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# Climate Change Is Driving Shifts in Dragonfly Species Richness across Europe via Differential Dynamics of Taxonomic and Biogeographic Groups

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**Abstract:** Understanding how changes in species richness pattern correlate with range changes in different taxonomic and biogeographic groups is important for conservation because it allows for generalizations about which species are at greatest risk. Here, we assessed whether changes in species richness patterns result from generalized range shifts across taxonomic and biogeographic groups or from changes in specific subsets of species. Using data from 1988 and from 2010, we studied changes in distributional range of European dragonfly species, using outline distribution maps for all dragonflies combined and separately for taxonomic suborders (Zygoptera and Anisoptera) and biogeographic groups (Boreo-alpine, Eurasian, Mediterranean, and Tropical). The results demonstrated differing range dynamics for Zygoptera and Anisoptera, with Anisoptera driving local turnover in species richness to a greater extent than Zygoptera. The distributional range of Tropical and Mediterranean species had expanded to a much greater extent than that of Eurasian and Boreo-alpine species. Large-scale changes in species richness arose from several divergent, group-specific processes. Overall, local diversity especially declined in parts of southern and south-eastern Europe, reflecting local losses in multiple species rather than major range contractions among Mediterranean or Eurasian species. In fact, among the biogeographic groups, overall range declines were most prominent among Boreo-alpine species, highlighting the particular threat from climate change to this group.

**Keywords:** biodiversity; geographic range expansion; Odonata; range dynamics; range size; species distribution; species richness; zoogeography

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## 1. Introduction

The latitudinal gradient of species richness is well documented for most higher taxa in both terrestrial and aquatic environments [1]. Current environmental changes are causing shifts in geographical distributions of species, leading to new patterns of species richness and assemblages at regional and local scales. Human-driven climate change is already profoundly affecting species distributions, causing substantial range shifts and expansions in species that can keep pace with changes in climate and resources [2] or that can adapt to new resource conditions and exploit formerly unsuitable habitats [3,4]. Species that cannot do either will experience range contraction or local extinction [5]. Habitat loss and degradation may cause range shifts to lag behind changes in climate and resources if unsuitable habitat restricts or blocks emigration by spatially isolated and small populations [6]. In such cases, small local populations can become more susceptible to extinction [7] because of stochastic events such as extreme weather or climatic variation at range boundaries where individuals live at the limits of their physiological tolerances [8]. The overall consequences of these range shift dynamics are changes in local species richness and assemblages, which eventually may lead to shifts in the latitudinal richness gradient [9]. Climate change is expected to reduce the number of species globally [10], but species richness at regional and local scales could increase or decrease.

Different species from a variety of ecological systems are showing poleward range expansion in the Northern Hemisphere that is consistent with climate change [2], and this has had important effects on distributions and regional species richness [11]. Commonly used scenarios for future changes predict an increase in global temperature of 1.8–6.4 °C in this century [12]. Phenotypic plasticity may play a key role in surviving a changing climate [3,4], but such climatic changes will probably stress insects, which likely have insufficient adaptive potential to keep pace with the rate of change [13]. In principle, evolutionary adaptation could be a response [14,15], but niche conservatism in some insects including dragonflies suggests a limited scope for this strategy [16,17]. Most species therefore are expected to show altered distribution rather than adaptation to warmer temperatures in situ [18].

The ranges of several European dragonfly species (Odonata) have expanded or moved northward (e.g., [19–22]. In this taxonomic group, temperature is a major determinant of species distribution [21], life cycle regulation and larvae growth responses [23,24], shifts in voltinism and seasonal regulation [25,26], and phenology [25,27–29], as well as immune function capacity [30,31] and pigment production for thermoregulation [32]. These different effects and responses originate in the facts that (1) dragonflies are flying insects that lay eggs in aquatic habitats, with larvae strictly tied to water for months or even years prior to emergence; (2) climate changes influence distribution in space and time of habitats and food resources; and (3) their metabolic and physiological processes are temperature dependent [33].

Knowing the range dynamics of species affected by climate warming is imperative for understanding which species are most likely to experience expansion or contraction of their range in response to global climate change. In conservation, information about trends in species range shifts is needed for setting priorities and assigning threat status. Change in occurrence have been used by International Union for Conservation of Nature (IUCN) to determine species status in the European Red List, which shows that 15% of European dragonfly species are threatened, with 2% being critically endangered, 4% endangered, and 9% classified as vulnerable. A further 11% are considered to be near threatened within Europe [34]. Additionally, a representative global assessment of conservation status has been completed and analyzed for dragonflies, currently the only insect group for which that has been conducted [35]. Only a few studies have concentrated on more integrated measures of change, such as species richness and local species assemblage [36]. However, although species are expected to respond individually, the overall consequences of environmental changes will likely be shifts in local species richness and assemblage composition.

