well as for lentic and for lotic species. The regional pool is consistently richer in the south than in the north for all groups (Fig. 3, Table 1). Specifically, for lotic species, median local richness was significantly higher in Southern Europe compared to Northern Europe. In contrast, the pattern observed for all species as a whole closely resembles that of lentic species, with both groups showing significantly higher median local species richness in northern Europe (Table 1). This similarity arises because lentic species constitute the majority of Odonata species, thereby shaping the overall richness pattern of the group.

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

Current climate, past climate (measured as climate variation since LGM), and habitat availability shape all odonates' species richness patterns across Europe (Table 2 and Suppl. material 4). The spatial autocorrelation analysis (Moran's I ≈ 0) indicates that the spatial structure of the data is well accounted for by the predictors in our analyses, ensuring that observed patterns are not artefacts of spatial dependence. Current climate is a key driver of all odonates' richness: as expected, temperature is most influential in northern Europe (0.215; $p < 0.001$), while precipitation dominates in the south (0.151; $p < 0.001$).

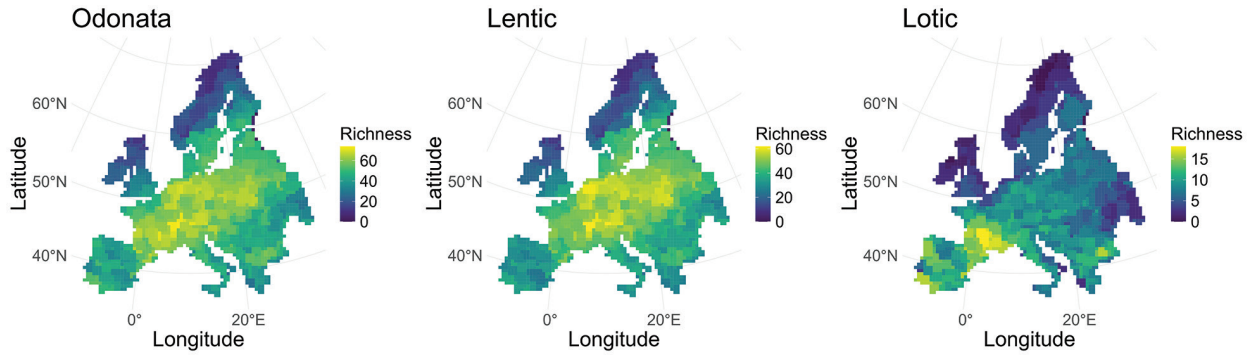

Figure 2. Geographic patterns of species richness per 50 × 50 km grid cell in Europe for the different groups analyzed in this work: all odonates, lentic species, and lotic species.

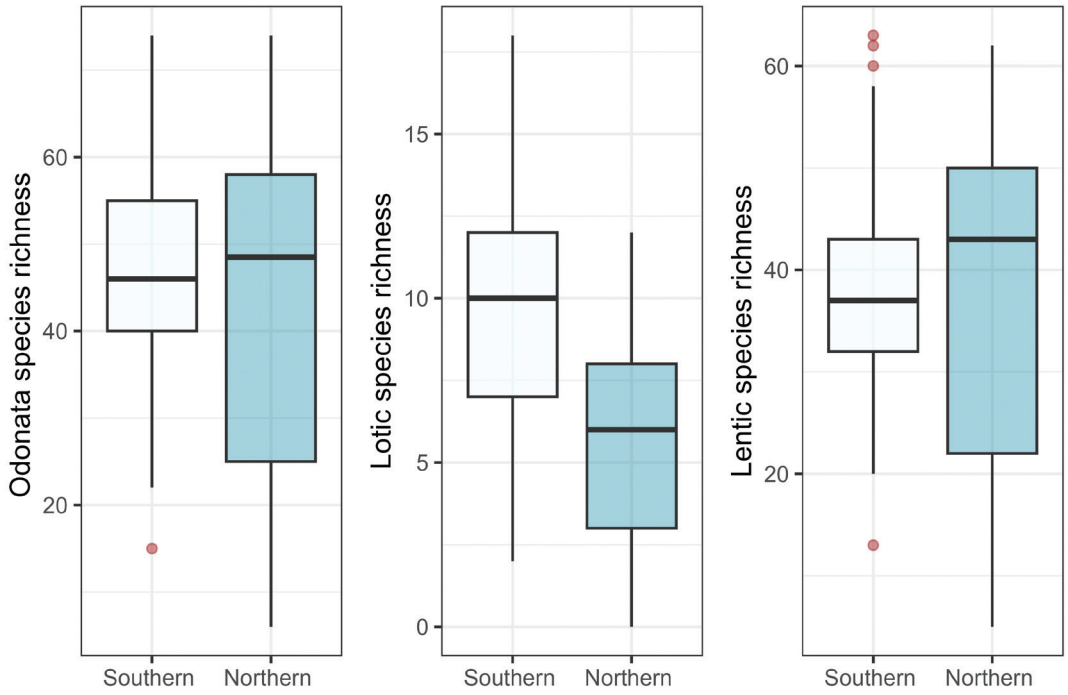

Figure 3. Box plots showing the differences in species richness per grid cell between Northern and Southern Europe for each study group: all odonates, lotic species, and lentic species.

