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Research

Evolutionary processes, dispersal limitation and climatic history shape current diversity patterns of European dragonflies

Stefan Pinkert, Klaas-Douwe B. Dijkstra, Dirk Zeuss, Christoph Reudenbach, Roland Brandl and Christian Hof

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Ecography

41: 795–804, 2018

doi: 10.1111/ecog.03137

Subject Editor:

Jens-Christian Svenning

Editor-in-Chief: Miguel Araújo

Accepted 24 May 2017

We investigated the effects of contemporary and historical factors on the spatial variation of European dragonfly diversity. Specifically, we tested to what extent patterns of endemism and phylogenetic diversity of European dragonfly assemblages are structured by 1) phylogenetic conservatism of thermal adaptations and 2) differences in the ability of post-glacial recolonization by species adapted to running waters (lotic) and still waters (lentic). We investigated patterns of dragonfly diversity using digital distribution maps and a phylogeny of 122 European dragonfly species, which we constructed by combining taxonomic and molecular data. We calculated total taxonomic distinctiveness and mean pairwise distances across 4192 50 × 50 km equal-area grid cells as measures of phylogenetic diversity. We compared species richness with corrected weighted endemism and standardized effect sizes of mean pairwise distances or residuals of total taxonomic distinctiveness to identify areas with higher or lower phylogenetic diversity than expected by chance. Broken-line regression was used to detect breakpoints in diversity–latitude relationships. Dragonfly species richness peaked in central Europe, whereas endemism and phylogenetic diversity decreased from warm areas in the south-west to cold areas in the north-east and with an increasing proportion of lentic species. Except for species richness, all measures of diversity were consistently higher in formerly unglaciated areas south of the 0°C isotherm during the Last Glacial Maximum than in formerly glaciated areas. These results indicate that the distributions of dragonfly species in Europe were shaped by both phylogenetic conservatism of thermal adaptations and differences between lentic and lotic species in the ability of post-glacial recolonization/dispersal in concert with the climatic history of the continent. The complex diversity patterns of European dragonflies provide an example of how integrating climatic and evolutionary history with contemporary ecological data can improve our understanding of the processes driving the geographical variation of biological diversity.



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Introduction

It was recognized early on that broad-scale patterns of species richness generally correlate well with gradients of current temperature and with available water and energy (Humboldt and Bonpland 1806). Statistical correlations inferred from contemporary macroecological patterns support the hypothesis that current environmental factors are major determinants of the spatial variation of biodiversity (Waide et al. 1999, Hawkins et al. 2003, Willig et al. 2003). However, studies focusing on species richness alone cannot take into account the evolutionary history of regions and lineages, even though this may carry important information on the major factors that have shaped the current distribution of biodiversity, such as dispersal and diversification (Ricklefs 2004). Therefore, the combination of macroecological and macroevolutionary, i.e. contemporary and historical approaches, should improve our understanding of the broad-scale variation of life on Earth (Ricklefs 2004, Wiens and Donoghue 2004, Mittelbach et al. 2007).

One promising approach for elucidating the macroecological and macroevolutionary processes (e.g. past dispersal and diversification events) that shape species assemblages is to analyse phylogenetic diversity in relation to expectations based on species richness and random assembly processes (Buckley et al. 2010, Cadotte et al. 2010, Fritz and Rahbek 2012). If, for instance, phylogenetic diversity is higher than expected by chance, this might be due to high levels of in situ diversification or immigration of multiple lineages, which may be caused by a long history of the region that provides more time for diversification and the accumulation of diversity (time-for-speciation effect; Stephens and Wiens 2003). Conversely, if phylogenetic diversity of an assemblage is lower than expected by chance, this might be an outcome of strong phylogenetic constraints restricting the evolution of the fundamental niches of species, which leads to the co-occurrence of closely related species, e.g. due to shared responses to similar environmental factors (Ackerly 2003).

Dragonflies and damselflies (together referred to as dragonflies for simplicity) are poikilothermic organisms that require energy from their abiotic environment for mobility (Huey and Kingsolver 1989) and for fundamental physiological processes (e.g. development time; Gillooly et al. 2002). This requirement links their fitness and survival and hence links their distribution directly to the climate of a geographical area (Huey and Kingsolver 1989). The ancestor of dragonflies is probably a warm-adapted taxon from the Carboniferous (Corbet 2004); nonetheless, they were able to colonize even the coldest and driest parts of all continents except Antarctica (Kalkman et al. 2008). Therefore, the present-day distribution of dragonfly diversity is considered to be the result of tropical niche conservatism that allowed only a few cold-adapted and, hence, younger lineages to colonize and persist in temperate climates (cf. Tillyard 1916, May 1976), generating a gradient of decreasing phylogenetic

diversity with decreasing temperature. However, this long-standing hypothesis is challenged by the fact that dragonfly species richness peaks within the latitudinal domains of North America and Europe around the mid-latitudes (Fig. 1 and Kalkman et al. 2008).