The combined latitudinal and altitudinal species richness gradient for European dragonflies, ranges from many species in warmer southern regions to fewer species in colder northern regions, and Europe overall is species-poor compared with the tropics [37]. The higher diversity of dragonflies in the mountains is influenced not only by temperature and rainfall but also by the greater diversity of habitats in these areas [38]. Nevertheless, the legacies of past climate may be important for understanding current species distributions. Traditionally, it has been thought that three major Pleistocene refugia on the Iberian, Italian, and Balkan peninsulas were the source of recolonization of most of the temperate part of Europe after the last ice age [39,40]. Recent studies based on plants, terrestrial vertebrates, and butterflies have revealed a much more complicated situation, however, and postglacial recolonization may have been sourced from the east and from small ice age refugia in Europe north of the Alps (e.g., Simonsen and Huemer [41], Ursenbacher et al. [42], Brochmann et al. [43], and Schmitt et al. [44]). For highly mobile species, present-day ranges are believed to be primarily governed by current environmental conditions rather than changes in environmental conditions over time. In contrast, current ranges of less mobile species may represent only partially incomplete post-glacial recolonization [45]. Dragonflies are believed to have high dispersal capacities in general [33], so that present day climate warming and resources should mainly drive changes from past distribution and geographical richness patterns; restrictions by physical barriers such as high-altitude ranges are expected to have a lesser influence by having prevented postglacial recolonization in certain regions.

The order Odonata consists of the two suborders: true dragonflies (Anisoptera) and damselflies (Zygoptera). True dragonflies are capable of using thoracic muscle vibration to heat their body and to a certain degree regulate their hemolymph circulation, adaptations which damselflies lack and as a consequence they are considered thermoconform [33]. Hence, true dragonflies and damselflies are affected differently by temperature [46] where true dragonflies in general are more tolerant to high and low temperatures than damselflies, despite living in the same latitudes or altitudes [17,33]. Furthermore, true dragonflies are generally large, robust, and physically strong, and their hind wings have a broad base and are larger than the front pair. Damselflies are typically smaller and therefore do not fly as fast as true dragonflies in active flight, and their front and hind wings are similar in shape. Most European dragonfly species are strong fliers that are able to move between suitable habitats. Commuting between roosting, foraging, and reproductive sites up to several kilometers apart does not lead to relocation of next generations into a different habitat. Dispersal, in contrast, is unidirectional and may be a response to unfavorable habitat conditions, mass emergence after unusual weather, or population increases following favorable weather conditions [47]. True dragonflies and damselflies may occupy suitable habitats for several generations and then move to other suitable regions when the original habitat deteriorates [33]. This mobility helps species to maintain continuity of reproduction in the face of discontinuous habitat suitability, and as a result, their distributional range and biogeographic species assemblage becomes dynamic.

Environmental change can have strong effects on the population dynamics, distribution, and diversity of dragonflies [22,23,37,48], making them well suited for evaluating the mechanisms of these changes. Their sensitivity to habitat quality, amphibious life cycle, and ease of identification combined with the substantial knowledge about their distribution and ecological requirements uniquely suit them for studies of the effects of environmental changes in the short term (water pollution, structural changes in running and standing water) and the long term (species conservation and biogeography).

For our work here, we used distribution maps of European dragonflies from 1988 [49] and 2010 [34] to identify how their species ranges have changed during those 22 years. Our scope was to track temporal changes in distribution and to highlight patterns in the latitudinal and longitudinal movements at the margins of the dragonfly ranges. For this purpose, we analyzed geographic patterns of change in species richness with the aim of identifying species groups sharing functional and biogeographic traits that primarily drive local turnover in species assemblages and cause geographical shifts in species richness patterns. The five specific questions we addressed are as follows: (1) Are increases in ranges of true dragonflies greater than those of damselflies? (2) Have the ranges of southern species increased more than the ranges of continental and northern species? (3) Will northern species and high-elevation species experience reduced overall ranges as their realized climatic envelopes shrink because of global warming? (4) Are northwards range shifts greater than movements at other range margins reflecting a directional poleward shift rather than a non-directional range expansion? (5) Are geographical shifts in species richness patterns driven mainly by southern species rather than by species from a more continental and northern origin? We argue that these measures would be particularly useful for detecting effects of environmental changes and highlighting the importance of using insects—and especially dragonflies—as first-level indicators of environmental health.