Table 1. Mann-Whitney U-test results comparing Northern and Southern Europe species richness per grid cell. Median values of richness (see Fig. 3) and the regional species pool.

Group	*p*	U	Median richness		Regional pool	
			South	North	South	North
All odonates	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

These results confirm that all species 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 all odonates' richness and that its impact varies between northern and southern regions (H2 and P2.1). Additionally, including lentic (-0.041; $p < 0.001$) and lotic (0.066; $p < 0.001$) habitats, affects the richness of all species, particularly in the north, confirming that species richness is influenced by habitat availability (H3).

When subdividing all odonates into lotic and lentic species, we found consistent patterns explained primarily by the water-energy hypothesis and past climate (Table 2 and Suppl. material 4). 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 (0.206; $p < 0.001$). It is noteworthy that the availability of lotic habitats also has a positive effect on the species richness patterns of northern

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

	Variable	North		South	
		S.C.	*p*	S.C.	*p*
All odonates	Variation in temperature	-0.190	< 0.001	0.017	0.044
	Variation in precipitation	0.049	< 0.001	-0.091	< 0.001
	Temperature	0.215	< 0.001	-0.008	0.220
	Precipitation	-0.169	< 0.001	0.151	< 0.001
	Availability of lentic habitat	-0.041	< 0.001	-0.014	0.006
	Availability of lotic habitat	0.066	< 0.001	0.014	0.010
	PCNM1	0.109	0.482	0.319	< 0.05
	Pseudo R^2	0.593		0.349	
Lotic species	Variation in temperature	-0.226	< 0.001	-0.185	< 0.001
	Variation in precipitation	0.028	< 0.001	-0.348	0.018
	Temperature	0.206	< 0.001	0.206	< 0.001
	Precipitation	-0.141	< 0.001	0.431	< 0.001
	Availability of lotic habitat	0.126	< 0.001	0.054	0.546
	PCNM1	-0.853	< 0.05	-0.504	0.117
	Pseudo R^2	0.444		0.229	
Lentic species	Variation in temperature	-0.197	< 0.001	0.065	< 0.001
	Variation in precipitation	0.060	0.186	-0.037	< 0.001
	Temperature	0.212	< 0.001	-0.055	< 0.001
	Precipitation	-0.191	< 0.001	0.092	< 0.001
	Availability of lentic habitat	-0.022	< 0.001	-0.003	< 0.001
	PCNM1	0.005	0.977	0.375	< 0.05
	Pseudo R^2	0.589		0.460	

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 Suppl. material 4). These results together highlight the strong influence of both past and current climate on European lotic and lentic odonates' richness patterns.

Partitioning of explained deviances

Our results highlight the primary roles of past and current climates in explaining the current species richness of all odonates in Europe. Deviance partitioning shows that in the south, current climate predominantly determines species richness of each study group (all odonates, 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 each group; 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 two study areas (Northern and Southern Europe) (Fig. 4).

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 and Ribera 2003). Nonetheless, we find support for the water-energy hypothesis in the form outlined by 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 all odonates 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 those obtained by Keil et al. (2008), where the pattern of all Odonata species richness in Europe and North Africa is studied in detail, and by Fattorini (2022) describing a southward decline in the Italian odonate richness pattern as an effect of the precipitation gradient.

We also obtain evidence that there is a clear effect of past climate in southern and northern Europe, being higher for the north than for the south, as found in Odonata before (Pinkert et al. 2018; Fattorini 2022) 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