In a previous study, we have shown that patterns of species richness of European freshwater organisms that develop in still waters (lentic) show a hump-shaped latitudinal gradient, while the richness of species that develop in running waters (lotic) declines gradually towards the north (Hof et al. 2008). These two contrasting biogeographical patterns might reflect the ecological differences of lentic species that have evolved as an adaptation to the lower spatial and temporal stability and persistence of lentic habitats (Ribera et al. 2003). Indeed, lentic species seem to have more northern ranges (Hof et al. 2006) and greater dispersal propensity (Ribera et al. 2003, Hof et al. 2012, Grewe et al. 2013) than lotic species. Some lentic species are also able to avoid inhospitable conditions through long-distance migration or a diapause state (Corbet 2004, p. 385). Owing to these adaptations, lentic species should have an advantage over lotic species in colonizing and persisting in ditches and seasonal ponds, but also in areas with pronounced seasonal temperature variation.

Since only a few extant dragonfly species are found at annual mean temperatures below the freezing point (Fig. 1), most of them probably retreated from large parts of northern and central Europe during the Last Glacial Maximum (LGM). Hence, the diversity of contemporary assemblages might be mainly recruited from refugia in the Mediterranean basin and Siberia (Sternberg 1998). If the ecological differences between lentic and lotic species carry a phylogenetic

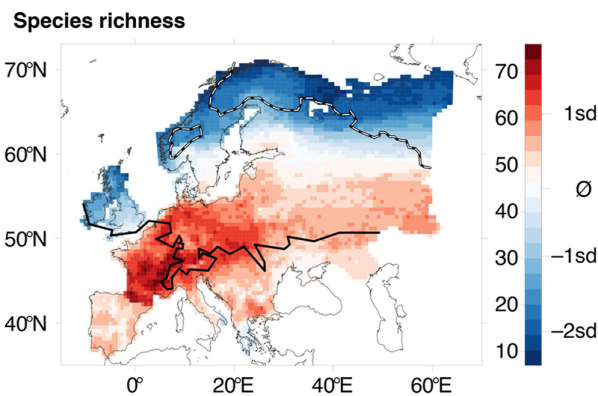


Figure 1. Geographical distribution of the total species richness across 4192 assemblages of European dragonflies (EPSG: 4326; equal-area grid CGRS). The solid black line indicates the location of the 0°C isotherm at the Last Glacial Maximum (21 ka); the dashed black line indicates its present location. Colour class intervals are scaled according to equal class breath, centred on the mean in a bipolar colour space. Note that only a few extant dragonfly species are found in areas with annual mean temperatures below the freezing point. The relationship between species richness of dragonfly assemblages and latitude is not a monotonic gradient, but rather a hump-shaped curve.

signal, we would expect that assemblages in previously glaciated areas are composed of a closely related subset of lentic species. By contrast, the climatic stability of unglaciated areas in the Mediterranean basin should have supported the accumulation of both lentic and lotic lineages. Given the limited time available since the LGM, we would furthermore predict that incomplete recolonization results in a marked decrease in the diversity of dragonfly assemblages at a certain latitudinal breakpoint (Castro-Insua et al. 2016), for instance at the southern border of the zone of discontinuous permafrost at the LGM along the historical 0°C isotherm.

Here, we investigated to which extent contemporary and historical factors have influenced current diversity patterns of European dragonfly assemblages. We hypothesized that patterns of endemism and phylogenetic diversity are influenced 1) by phylogenetic conservatism of thermal adaptations, and 2) by differences in post-glacial recolonization that are related to the habitat preferences of species. As lentic species are assumed to have stronger dispersal abilities, they might also have an advantage in recolonizing previously glaciated areas. Based on these hypotheses, we predict that endemism and phylogenetic diversity decrease 1) with decreasing temperature, and 2) with an increasing proportion of lentic species. Furthermore, both relationships should show a marked change around the 0°C isotherm during the LGM.

Material and methods

For our analysis, we combined distribution data and a phylogenetic tree of 122 European dragonfly species with information on their habitat preferences and data on the contemporary climate. Sixteen other European dragonfly species were not considered because their systematic position was unclear, but these species either occur only marginally in the far south or do not maintain stable populations in Europe at all (for a species list with brief explanations, see Supplementary material Appendix 1 Table A1).

Distribution and trait data

Digital distribution maps from two IUCN Red List assessments (Riservato et al. 2009, Kalkman et al. 2010) were reassigned to an equal-area grid (CGRS, cell size of approximately 50 × 50 km) with functions provided in the R-package 'RSAGA' (Brenning 2008). Distribution ranges of three additional species were digitized from contour maps published in Dijkstra and Lewington (2006) using QGIS (see maps in Supplementary material Appendix 1 Fig. A1). All islands, except Ireland and Great Britain, and grid cells with less than five species were excluded to avoid the effects of very low sampling sizes for the analysis at the assemblage level (see also Pinkert et al. 2016). Information on habitat preferences (running waters, lotic; still waters, lentic) of dragonfly larvae