We expect the current findings to support conservation efforts by providing additional means of determining species and species groups most at risk.

## 2. Materials and Methods

### *2.1. Study Area*

Our study area covered 6,331,488 km$^2$ of the westernmost peninsula of Eurasia (=Europe) limited by the Arctic Ocean to the north, by the Atlantic Ocean to the west, and by the Mediterranean Sea to the south (see Figure 2 in Olsen et al. [22]). The eastern border of the study area followed a combination of the 35° E longitude and the eastern margin used in outline range maps in Askew [49]. All larger European islands in the Mediterranean Sea were included as in Olsen et al. [22].

### *2.2. Data*

#### 2.2.1. Species Distribution Data

Distributional ranges of dragonflies in Europe were obtained from two points taken 22 years apart, based on outline maps in Askew [49] and Kalkman et al. [34]. The maps do not always present the full distributional range and sometimes represent only the part that falls within the westernmost Eurasian peninsula. We excluded data from east of 35° E and south of the Mediterranean Sea because dragonfly occurrences in these regions are not well documented (e.g., Dijkstra and Lewington [50]).

Of the 130 species of dragonflies known to occur within the study area, we constructed outline range maps for 123, after excluding vagrant species, species new to science since 1988, and species without a range map in Askew [49] or Kalkman et al. [34] (see Table S1 for a list of excluded species, species that in 2010 were included as new in Europe, taxonomic and nomenclatural changes, and modifications to species ranges). Of the 123 included species, 4 colonized Europe during the 22-year period, whereas 119 species occurred in both data sets (see Table A1 and Table S1 for a list of the 4 and 119 species).

Maps from Askew [49] were georeferenced in ArcGIS 10.2 [51] based on scanned TIFF images, whereas maps from [34] were provided as shape files from the Freshwater Biodiversity Unit under the IUCN Global Species Program. All species ranges categorized as extant in Kalkman et al. [34] were included, whereas all ranges with a signature of extinction were omitted. The distribution maps in 1988 and 2010 were cut with the same European coastline layer in ArcGIS 10.2 [51] to ensure that species ranges followed the same extent of land cover and to facilitate direct comparison.

#### 2.2.2. Species Classification

As functional traits, we used the morphological characteristics that distinguish the taxonomic suborders of European dragonflies—damselfly (Zygoptera) ($n$ = 41) and true dragonfly (Anisoptera) ($n$ = 82) species (see Table A1 for a list of species in each suborder). For biogeographic traits, we used four groups—Tropical ($n$ = 14), Mediterranean ($n$ = 56), Eurasian ($n$ = 36), and Boreo-alpine ($n$ = 17) species (see Table A1 for a list of species in each group). These subdivisions by functional and biogeographic traits based on Dijkstra and Lewington [50], Sternberg [52], and Beschovski et al. [53] allowed us to distinguish species responses and differential changes in species richness patterns arising from southern Mediterranean fauna elements (Tropical and Mediterranean groups) from the species responses with a more continental distribution in central and northern Europe (Eurasian and Boreo-alpine groups). It also allowed us to capture effects caused by species with an Afrotropical and Oriental origin (Tropical group) from the more extreme habitat specialists, such as the Boreo-alpine species.

### *2.3. Data Analysis*

#### 2.3.1. Range Shifts

In ArcGIS 10.2 [51], we transformed the outline distributions into gridded maps with 880 cells of 100 × 100 km to estimate distributional range as an occupancy of grid cells. The large grid resolution allowed us to minimize artefacts from outline range maps, including false absences or more commonly false presences, and thus avoid overestimating the extent of occurrence of species [22]. To address questions 1–3 of our study, we calculated differences in total species range ($\Delta R$) between 1988 and 2010 for stable ($\Delta R = 0$), contracting (negative $\Delta R$), and expanding (positive $\Delta R$) species as relative change, giving the percentage change in the number of occupied cells.

To address question 4 of our study, we measured change in distributional range as shifts in northern, southern, eastern, and western boundaries, calculated by subtracting minimum and maximum latitude and longitude for each species in 1988 from the values in 2010. All range shift distances were standardized so that expansions and contractions were expressed with positive and negative values, respectively.

To further address question 4, we determined directionality in range shifts by calculating direction (0–360°) and compass distance of range centroid shifts. All distances were calculated using an equidistant projection in ArcGIS 10.2 [51].