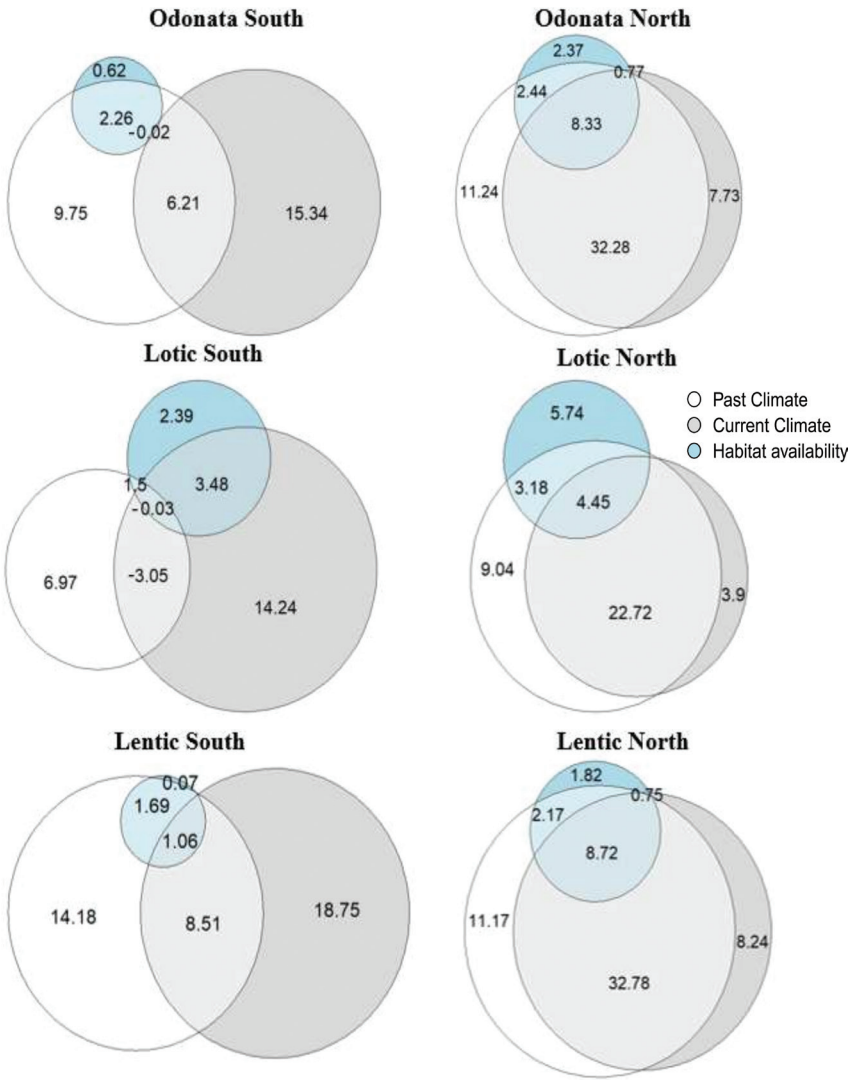

Figure 4. Deviance partitioning results expressed as percentages of explained deviance of each independent and joint fraction of the predictors for each study group (all odonates, lotic species, lentic species) in the two study areas (Northern and Southern Europe).

temperature north of the 0 °C isotherm at 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, the past climate influences all 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 deviance partitioning provides additional support for this pattern, showing that past climate explains more of the variation in species richness than current climate, particularly in the north.

The effect of the past climate on the species richness can, at least in part, be attributed to the extensive ice and snow glacial sheets that covered the north, resulting in an impoverished fauna and flora (Hewitt 1999; Hortal et al. 2011; Kalkman et al. 2018; Calatayud et al. 2019). In fact, deviance partitioning results show that in northern Europe, the combined effect of past and present climate accounts for most of the explained variation, suggesting that their spatial patterns are strongly correlated and difficult to disentangle. This overlap likely reflects the long-lasting imprint of glacial history on present-day environmental conditions and species distributions (Hewitt 1999; Hortal et al. 2011; Calatayud et al. 2019). This contrasts with southern Europe, where current climate alone explains a larger part of the variation for lentic species, which is reflected in the overall models for all odonates. This is likely a result linked to this particular region as it is not so exposed to climatic oscillations and, moreover, a climatic refugia (Kalkman et al. 2018; see Morales-Barbero 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 (Adams and Woodward 1989; Blondel and Mourer-Chauviré 1998; Gaston and Blackburn 2000). Interestingly,

although habitat availability has a minor effect compared to current climate and climate variability, its effect on lotic species is relevant regardless of the region.

The species richness patterns for all odonates observed in this study resemble 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 results and Kalkman et al. (2018). This difference may be due to the data used, since we consider a larger number of species compiled from multiple sources, thus providing a more comprehensive dataset. On the other hand, there are large differences in the distribution patterns shown by lentic and lotic species, a result previously found by other studies (Ribera and Vogler 2000; Ribera et al. 2003; 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 (Ribera et al. 2001; Hof et al. 2006). Lotic species have a more southern distribution, with the peak of richness centered in the south of France and the north of Spain, mainly in the Massif Central and the Pyrenees. In contrast, lentic species are found mainly in central and western Europe. These differences may be due to the spatio-temporal characteristics of both habitat types. Since lentic habitats 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 (Ribera and Vogler 2000; 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 northwards after the glaciations. These observations confirm that the differences in richness would be more pronounced for lotic species, which are worse dispersers, compared to lentic species (P2.3). 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 higher in southern Europe for each of the species groups we studied. 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 (Ribera and Vogler 2000; Ribera et al. 2003; Hof et al. 2006).