was compiled from Dijkstra and Lewington (2006). We converted the three possible categories – only lentic, both lentic and lotic, and only lotic – to ordinal values, i.e. 0, 0.5, and 1, respectively, and averaged this value for all co-occurring species across grid cells (i.e. the proportion of lentic/lotic habitat preferences). The phylogenetic signal in habitat preferences of European dragonfly species was evaluated using Bloomberg's K and Pagel's lambda implemented in the R-package 'phytools' (Revell 2017). These two measures were designed for continuous traits; hence, when we apply them to our data, we imply that the evolution of habitat preferences from lentic to lotic or from lotic to lentic will pass through a mixed strategy, of being generalists. However, this assumption about the evolution of habitat preferences of freshwater species has not been tested. Consequently, we calculated the D statistic (Fritz and Purvis 2010) implemented in the R-package 'caper' (Orme et al. 2013) also for a set of binary habitat preference data in which all species that are adapted to both lentic and lotic habitat are considered only lotic as well as a set in which they are considered only lentic.

Environmental data

The importance of climatic factors for shaping the patterns of endemism and phylogenetic diversity of European dragonfly assemblages was evaluated using 19 biologically relevant temperature and precipitation variables. All variables were downloaded with a resolution of 2.5 arc min from worldclim.org (BIOCLIM; ver. 1.4; current condition records; Hijmans et al. 2005) and reassigned to the resolution of our grid with functions of the R-packages 'raster' (Hijmans 2016). Our primary interest was to show general trends in the relationships between environmental variables and measures of dragonfly diversity; therefore, we summarized temperature and precipitation variables based on a correlation matrix in two principal components, each with functions provided in the R-package 'psych' (Revelle 2016). Because multicollinearity can overemphasize the importance of shared trends in the principal components (i.e. the first principal component might explain most of the variation in the temperature variables, but it does not have to be an important predictor of diversity patterns), we evaluated whether it improves the model fit of our multiple regressions when we select only those four climate variables that contribute most to the principal components. For all of these regressions, the model fit was lower than for the regressions that included the two first principle components of all precipitation variables and temperature variables (Supplementary material Appendix 1 Table A5).

To evaluate the importance of Europe's climatic history, we reconstructed the historical 0°C isotherm based on a downscaled simulation of mean annual temperature at the LGM (21 ka; FGOALS earth system model; Schmatz et al. 2015) using R-packages 'raster' (Hijmans 2016) and 'ncdf4' (Pierce 2017). The geometry of the resulting spatial line object was simplified using the Douglas–Peucker algorithm with functions provided in the R-package 'rgeos' (Bivand and

Rundel 2016). Only the section of the isotherm along the shore was considered. Because there were no data available for the area between 40°E and 48°E, we simply continued the isotherm along 50°N latitude. Note that this part coincides with previous reconstructions of lower resolution (Hortal et al. 2011). In the following, we used the historical 0°C isotherm to categorize unglaciated areas south of the isotherm and previously glaciated areas north of the isotherm.

Statistical analyses

Phylogenetic analysis

Since no phylogeny that includes all European dragonfly species is currently available, we constructed a phylogeny based on taxonomic information and published molecular data. The final phylogeny was calculated from sequences for up to nine different loci and 121 dragonfly species. This included the slowly-evolving loci 5.8S, 18S and 28S for higher-level relationships and the fast-evolving loci ITS, ITS2, 12S, 16S, COI and COII for relationships at lower taxonomic ranks (Storch et al. 2013). Taxonomic information was integrated by enforcing monophyly at 90 internal nodes of the phylogeny (Supplementary material Appendix 1 Fig. A2). The phylogeny that we used in our analysis thus does not challenge the current taxonomic consensus, but instead integrates the detail of molecular differences among species into our current phylogenetic understanding (Supplementary material Appendix 1 Fig. A3). Branch lengths were inferred with an estimated lognormal relaxed molecular clock for 50 million MCMC simulations using Bayesian analysis implemented in BEAST (Drummond et al. 2012; see Supplementary material Appendix 1 for further details). For *Orthetrum cancellatum*, no phylogenetic information, but extensive information on the taxonomic position was available. Therefore, we inserted *O. cancellatum* manually by halving the terminal branch of its sister taxon, *O. albistylum* (Dijkstra and Kalkman 2012; Supplementary material Appendix 1 Table A1).

Measures of diversity

We investigated patterns of dragonfly diversity in terms of three different aspects: species richness, endemism and phylogenetic diversity. Endemism is commonly defined as the proportion of species that are restricted to a certain geographical area. According to this definition, only 18 dragonfly species are endemic to Europe (Kalkman et al. 2010). However, 120 of 138 species have ranges that reach into Asia, northern Africa or the Orient, whose exclusion would have resulted in the loss of relevant information for our analyses. Thus, to integrate these species as well, we used the corrected weighted endemism across grid cells, i.e. the geometric mean of the inverse occupancy of co-occurring species (Williams 2000). Owing to the way it is calculated, corrected weighted endemism places greater emphasis on species with small ranges in Europe. For instance, a species that occurs in one assemblage has a weight of 1 (1/1), whereas a species that occurs in two

assemblages has the weight of 0.5 (1/2). Hence, we interpret high levels of corrected weighted endemism in a region as a high proportion of narrow-ranging species, rather than high endemism in sensu stricto.