#### 2.3.2. Species Richness

To address question 5 of our study, we calculated latitudinal species richness (number of species in 100-km latitudinal intervals) to evaluate changes in species richness in each biogeographic group between 1988 and 2010. We subdivided our study area into 10 × 10 km grid cells (total 67.374) and calculated local species richness (number of species in each grid cell) by overlaying the grid onto the outline distribution maps. We then subtracted the number of species in each grid cell in 1988 from the number in 2010 to evaluate geographic patterns in diversity changes over the 22-year period. When plotting geographical patterns of species richness, we chose to reduce the grid cell size to 10 × 10 km because higher resolution allowed us visually to detect patterns at a more local scale than if we used the 100 × 100 km grid as applied in the statistical analysis.

### *2.4. Statistical Analysis*

The various measures of range shifts (overall range shift; range shift at the four range margins: north, south, east, and west; and shift in range centroid) in European damselfly (Zygoptera) and true dragonfly (Anisoptera) species were analyzed with the taxonomic suborders—Zygoptera and Anisoptera—used as unmatched test groups in a Mann–Whitney–Wilcoxon test.

The various measures of range shifts (overall range shift; range shift at the four range margins: north, south, east, and west; and shift in range centroid) in biogeographical groups of European dragonfly species were analyzed with the biogeographic groups—Tropical, Mediterranean, Eurasian, and Boreo-alpine—used as unmatched test groups in a Kruskal–Wallis test.

Range shifts at range margins for all species, for damselfly species and true dragonfly species, and for species in the four biogeographical groups—Tropical, Mediterranean, Eurasian, and Boreo-alpine—were analyzed with the northern margin and the southern, eastern, and western margins combined (=other margins) used as unmatched test groups in a Mann–Whitney–Wilcoxon test.

All statistical tests were performed using R [54], and polar plots were made with the plotrix package [55].

## **3. Results**

### *3.1. Range Shift Pattern*

On average, range sizes increased between 1988 and 2010. Median change in overall range size was 254,965 km$^2$, median percentage change in range was 18%, and median change in number of 100 × 100 km grid cells was 35. Of the 123 species, 106 had expanding ranges (including 4 that colonized Europe between 1988 and 2010), 3 species (all damselflies) had stable range sizes, and 14 species experienced range contractions (7 damselflies and 7 true dragonflies) (Tables A1 and S2).

Percentage change in range was significantly larger in true dragonflies than in damselflies (Figure 1A, Table S3). The magnitude of the range changes differed significantly among biogeographic groups, with the largest increase in Tropical and Mediterranean species compared with Eurasian and Boreo-alpine taxa. With separate analyses for the two suborders, however, the changes were significant only for true dragonflies (Figure 1A, Table S4). Within the Boreo-alpine group, 13 species had expanding ranges, 1 species had a stable range size, and 3 species showed range contractions (Tables A1 and S2).

Latitudinal shifts are much larger than longitudinal shifts. The latitudinal shift at the northern range margin was significantly larger than shifts at the other three margins combined, and when accounting for suborder, the differences were significant for both damselflies and true dragonflies (Table S5). When accounting for biogeographic group, shifts in the northern range margin were significantly larger than shifts in the other three directions for Tropical, Mediterranean, and Eurasian species, but not for Boreo-alpine species (Table S5). When shifts at the four range margins were analyzed separately rather than together, we found a significant difference between damselfly and true dragonfly species only at the western border (Figure 1C–F, Table S3). In addition, we found a significant difference among the four biogeographic groups at the eastern border, but when suborder was considered, the differences were significant only for true dragonflies (Figure 1C–F, Table S4).

The centroid of dragonfly ranges shifted by 176 km on average (median 138 km), with a significant difference between damselfly and true dragonfly species (Figure 1B, Table S3) and among the four biogeographic groups (Figure 1B, Table S4). However, when accounting for suborder, the differences between biogeographical groups were not significant for either damselflies or true dragonflies (Table S4). Centroids of dragonfly ranges moved in all directions, with a mean shift towards south–southwest (202°) (Figure 2). Damselfly and true dragonfly species did not differ significantly in the direction of the range shifts (Figure 2, Table S3), but the biogeographic groups did show differences (Figure 2, Table S4).

### *3.2. Species Richness Pattern*

On average, the latitudinal species richness (number of species in 100 km latitudinal intervals) increased from 1988 to 2010 by 5.4 species (median 5.0 species), representing 1.3 damselfly and 4.1 true dragonfly species (Figure 3). The largest increase was between the Mediterranean Sea and 46° N, with an average of 7.1 species (1.3 damselfly and 6.3 true dragonfly), and between 52° N and 63° N, with an average of 7.4 species (2.8 damselfly and 4.6 true dragonfly).