Both the current and past climate have had 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 (Dynesius and Jansson 2000; Kalkman et al. 2018). This idea is corroborated for tropical species according to McCauley (2007) and Harabiš and Dolný (2011). If this holds for temperate environments, it could also explain why species adapted to lotic ecosystems do not disperse northward (Fig. 2): being habitat specialists, they would need stepping stones in intermediate areas to move.

Besides that, all odonates' species richness presents a positive relationship with lotic habitat availability, and a negative relationship with lentic habitat availability. Indeed, lotic species richness shows a positive and significant relationship with habitat availability, both in southern and northern Europe. 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 that species richness of all odonates increases in areas where habitat availability is higher (P3.1), and that lotic species richness is positively correlated with the amount of river streams (P3.2). This supports the idea that habitat availability acts as a key driver of species richness by providing more resources, niches, and/or opportunities for species establishment and persistence. In contrast, in southern Europe the observed relationship between these variables is not significant, failing to confirm our prediction that lentic species richness is expected to be higher in areas with more ponds and lakes (P3.6). 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 (Ribera and Vogler 2000; Grewe et al. 2013). Having a greater dispersal capacity, they exhibit broader species distributions, and are less dependent on habitat availability. In contrast, lotic species have a lower dispersal capacity, making them more dependent on habitat availability (Ribera and Vogler 2000; 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 all odonates is primarily determined by the effects of current climate and past climatic changes, and to a lesser extent by habitat availability. Our findings underline the dominant role of water-energy balance in shaping the distribution of European odonate species richness, with temperature driving the decline towards the north and precipitation influencing the southern limits, as conjectured by Hawkins et al. (2003). Additionally, the legacy of past climate oscillations is still evident in current species richness patterns, reinforcing the importance of historical climate dynamics in shaping biodiversity. In northern Europe, past climate influences more than current climate, for all species (both lotic and lentic and therefore in all odonates), while in southern Europe the current climate alone has a greater influence for lentic species, which in turn is reflected in all odonates as a whole. These results underscore the interplay between equilibrium (current climate) and non-equilibrium (historical events) processes in shaping biodiversity patterns.

Our study highlights how ecological and evolutionary constraints related to habitat specialization contribute to diversity patterns, as evidenced by the significant differences in the distribution 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, which tend to be more habitat-specialized, remain concentrated in southern Europe, potentially reflecting limitations in their dispersal capacity. In contrast, the lower temporal stability of lentic habitats has likely favoured greater dispersal capacity in lentic species, facilitating their broader northern distribution (see also Hof et al. 2006; Kalkman et al. 2018). These differences in the responses of lotic and lentic species emphasize the need to integrate species' ecological traits when interpreting diversity patterns.

Overall, our findings contribute to the understanding of diversity gradients in semi-aquatic insects, offering perspective that may be appropriate to other taxa with life cycles that depend on the aquatic environment. The opposite responses of lotic and lentic species suggest that the equilibrium between dispersal and habitat specialization is a crucial factor that determines the large-scale diversity patterns. 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 capabilities in natural versus human-altered habitats; and (3) explore how species interactions (competition, predation, mutualism) vary between lotic and lentic habitats and how these interactions influence dispersal and community structure.

Acknowledgements

This work was funded by Spanish AEI projects NICED (grant PID2022-140985NB-C21) and SCENIC (grant PID2019-106840GB-C21), funded by MCIN/AEI/10.13039/501100011033 / FEDER, EU. MGV was funded by AEI / PRE23_MNCN_207. FA-M was supported via the European Union's Horizon 2020 research and innovation programme under the ERA Chairs (grant agreement #854248; project: TROPIBIO).

Author contributions

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

Data accessibility statement

Data for this work comes from open access databases available in digital.CSIC at 10.20350/digitalCSIC/12535. R Code and cleaned dataset used for the analyses are available in https://github.com/mgomezv26/European_odonate_species_richness_2024.