In addition, we used two different approaches to identify areas with higher or lower levels of phylogenetic diversity than expected by chance. Both of these approaches are based on the assumption that co-occurring species would represent the same phylogenetic diversity if species-neutral processes had determined their assembly. In the first approach, based on our fully-resolved phylogeny and for each grid cell, we calculated Faith's phylogenetic diversity index, i.e. the sum of the branch lengths of the minimum spanning tree among co-occurring species (Faith 1992), and total taxonomic distinctiveness, i.e. the average phylogenetic distinctiveness summed over all co-occurring species (Warwick and Clarke 2001). We used the function 'ecospat.calculate.pd' provided in the R-packages 'ecospat' (Broennimann et al. 2016) to calculate these metrics, and functions of the R-package 'ape' to handle phylogenetic data in R (Paradis et al. 2004). Following Fritz and Rahbek (2012), we interpreted the residuals of Faith's phylogenetic diversity and total taxonomic distinctiveness against species richness as the signature of evolutionary history (for model statistics, see Table 1). The residuals were calculated with a spline-based smoothed regression, as implemented in generalized additive models and generalized mixed models of the R-package 'mgcv' (Wood 2011). We chose only these two out of a wide range of metrics, based on the comparison of ten commonly used measures of phylogenetic diversity (Schweiger et al. 2008) which showed that only Faith's phylogenetic diversity and total taxonomic distinctiveness do not increase if species are missing or decrease if species are added. Furthermore, Fritz and Rahbek (2012) found that although Faith's phylogenetic diversity and total taxonomic distinctiveness should be strongly correlated with species richness, residuals of these relationships satisfy homoscedasticity. However, in the specific case of European dragonflies, residuals of the correlation between Faith's phylogenetic diversity and species richness increased at larger fitted values, which indicated heteroscedasticity (Supplementary material Appendix 1 Fig. A4). We therefore decided to discuss only the results based on total taxonomic distinctiveness. In the second approach, we calculated the standardized effect sizes of the mean pairwise distances (MPD) across grid cells, i.e. the observed MPD minus the random MPD divided by the standard deviation of the random MPD values, with functions of the R-package 'picante' (Webb et al. 2008). Random MPD represents the average of 10 000 calculations of MPD, for which taxon labels of our phylogeny were randomly shuffled each time.

Regression models

To assess which factors determine patterns of species richness, corrected weighted endemism, and phylogenetic diversity (i.e. total taxonomic distinctiveness and MPD),

Table 1. Beta coefficients, per cent explained deviance (D) and generalized cross validation scores (GCV) from multiple regressions (gam) of five different measures of diversity against seven predictor variables. Predictors were z-standardized species richness, four principal components that describe temperature and precipitation, the proportion of lentic to lotic species and the location of the 0°C isotherm at the Last Glacial Maximum (LGM; 21 ka; unglaciated areas south of it = 1, glaciated areas north of it = 0) of 4192 assemblages of European dragonflies. Except those models with species richness as dependent variable, models were corrected for species richness using a smoothing term; only effective degrees of freedom (edf) and per cent explained deviance from single regressions are presented. Positive or negative values indicate the positive or negative tendency of the relationship; n.s., not significant at $p > 0.001$. Variable abbreviations: Richness, total species richness; CWE, corrected weighted endemism (i.e. geometric mean of the inverse occupancy of co-occurring species); TTD, total taxonomic distinctiveness (i.e. sum of pairwise distances); SES MPD, standardized effect sizes of mean pairwise distances. The first principal component of temperature, the proportion of lentic to lotic species and the 0°C isotherm at LGM are consistently strong predictors of patterns in all measures of diversity.

Model	edf		Standardized beta coefficients							D	GCV
	Richness (smoothed)	D	PC 1 temp.	PC 2 temp.	PC 1 preci.	PC 2 preci.	Lentic/lotic	LGM iso.			
Richness	–	–	+0.52	+0.93	n.s.	+0.43	–0.05	–0.28	63.8	0.364	
CWE	8.7	12.0	+0.28	n.s.	+0.08	–0.40	–0.46	+0.12	77.6	0.226	
TTD	9.0	99.8	+0.02	+0.00	n.s.	n.s.	–0.02	+0.02	99.9	0.012	
SES MPD	8.9	35.7	+0.36	+0.09	n.s.	+0.05	–0.27	+0.25	77.6	0.001	

we used generalized additive models implemented in the R-package ‘mgcv’ (Wood 2011). In all of these models, we considered measures of diversity as dependent variables, and environmental variables as well as the proportion of lentic to lotic species and the location of the 0°C isotherm during the LGM as independent variables. We chose generalized additive models over generalized linear models to be able to fit smoothing terms and thereby increase homoscedasticity in the model residuals for hump-shaped and other non-linear relationships. Model parameters for the five models of different measures of diversity were: endemism = quasi-Poisson distribution; standardized effect sizes of MPD = Gaussian distribution; and richness, Faith’s phylogenetic diversity and total taxonomic distinctiveness = gamma distribution. To compare effect sizes within models, we z-standardized independent variables with functions of the R-package ‘QuantPsych’ (Fletcher 2012). Breakpoints in segmented relationships between the proportion of lentic to lotic species, endemism, evolutionary history and latitude were calculated with broken-line regressions using functions provided in the R-package ‘segmented’ (Mugge 2003).