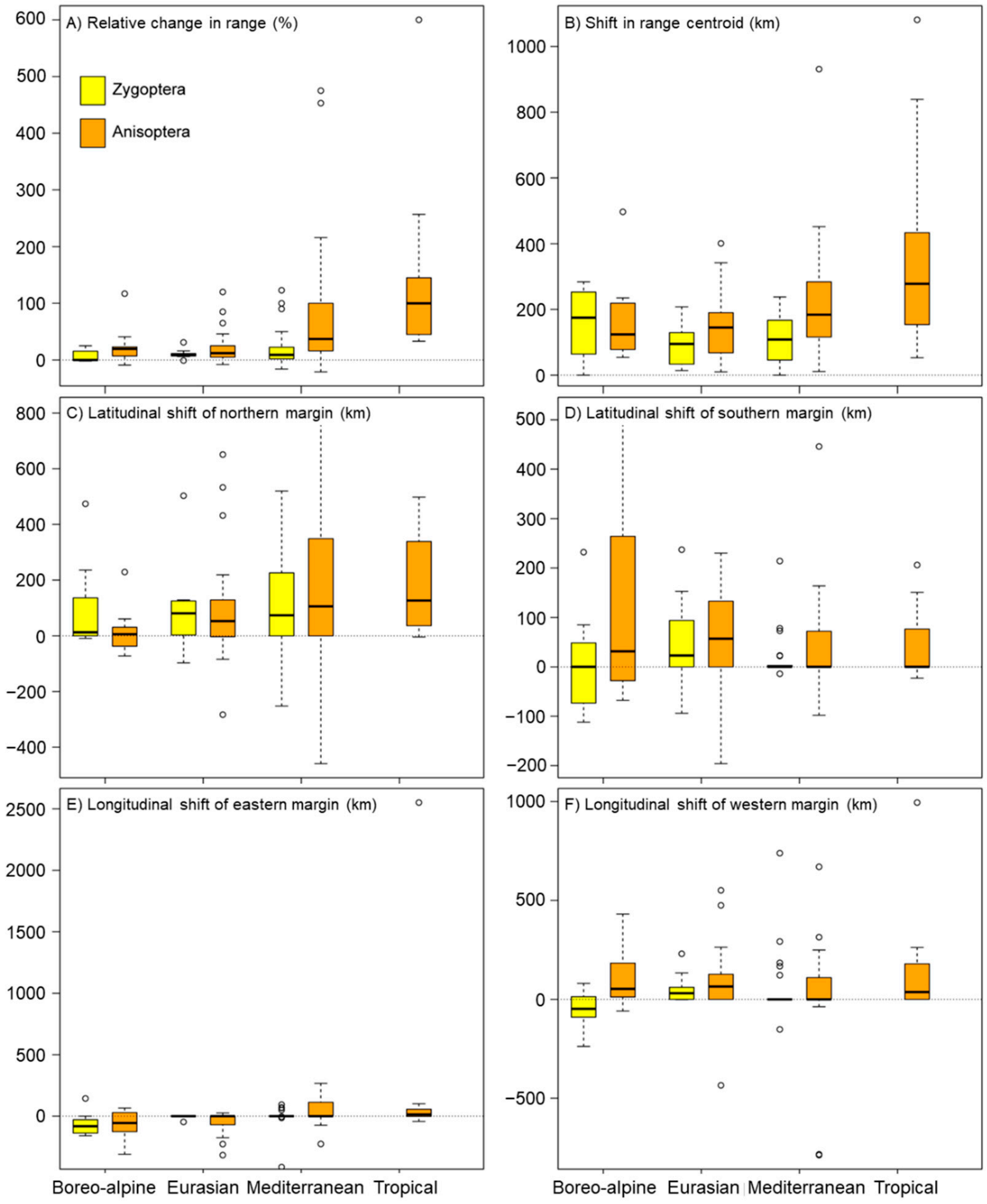

**Figure 1.** Range shifts in European dragonfly (Odonata) species from 1988 to 2010. (**A**) Relative change in range (percent change in number of occupied 100 × 100 km grid cells). (**B**) Distance shift of range centroid. (**C**) Latitudinal shift of northern range margin. (**D**) Latitudinal shift of southern range margin. (**E**) Longitudinal shift of eastern range margin. (**F**) Longitudinal shift of western range margin. Data separated by biogeographical groups (Tropical, Mediterranean, Eurasian, and Boreo-alpine) for damselflies (Zygoptera, yellow) and true dragonflies (Anisoptera, orange). The box-and-whisker plots illustrate the spread and skewness of the data through their quartiles and the median (thick black middle line). The whiskers extending from the box show data variability outside the upper and lower quartiles. Outlier points that differed significantly from the rest of the dataset are plotted as individual points (empty circles) beyond the whiskers.