References

Adams JM, Woodward FI (1989) Patterns in tree species richness as a test of the glacial extinction hypothesis. Nature 339: 699–701. https://doi.org/10.1038/339699a0

Alves-Martins F, Calatayud J, Medina NG, De Marco P, Juen L, Hortal J (2019) Drivers of regional and local diversity of Amazonian stream Odonata. Insect Conservation and Diversity 12: 251–261. https://doi.org/10.1111/icad.12327

Alves-Martins F, Stropp J, Juen L, Ladle RJ, Lobo JM, Martinez-Arribas J, Júnior PDM, Brasil LS, Ferreira VRS, Bastos RC, Córdoba-Aguilar A, Medina-Espinoza EF, Dutra S, Vilela DS, Cordero-Rivera A, del Palacio A, Ramírez A, Carvalho-Soares AA, Farias ABS, de Resende BO, dos Santos B, Bota-Sierra CA, Mendoza-Penagos CC, Veras DS, Anjos-Santos D, Périco E, González-Soriano E, de Oliveira Roque F, Lozano F, de Carvalho FG, Lencioni FAA, Palacino-Rodríguez F, Ortega-Salas H, Venâncio H, Sanmartín-Villar I, Muzón J, Santos JC, Montes-Fontalvo J, da Silva Brito J, da Silva Pereira JL, Oliveira-Junior JMB, Dias-Silva K, Ferreira KG, Calvão LB, Pérez-Gutiérrez LA, Rodrigues ME, Dalzochio MS, Rocha-Ortega M, von Ellenrieder N, Hamada N, Pessacq P, Rodríguez P, Martins RT, Guillermo-Ferreira R, Koroiva R, Miguel TB, Mendes TP, Neiss UG, de Almeida WR, Hortal J (2024) Sampling completeness changes perceptions of continental scale climate-species richness relationships in odonates. Journal of Biogeography 51: 1148–1162. https://doi.org/10.1111/jbi.14810

Allen AP, Gillooly JF, Brown JH (2007) Recasting the species-energy hypothesis: the different roles of kinetic and potential energy in regulating biodiversity. In: Storch D, Marquet P, Brown J (Eds) Scaling Biodiversity. Cambridge University Press, Cambridge, 283–299. https://doi.org/10.1017/CBO9780511814938.016

Askew RR (2004) The Dragonflies of Europe (revised edn). Harley Books, Colchester, United Kingdom, 308 pp. https://doi.org/10.1163/9789004474383

Araújo MB, Nogués-Bravo D, Diniz-Filho JAF, Haywood AM, Valdes PJ, Rahbek C (2008) Quaternary climate changes explain diversity among reptiles and amphibians. Ecography 31: 8–15. https://doi.org/10.1111/j.2007.0906-7590.05318.x

Auguie B, Antonov A (2017) gridExtra: Miscellaneous Functions for "Grid" Graphics. https://cran.r-project.org/web/packages/gridExtra/index.html [June 12, 2025]

Beatty CD, Alves-Martins F, Smith BD, Verheyen J (2022) Biogeographical ecology in Odonata. In: Cordoba-Aguilar A, Beatty C, Bried J (Eds) Dragonflies and Damselflies: Model Organisms for Ecological and Evolutionary Research. Oxford University Press, 0. https://doi.org/10.1093/oso/9780192898623.003.0013

Blondel J, Mourer-Chauviré C (1998) Evolution and history of the western Palaearctic avifauna. Trends in Ecology & Evolution 13: 488–492. https://doi.org/10.1016/S0169-5347(98)01461-X

Boudot JP, Kalkman VJ (2015**)** Atlas of the European dragonflies and damselflies. KNNV Publishing, Netherlands.

Braconnot P, Otto-Bliesner B, Harrison S, Joussaume S, Peterchmitt J-Y, Abe-Ouchi A, Crucifix M, Driesschaert E, Fichefet T, Hewitt CD, Kageyama M, Kitoh A, Laîné A, Loutre M-F, Marti O, Merkel U, Ramstein G, Valdes P, Weber SL, Yu Y, Zhao Y (2007) Results of PMIP2 coupled simulations of the Mid-Holocene and Last Glacial Maximum – Part 1: experiments and large-scale features. Climate of the Past 3: 261–277. https://doi.org/10.5194/cp-3-261-2007

Calatayud J, Hortal J, Medina NG, Turin H, Bernard R, Casale A, Ortuño VM, Penev L, Rodríguez MÁ (2016) Glaciations, deciduous forests, water availability and current geographical patterns in the diversity of European Carabus species. Journal of Biogeography 43: 2343–2353. https://doi.org/10.1111/jbi.12811

Calatayud J, Rodríguez MÁ, Molina-Venegas R, Leo M, Horreo JL, Hortal J (2019) Pleistocene climate change and the formation of regional species pools. Proceedings of the Royal Society B: Biological Sciences 286: 20190291. https://doi.org/10.1098/rspb.2019.0291

Cancellario T, Miranda R, Baquero E, Fontaneto D, Martínez A, Mammola S (2022) Climate change will redefine taxonomic, functional, and phylogenetic diversity of Odonata in space and time. npj Biodiversity 1: 1–14. https://doi.org/10.1038/s44185-022-00001-3

Corbet PS (1999) Dragonflies: Behaviour and Ecology of Odonata. Harley Books, Colchester, United Kingdom.