Spatial autocorrelation can lead to an overestimation of the degrees of freedom, due to the inherent non-independence of the neighbouring samples from the environmental template, and hence to false parameter estimates and model inference (Dormann et al. 2007). We used two alternative approaches to account for such systematic bias. In the first approach, we modelled all multiple regressions with a trend surface (i.e. smoothed term) of geographical coordinates as an additional predictor in generalized additive models. Effective degrees of freedom of the trend surface term were estimated (i.e. not fixed) to obtain best fit. In the second approach, we modelled autocorrelation in the model errors using a Gaussian spatial correlation structure of geographical coordinates (Manhattan distance metric, initial value 0.5) in generalized additive mixed models. For species richness, this model was a generalized least-squares model, i.e. the models were without a random effect. Spatial autocorrelation

structure was evaluated using spatial correlograms generated with the R-package ‘ncf’ (Bjornstad 2016). Correlograms for the residuals of the regressions modelled with and without the trend surface term or a Gaussian spatial correlation structure were, however, very similar, indicating that the other environmental variables (e.g. temperature and precipitation) already reduced spatial autocorrelation to a minimum (spatial independence was reached at about 500 km; Supplementary material Appendix 1 Fig. A5). We therefore do not report the results of models corrected for spatial autocorrelation.

Despite being a potential source of bias, the spatial (autocorrelation) structure of variables also includes additional information. As explained in the introduction, we would for instance expect that phylogenetic diversity measures show clear spatial structure if macroevolutionary processes and past dispersal have shaped the distribution of dragonfly lineages across Europe (see also Fritz and Rahbek 2012). We evaluated this prediction using spatial correlograms as an estimate of (non-random) spatial structure in diversity measures.

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.78j8g>> (Pinkert et al. 2017).

Results

Diversity measures of European dragonfly assemblages showed a clear spatial structure (spatial independence was reached at about 2000 km for most measures; Supplementary material Appendix 1 Fig. A6). In northern Europe, most co-occurring species are closely related representatives of only a few temperate lineages of Asian origin. The majority of these species belong to the families Aeshnidae, Coenagrionidae and Libellulidae and mainly to the genera *Aeshna*, *Coenagrion*, *Leucorrhinia* and *Sympetrum*. Nearly all of them are widespread across Europe and none are endemic to

Europe. By contrast, the ranges of all European endemics, as well as the ranges of numerous warm-adapted lineages with a few species from Asia and Africa, e.g. *Diplacodes*, *Trithemis* and *Zygonyx* (see tree in Supplementary material Appendix 1 Fig. A2), overlap in the southern half of Europe.

Importance of thermal adaptations for diversity patterns

Species richness peaked in central Europe (Fig. 1), whereas all considered measures of endemism and evolutionary history decreased gradually from south-western to north-eastern Europe (Fig. 2). Several aspects of contemporary climate were important predictors of the spatial variation in species richness (Table 1). The single most important environmental predictor of the spatial variation in endemism and evolutionary history was the first principal component of temperature, which mainly represented annual mean temperature and minimum temperature of the coldest month (see component loadings in Supplementary material Appendix 1 Table A4 and maps in Fig. A7).

Signature of limited post-glacial recolonization

All considered measures of diversity were significantly correlated with the proportion of lentic to lotic species and the location of the 0°C isotherm at the LGM (Table 1 and Fig. 2). With an increasing proportion of lentic species, dragonfly assemblages were composed of on average more widespread (lower levels of endemism) and closely-related species. Furthermore, we found a strong phylogenetic signal in habitat preferences of European dragonfly species (Bloomberg's K [10 000 permutations] = 0.43, $p < 0.001$; Pagel's $\lambda = 0.82$, $p < 0.001$). D statistics for binary data rejected the hypothesis of random phylogenetic structure in habitat preferences of European dragonflies, both when we considered species that are adapted to lentic and lotic habitats as being only lotic (D [10 000 permutations] = -0.18) and when we considered them as being only lentic (D [10 000 permutations] = -0.17). Endemism and measures of evolutionary history were lower in previously glaciated areas north of the historical 0°C isotherm than in unglaciated areas south of it. Only species richness showed the reverse pattern. Broken-line regressions supported the relevance of the historical isotherm for differences in the composition of European dragonfly assemblages; breakpoints were recovered in the relationships between endemism, measures of evolutionary history and the proportion of lentic to lotic species at latitudes close to the reconstruction of the historical isotherm (Fig. 2; breakpoint estimates \pm SE: richness = 50.9 ± 0.137 , endemism = 46.5 ± 0.0892 , residuals of total taxonomic distinctiveness against species richness = 51.3 ± 0.178 , standardized effect sizes of MPD = 50.3 ± 0.421 , lentic/lotic = 50.4 ± 0.183). The slope of these relationships changed from a steep decrease across assemblages south of the breakpoint to a shallow

decrease (for total taxonomic distinctiveness, the increase was very shallow) across assemblages north of it (Fig. 2).