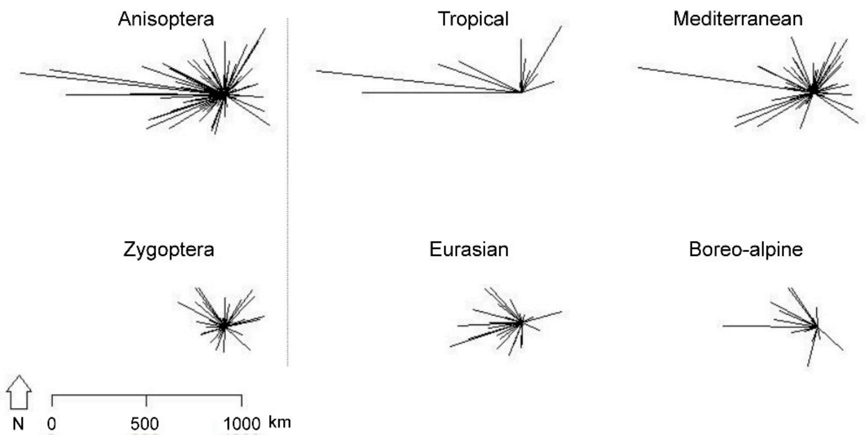

**Figure 2.** Plots showing shifts (1988–2010) in the range centroids of European (Odonata) dragonflies. Distance (km) and compass direction (°) of range shifts in range centroids in species from 1988 to 2010. Data separated by taxonomic suborder (damselflies [Zygoptera] and true dragonflies [Anisoptera]) and biogeographical groups (Tropical, Mediterranean, Eurasian, and Boreo-alpine).