European Union's Copernicus Land Monitoring Service (2018) CORINE Land Cover Change 2012–2018 (vector/raster 100 m), Europe, 6-yearly. https://land.copernicus.eu/pan-european/corine-land-cover/lcc-2012-2018 [Visited on 12/06/2025]

Dray S, Legendre P, Peres-Neto PR (2006) Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling 196: 483–493. https://doi.org/10.1016/j.ecolmodel.2006.02.015

Dehling DM, Hof C, Brändle M, Brandl R (2010) Habitat availability does not explain the species richness patterns of European lentic and lotic freshwater animals. Journal of Biogeography 37: 1919–1926. https://doi.org/10.1111/j.1365-2699.2010.02347.x

Dijkstra KDB, Lewington R (2006) Field Guide to the Dragonflies of Britain and Europe. British Wildlife Publishing, Gillingham, Dorset.

Dynesius M, Jansson R (2000) Evolutionary consequences of changes in species' geographical distributions driven by Milankovitch climate oscillations. Proceedings of the National Academy of Sciences 97: 9115–9120. https://doi.org/10.1073/pnas.97.16.9115

European Environment Agency (2018) EEA reference grids. https://www.eea.europa.eu/data-and-maps/data/eea-reference-grids-2 [Visited on 12/06/2025]

EuroGeographics (2021) EuroGlobalMap. https://www.mapsforeurope.org/datasets/euro-global-map [Visited on 12/06/2025]

Fahrig L (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. Journal of Biogeography 40: 1649–1663. https://doi.org/10.1111/jbi.12130

Fattorini S (2022) Odonate Diversity Patterns in Italy Disclose Intricate Colonization Pathways. Biology 11: 886. https://doi.org/10.3390/biology11060886

Gaston KJ, Blackburn TM (2000) Pattern and process in macroecology. Blackwell Science, Oxford, United Kingdom, 377 pp. https://doi.org/10.1002/9780470999592

GBIF (2020) GBIF Occurrence Download. https://doi.org/10.15468/dl.r9m6nw

Gómez Vadillo M, Ronquillo C, Hortal J (2020) Mapas de distribución geográfica de Odonatos de Europa a partir de Atlas de distribución y bases de datos online. DIGITAL.CSIC, Madrid.

Grewe Y, Hof C, Dehling DM, Brandl R, Brändle M (2013) Recent range shifts of European dragonflies provide support for an inverse relationship between habitat predictability and dispersal. Global Ecology and Biogeography 22: 403–409. https://doi.org/10.1111/geb.12004

Hanski I (2015) Habitat fragmentation and species richness. Journal of Biogeography 42: 989–993. https://doi.org/10.1111/jbi.12478

Harabiš F, Dolný A (2011) The effect of ecological determinants on the dispersal abilities of central European dragonflies (Odonata). Odonatologica 40: 17

Hawkins BA, Field R, Cornell HV, Currie DJ, Guégan J-F, Kaufman DM, Kerr JT, Mittelbach GG, Oberdorff T, O'Brien EM, Porter EE, Turner JRG (2003) Energy, water, and broad-scale geographic patterns of species richness. Ecology 84: 3105–3117. https://doi.org/10.1890/03-8006

Hawkins BA, Diniz-Filho JAF, Soeller SA (2005) Water links the historical and contemporary components of the Australian bird diversity gradient. Journal of Biogeography 32: 1035–1042. https://doi.org/10.1111/j.1365-2699.2004.01238.x

Heiser M, Schmitt T (2010) Do different dispersal capacities influence the biogeography of the western Palaearctic dragonflies (Odonata)? Biological Journal of the Linnean Society 99: 177–195. https://doi.org/10.1111/j.1095-8312.2009.01349.x

Hewitt GM (1999) Post-glacial re-colonization of European biota. Biological Journal of the Linnean Society 68: 87–112. https://doi.org/10.1111/j.1095-8312.1999.tb01160.x

Hof C, Brändle M, Brandl R (2006) Lentic odonates have larger and more northern ranges than lotic species. Journal of Biogeography 33: 63–70. https://doi.org/10.1111/j.1365-2699.2005.01358.x

Hof C, Brändle M, Brandl R (2008) Latitudinal variation of diversity in European freshwater animals is not concordant across habitat types. Global Ecology and Biogeography 17: 539–546. https://doi.org/10.1111/j.1466-8238.2008.00394.x

Hortal J, Triantis KA, Meiri S, Thébault E, Sfenthourakis S (2009) Island Species Richness Increases with Habitat Diversity. The American Naturalist 174: E205–E217. https://doi.org/10.1086/645085

Hortal J, Carrascal LM, Triantis KA, Thébault E, Meiri S, Sfenthourakis S (2013) Species richness can decrease with altitude but not with habitat diversity. Proceedings of the National Academy of Sciences 110: E2149–E2150. https://doi.org/10.1073/pnas.1301663110