Discussion

Overall, European dragonflies show a pronounced spatial structure in patterns of endemism and phylogenetic diversity that contrasted with the pattern of species richness. More specifically, areas south of the 0°C isotherm during the LGM show higher phylogenetic diversity and contained more species with small distributions. This pattern corresponds to the spatial distribution of habitat preferences, i.e. the northward increase in the proportion of lentic species, which are assumed to be stronger colonizers (Grewe et al. 2013). These findings support our hypothesis that the combination of phylogenetic conservatism in thermal adaptations and perhaps the varying colonization/dispersal abilities of species with different habitat preferences have left a strong imprint on the current diversity patterns of European dragonflies.

Phylogenetic conservatism in thermal adaptation

The decline of phylogenetic diversity from southern to northern Europe, which corresponds to decreasing ambient temperatures, is mainly due to the limited number of lineages that can cope with harsher and more variable climatic conditions. Dragonflies do not mainly use metabolic heat to be active, but rather external heat. To cope with temperature variation, however, they have evolved several behavioural strategies (e.g. active 'wing whirring' or exposure) and physiological adaptations (e.g. frost tolerance; reviewed by May 1976). Our results demonstrated that closely related species tend to have more similar distributions than expected by chance (i.e. phylogenetic conservatism). Thus, assuming that similar distributions also reflect similar climatic preferences and thermal requirements, these traits should be phylogenetically conserved as well.

Only few physiological traits appear to be sufficiently general (mechanistic) to have determined the evolution of thermal tolerances in dragonflies, among them body size and surface colour. Both traits regulate heat gain and loss through fundamental physical principles (reviewed by Clusella-Trullas et al. 2007 and Shelomi 2012). There is evidence that body size variation influences the distribution of dragonflies (Zeuss et al. 2016), but so far only a few studies on this topic have been carried out. Furthermore, dragonfly assemblages across Europe and North America tend to be darker in cold regions than in warm regions – a pattern that is in part driven by ancestral adaptations in colouration (Zeuss et al. 2014, Pinkert et al. 2016). Phylogenetic conservatism in thermal adaptations such as colour lightness could thus have filtered certain phylogenetic lineages along a gradient of progressively cooler temperatures.

Only about one-sixth of all dragonfly species globally and one-quarter of all genera and families are found in the Holarctic, and the richness across all taxonomic ranks peaks