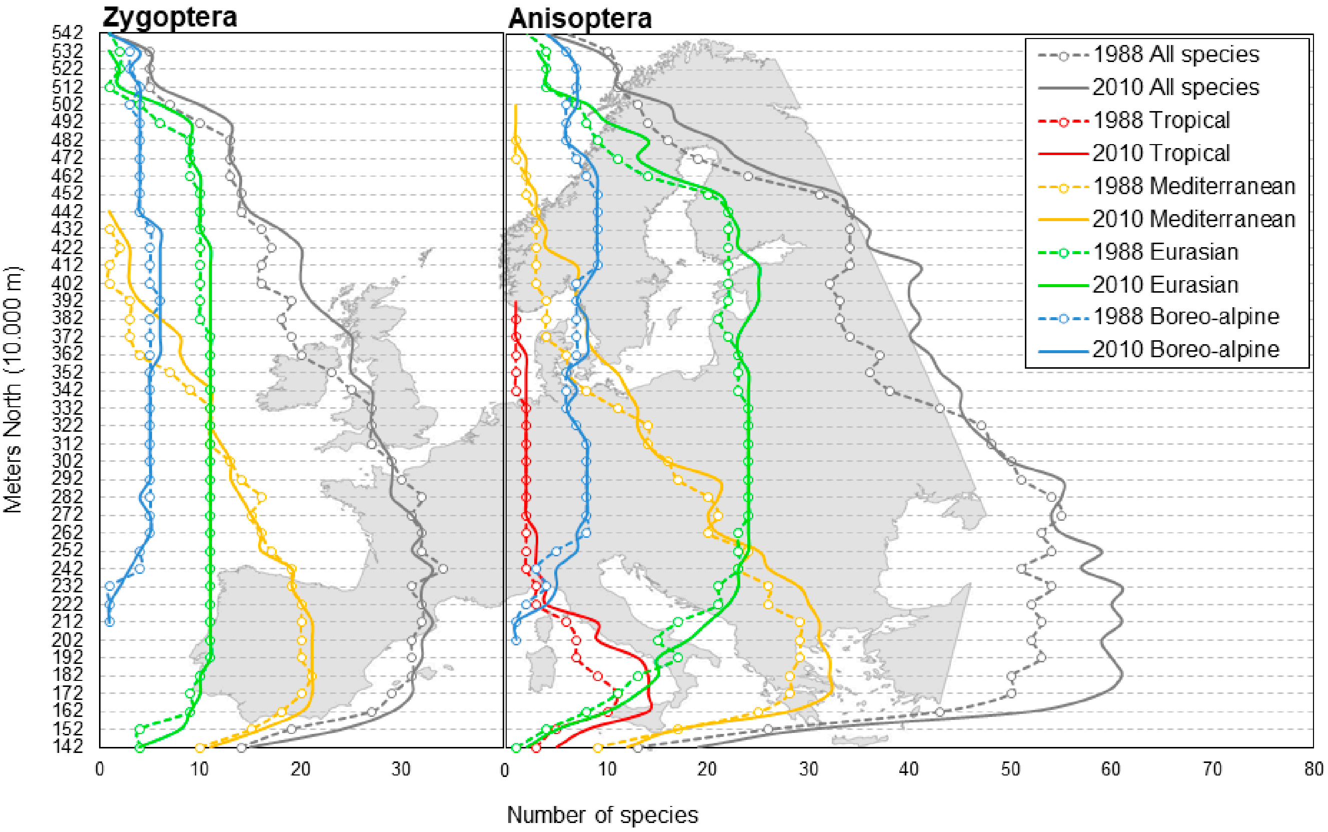

**Figure 3.** Shift in latitudinal species richness of European dragonfly (Odonata) species, plotted against latitude. Species richness presented as number of species in 100-km latitudinal intervals in species from 1988 to 2010. Data separated by biogeographical groups (Tropical—*red*, Mediterranean—*yellow*, Eurasian—*green*, and Boreo-alpine—*blue*) for damselflies (Zygoptera, *left*) and true dragonflies (Anisoptera, *right*).

The biogeographic group of damselflies with the largest increase in latitudinal species richness was the Mediterranean, where richness increased most at Scandinavian latitudes, so that the expansion of their northern range included a shift from Central Europe into the Scandinavian zone (Figure 3). Additionally, the true dragonfly fauna that accounted for the largest increase were the Tropical and Mediterranean in Southern Europe, and Mediterranean and Eurasian in Central and Northern Europe (Figure 3).

Average local species richness (number of species in 10 km × 10 km grid cells) increased by 7.3 species (median 7.0 species), with 2.0 damselfly and 5.3 true dragonfly species. The highest values for local species richness were observed in eastern and central Europe, with a maximum (>64) in the lowlands north of the Alps and Carpathian Mountains, and in the region west of the western Alps (Figure 4). Local species richness of the two suborders followed a similar geographic pattern, although a hotspot west of the Alps was more pronounced in damselflies compared with true dragonflies, and true dragonflies were more species rich than damselflies in lowlands north of the Alps and Carpathian Mountains (Figure 4). The diversity center for damselflies was located around the "Massif Central" in France (28 species), whereas the diversity center for true dragonflies (46 species) was located west of the northwestern pre-Alps and areas in northern Slovakia along the Carpathian Mountains (Figure 4).

The geographic pattern of changes in local species richness differed among biogeographic groups (Figure S1), which followed variation in the percentages of 10 km × 10 km grid cells in which the number of Tropical, Mediterranean, Eurasian, or Boreo-alpine species increased, decreased, or remained unchanged between 1988 and 2010. The Boreo-alpine group showed the largest decline in the percentage of 10 × 10 km grid cells where species from that group occurred in 1988 compared with the similar decline in species from Tropical, Mediterranean, and Eurasian groups. In contrast, the Mediterranean and Eurasian species showed the largest percentage of cells with increasing diversity (Figure 5).