Hortal J, Diniz-Filho JAF, Bini LM, Rodríguez MÁ, Baselga A, Nogués-Bravo D, Rangel TF, Hawkins BA, Lobo JM (2011) Ice age climate, evolutionary constraints and diversity patterns of European dung beetles. Ecology Letters 14: 741–748. https://doi.org/10.1111/j.1461-0248.2011.01634.x

Kalkman VJ, Boudot J-P, Bernard R, De Knijf G, Suhling F, Termaat T (2018) Diversity and conservation of European dragonflies and damselflies (Odonata). Hydrobiologia 811: 269–282. https://doi.org/10.1007/s10750-017-3495-6

Keil P, Simova I, Hawkins BA (2008) Water-energy and the geographical species richness pattern of European and North African dragonflies (Odonata). Insect Conservation and Diversity 1: 142–150. https://doi.org/10.1111/j.1752-4598.2008.00019.x

Larsson J, Godfrey AJR, Gustafsson P, Eberly DH, Huber E, Privé F (2024) eulerr: Area-Proportional Euler and Venn Diagrams with Ellipses. https://cran.r-project.org/web/packages/eulerr/index.html [Visited on 12/06/2025]

MacArthur RH (1964) Environmental Factors Affecting Bird Species Diversity. The American Naturalist 98: 387–397. https://doi.org/10.1086/282334

McCauley SJ (2007) The role of local and regional processes in structuring larval dragonfly distributions across habitat gradients. Oikos 116: 121–133. https://doi.org/10.1111/j.2006.0030-1299.15105.x

Morales-Barbero J, Martinez PA, Ferrer-Castán D, Olalla-Tárraga MÁ (2018) Quaternary refugia are associated with higher speciation rates in mammalian faunas of the Western Palaearctic. Ecography 41: 607–621. https://doi.org/10.1111/ecog.02647

Moran PAP (1948) The Interpretation of Statistical Maps. Journal of the Royal Statistical Society: Series B (Methodological) 10: 243–251. https://doi.org/10.1111/j.2517-6161.1948.tb00012.x

O'Brien E (1998) Water-energy dynamics, climate, and prediction of woody plant species richness: an interim general model. Journal of Biogeography 25: 379–398. https://doi.org/10.1046/j.1365-2699.1998.252166.x

Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Solymos P, Stevens MHH, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Borman T, Carvalho G, Chirico M, Caceres MD, Durand S, Evangelista HBA, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill MO, Lahti L, Martino C, McGlinn D, Ouellette M-H, Cunha ER, Smith T, Stier A, Braak CJFT, Weedon J (2025) vegan: Community Ecology Package. https://cran.r-project.org/web/packages/vegan/index.html [Visited on 12/06/2025]

Paradis E, Schliep K (2019) ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. Bioinformatics 35: 526–528. https://doi.org/10.1093/bioinformatics/bty633

Pedersen TL (2024) patchwork: The Composer of Plots. https://cran.r-project.org/web/packages/patchwork/index.html [Visited on 12/06/2025]

Pinkert S, Dijkstra KDB, Zeuss D, Reudenbach C, Brandl R, Hof C (2018) Evolutionary processes, dispersal limitation and climatic history shape current diversity patterns of European dragonflies. Ecography 41: 795–804. https://doi.org/10.1111/ecog.03137

Rangel TF, Diniz-Filho JAF, Bini LM (2010) SAM: a comprehensive application for Spatial Analysis in Macroecology. Ecography 33: 46–50. https://doi.org/10.1111/j.1600-0587.2009.06299.x

Ribera I, Ribera AP (2000) Habitat type as a determinant of species range sizes: the example of lotic-lentic differences in aquatic Coleoptera. Biological Journal of the Linnean Society 71: 33–52. https://doi.org/10.1111/j.1095-8312.2000.tb01240.x

Ribera I, Barraclough TG, Vogler AP (2001) The effect of habitat type on speciation rates and range movements in aquatic beetles: inferences from species-level phylogenies. Molecular Ecology 10: 721–735. https://doi.org/10.1046/j.1365-294x.2001.01218.x

Ribera I, Foster GN, Vogler AP (2003) Does habitat use explain large scale species richness patterns of aquatic beetles in Europe? Ecography 26: 145–152. https://doi.org/10.1034/j.1600-0587.2003.03271.x

Rodríguez MÁ, Belmontes JA, Hawkins BA (2005) Energy, water and large-scale patterns of reptile and amphibian species richness in Europe. Acta Oecologica 28: 65–70. https://doi.org/10.1016/j.actao.2005.02.006

R Core Team (2023) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/ [Visited on 12/06/2025]