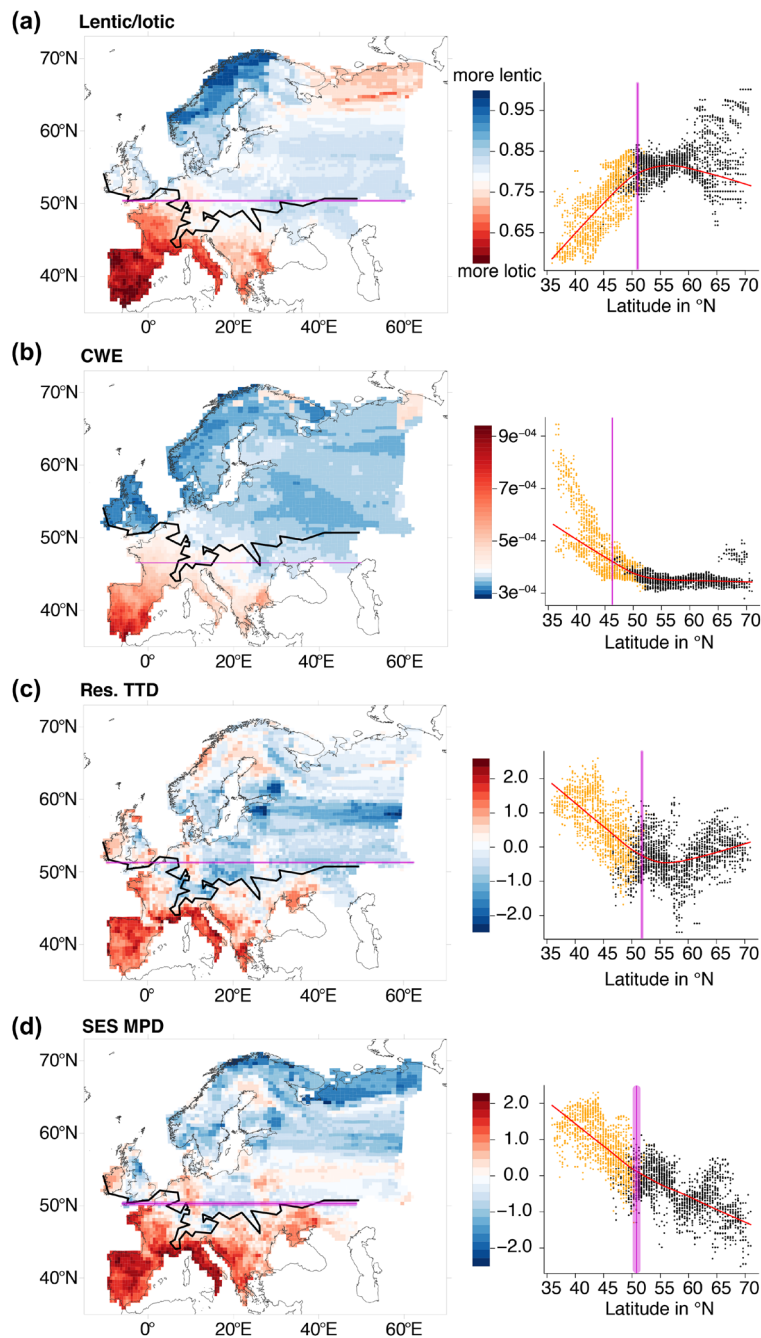


Figure 2. Spatial variation in four different measures of diversity across 4192 assemblages of European dragonflies (EPSG: 4326; equal-area grid CGRS). Left panels geographical distribution of (a) the proportion of lentic to lotic species (lentic/lotic), (b) corrected weighted endemism (CWE; i.e. geometric mean of the inverse occupancy of co-occurring species), (c) residuals of a spline-based smoothed regression of total taxonomic distinctiveness (i.e. sum of pairwise distances) against species richness (Res. TTD) and (d) standardized effect sizes of mean pairwise distances (SES MPD) of dragonfly assemblages. Colour class intervals are scaled according to equal class breadth, centred on the mean in a bipolar colour space. Black lines indicate the location of the 0°C isotherm at the Last Glacial Maximum (21 ka); purple and semi-transparent purple lines indicate breakpoint estimates and their standard deviations from broken-line regressions of the relationships in the right panels, respectively. Right panels correlations of measures (a–d) with latitude across 4192 assemblages of European dragonflies. Red curves were fitted by spline-based smoothed regressions. Purple and semi-transparent purple lines indicate breakpoint estimates and their standard deviations from broken-line regressions, respectively. Assemblages north of the historical 0°C isotherm are indicated by black data points; assemblages south of the isotherm are indicated by orange data points. Note that endemism and phylogenetic diversity measures consistently decrease with decreasing temperature and increasing proportion of lentic species. Breakpoints in the relationship of dragonfly diversity and latitude roughly coincide with the location of the historical 0°C isotherm. Thus, assemblages become abruptly more homogenous in previously glaciated areas, and are composed of more lentic, widespread (lower CWE) and closely-related species.

near the equator. For instance, 12 of the 31 extant families of dragonflies are confined to the tropics (Kalkman et al. 2008). Already a century ago, Tillyard (1916) hypothesized that temperature is the most important factor for these differences in the distribution of dragonfly clades (cf. Tillyard 1916, p. 295). Although both the phylogenetic and spatial scales of our study are limited to Europe, our finding that the evolutionary history of dragonfly assemblages decreases with decreasing temperature provides to our knowledge the first empirical support for this long-standing hypothesis.

Recent range shifts of dragonflies are among the most obvious responses of insects to changing climatic conditions (Hassall and Thompson 2008, Grewe et al. 2013, Zeuss et al. 2014). Over the last decades, some dragonfly species have shifted their range edges hundreds of kilometres northwards. These species are in most cases generalists and often represent the only member of their genus in Europe (e.g. *Crocothemis erythraea*, *Selysiothemis nigra*, *Trithemis annulata*; Grewe et al. 2013). Hence, they might have contributed to high levels of phylogenetic diversity in northern Europe only recently. The strong correlation between contemporary temperature and spatial variation in evolutionary history of dragonflies might, therefore, indicate that recent expansion trends continue to occur in a closely related subset of species owing to conservatism in thermal adaptations.

Historical signals in diversity patterns

In addition to evolutionary constraints on geographical distributions via thermal adaptations, our results also indicated that Europe's climatic history has left a strong signal in the phylogenetic structure of dragonfly assemblages. We found that both the latitudinal patterns of endemism and evolutionary history and the proportion of lentic to lotic species showed a marked change around the location of the 0°C isotherm during the LGM. We argue that this pattern is the outcome of the longer time available for diversification in unglaciated areas and of limited recolonization of previously glaciated areas in Europe.

During the LGM, large parts of central and northern Europe were uninhabitable for dragonflies (Sternberg 1998). Thus, all previously glaciated areas, including those with currently the highest levels of dragonfly species richness in central Europe, were colonized later. Our results indicate that this colonization process was probably dominated by a lentic and closely-related subset of species from southern refugia. Localized exceptions to this pattern, with comparatively high levels of phylogenetic diversity, seem to represent relict populations of several *Somatochlora*, *Aeshna* and *Leucorrhinia* species in Scandinavia, the Scottish Highlands, the Central German Uplands [see Sternberg (1998) for a discussion of their potential migration routes]. In general, however, the highest levels of evolutionary history are clearly found in the south-western and south-eastern Mediterranean basin.