Ronquillo C, Stropp J, Hortal J (2024) OCCUR Shiny application: A user-friendly guide for curating species occurrence records. Methods in Ecology and Evolution 15: 816–823. https://doi.org/10.1111/2041-210X.14271

RStudio Team (2024) RStudio: Integrated Development Environment for R (Version 2023.12.1+402 "Ocean Storm" Release). RStudio, PBC, Boston, MA. https://www.rstudio.com/ [Visited on 12/06/2025]

Santos AMC, Cianciaruso MV, Barbosa AM, Bini LM, Diniz-Filho JAF, Faleiro FV, Gouveia SF, Loyola R, Medina NG, Rangel TF, Tessarolo G, Hortal J (2020) Current climate, but also long-term climate changes and human impacts, determine the geographic distribution of European mammal diversity. Global Ecology and Biogeography 29: 1758–1769. https://doi.org/10.1111/geb.13148

Segovia RA (2023) Temperature predicts maximum tree-species richness and water availability and frost shape the residual variation. Ecology 104: e4000. https://doi.org/10.1002/ecy.4000

Stefanescu C, Carnicer J, Peñuelas J (2011) Determinants of species richness in generalist and specialist Mediterranean butterflies: the negative synergistic forces of climate and habitat change. Ecography 34: 353–363. https://doi.org/10.1111/j.1600-0587.2010.06264.x

Storch D, Konvicka M, Benes J, Martinková J, Gaston KJ (2003) Distribution patterns in butterflies and birds of the Czech Republic: separating effects of habitat and geographical position. Journal of Biogeography 30: 1195–1205. https://doi.org/10.1046/j.1365-2699.2003.00917.x

Svenning JC, Skov F (2007a) Could the tree diversity pattern in Europe be generated by postglacial dispersal limitation? Ecology Letters 10: 453–460. https://doi.org/10.1111/j.1461-0248.2007.01038.x

Svenning JC, Skov F (2007b) Ice age legacies in the geographical distribution of tree species richness in Europe. Global Ecology and Biogeography 16: 234–245. https://doi.org/10.1111/j.1466-8238.2006.00280.x

Svenning JC, Normand S, Skov F (2008) Postglacial dispersal limitation of widespread forest plant species in nemoral Europe. Ecography 31: 316–326. https://doi.org/10.1111/j.0906-7590.2008.05206.x

Termaat T, van Strien AJ, van Grunsven RHA, De Knijf G, Bjelke U, Burbach K, Conze K-J, Goffart P, Hepper D, Kalkman VJ, Motte G, Prins MD, Prunier F, Sparrow D, van den Top GG, Vanappelghem C, Winterholler M, WallisDeVries MF (2019) Distribution trends of European dragonflies under climate change. Diversity and Distributions 25: 936–950. https://doi.org/10.1111/ddi.12913

Vilela B, Villalobos F (2015) letsR: a new R package for data handling and analysis in macroecology. Methods in Ecology and Evolution 6: 1229–1234. https://doi.org/10.1111/2041-210X.12401

Vogler AP, Ribera I (2003) Evolutionary analysis of species richness patterns in aquatic beetles: why macroecology needs a historical perspective. In: Blackburn TM, Gaston KJ (Eds) Macroecology: Concepts and Consequences. Blackwell Science, Oxford, United Kingdom, 17–30.

Whittaker RJ, Nogués-Bravo D, Araújo MB (2007) Geographical gradients of species richness: a test of the water-energy conjecture of using European data for five taxa. Global Ecology and Biogeography 16: 76–89. https://doi.org/10.1111/j.1466-8238.2006.00268.x

Wickham H, Chang W, Henry L, Pedersen TL, Takahashi K, Wilke C, Woo K (2023) ggplot2: Elegant Graphics for Data Analysis. R package version 3.5.0. https://ggplot2.tidyverse.org [Visited on 12/06/2025]

Supplementary materials

Supplementary material 1

Zygoptera species included in the analyses (.pdf)
Link: https://doi.org/10.21425/fob.18.136933.suppl1

Supplementary material 2

Species eliminated during the data cleaning and preparation process (.pdf)
Link: https://doi.org/10.21425/fob.18.136933.suppl2

Supplementary material 3

Preliminary analysis that evaluated the relevance of classifying all species according to their habitat type (lentic or lotic) rather than their suborder (Anisoptera or Zygoptera) (.pdf)
Link: https://doi.org/10.21425/fob.18.136933.suppl3

Supplementary material 4

Relationships between richness, climate, climate stability, and habitat availability (.pdf)
Link: https://doi.org/10.21425/fob.18.136933.suppl4

Supplementary material 5

Anisoptera species included in the analyses (.docx)
Link: https://doi.org/10.21425/fob.18.136933.suppl5