Temperature was the main predictor of the variation in endemism and phylogenetic diversity; nevertheless, endemism and phylogenetic diversity were also clearly influenced

by factors not captured by contemporary environmental conditions, but by the location of the 0°C isotherm during the LGM. Similar historical signals also underlie the present-day species richness patterns of European plants (Svenning and Skov 2007), amphibians and reptiles (Araújo et al. 2008), and dung beetles (Hortal et al. 2011). We argue that such general trends in regional assemblages of taxa with very different biologies are in part the result of the greater climatic stability in the Mediterranean basin during Quaternary climate oscillations. Hence, lower levels of extinction in addition to longer time available for speciation and immigration probably facilitated the accumulation of phylogenetic diversity in this area (Hewitt 1996, Wiens and Donoghue 2004). It is beyond the scope of our study to separate the contribution of these processes, but our results reconcile a number of previously documented distribution patterns of dragonflies. For instance, Kalkman et al. (2010) showed that the Mediterranean basin harbours by far the most subspecies and endemic dragonfly species, which indicates high niche differentiation and in situ diversification of multiple lineages (Wiens and Donoghue 2004). Furthermore, zoogeographical studies suggest that distinct elements of several faunal regions intermix in the Mediterranean due to its position between the three continents Asia (Siberia as well as the Oriental region), Europe and Africa (Sternberg 1998, Heiser and Schmitt 2010).

Differences in colonization and dispersal abilities

Dragonflies are generally considered to be a group with high dispersal ability. Nonetheless, the marked change in the relationship between the proportions of lentic to lotic species with latitude close to the historical 0°C isotherm indicates that lotic species might not be in equilibrium with current climate owing to limited post-glacial colonization and dispersal abilities. Indeed, according to our data, 33 of 42 lotic species are confined to roughly the southern half of Europe, among them 15 of the 18 total European endemics (Kalkman et al. 2010). By contrast, assemblages in previously glaciated areas are markedly more homogenous and are composed of predominantly lentic, widespread and closely-related species.

The classification into lentic and lotic species specifically refers to habitat preferences of dragonfly larvae. Thus, it could be argued that the observed pattern in the proportion of lentic to lotic species might be entirely due to spatial variation in the availability of both habitat types. However, Dehling et al. (2010) demonstrated that the species richness patterns of European freshwater animals are not correlated with habitat availability. Furthermore, it seems unlikely that grid cells of approximately 2500 km² size do not integrate a single body of still or running water. Instead, the probability of finding a species that is bound to a specific habitat would be lower for rare habitats. However, it is unlikely that this affected our results because the distribution ranges on the contour maps used for our analysis are interpolations between records.

Latitudinal gradients in habitat preferences are described for several freshwater taxa in Europe and North America

(Ribera et al. 2003, Hof et al. 2006, 2008) or even within species (e.g. *Gomphus pulchellus*; Dijkstra and Lewington 2006). It was therefore surprising to find that in Europe most lentic dragonfly species are either Coenagrionidae or Libellulidae, which is reflected by a strong phylogenetic signal in habitat preference (for maps of lentic and lotic species and of families, see Supplementary material Appendix 1 Fig. A8). In fact, although these two families represent different suborders of dragonflies, they share several particularities. For instance, Coenagrionidae and Libellulidae are the youngest (Rehn 2003) and largest families of dragonflies, they include the most widespread species and, unlike most other families, their relative species richness is greater in temperate regions than in tropical regions (Kalkman et al. 2008). Similar patterns are known for younger clades of birds and mammals, which had large radiations when the temperate climate zones began to expand. Interestingly, these clades also show opposite latitudinal species richness gradients (Buckley et al. 2010). Unfortunately, until more comprehensive phylogenies and dating of diversification events are available at the global scale, it remains speculative whether adaptations to lentic habitats such as wing morphology, could have driven the current evolutionary and distributional success of Coenagrionidae and Libellulidae in a similar way.

Conclusions

We conclude that historical processes are a major determinant of the current spatial patterns of dragonfly diversity in Europe. On the one hand, phylogenetic conservatism of thermal adaptations of dragonflies has probably allowed only a closely-related subset of dragonfly lineages to initially colonize and survive in temperate climates. On the other hand, ecological differences between lentic and lotic species, namely their differences in dispersal and colonization ability, may have limited the recolonization of previously glaciated areas by lotic species. Our findings highlight that only joint consideration of the different components of species diversity, their evolutionary history, and their ecological characteristics in concert with the contemporary and historical variation of climatic conditions allows a comprehensive understanding of the processes that shape the distribution of life in space and time.

Acknowledgements – The authors thank Martin Brändle and Jonas Hagge for their comments on earlier versions of the manuscript and Karen A. Brune for improving the text linguistically.

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Supplementary material (Appendix ECOG-03137 at <www.ecography.org/appendix/ecog-03137>). Appendix 1.