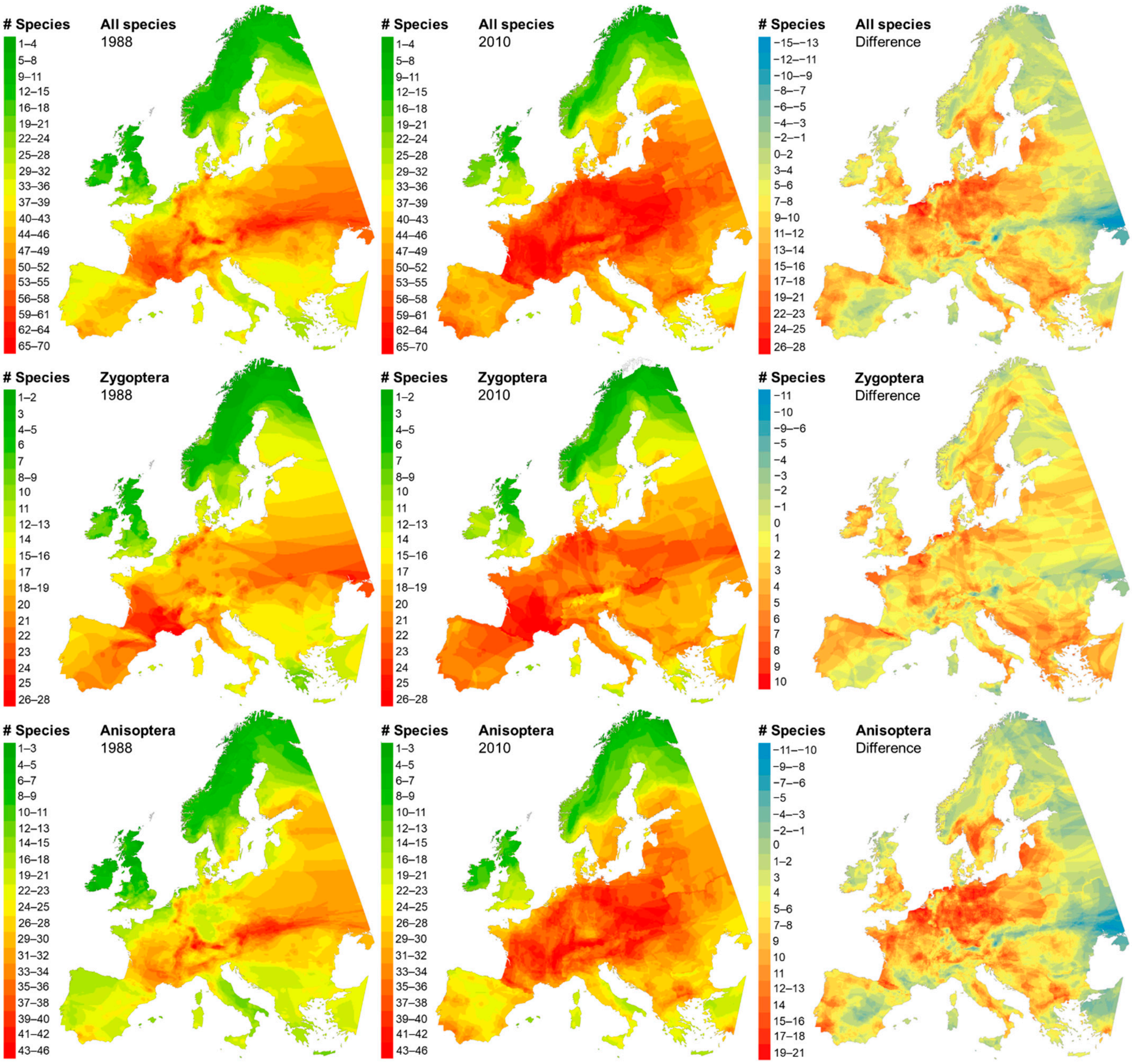

**Figure 4.** Geographical patterns of European dragonfly (Odonata) species richness and changes by taxonomic suborder. Observed species richness in 1988 according to Askew [49] (left column), observed species richness in 2010 according to Kalkman et al. [34] (middle column), and difference in observed species richness between 1988 and 2010 (negative value = decrease, positive value = increase) (right column). European data presented for all species (upper row), damselfly (Zygoptera) species (middle row), and true dragonfly (Anisoptera) species (lower row) at 10 km × 10 km grid resolution.

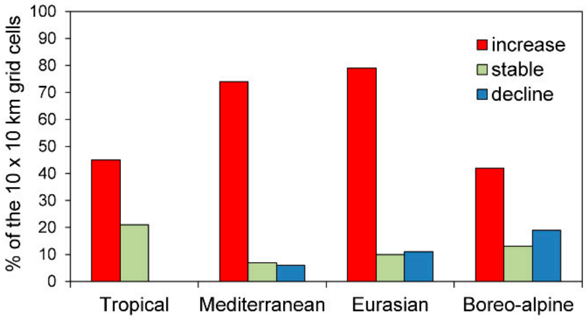

**Figure 5.** Percentages of 10 × 10 km grid cells (total 67.374 grid cells) where the number of European dragonfly (Odonata) species increased, decreased, or remained unchanged from 1988 to 2010, separated into biogeographic groups (Tropical, Mediterranean, Eurasian, and Boreo-alpine).

## 4. Discussion

### *4.1. Data Quality*

We used expert-drawn outline range maps to address how species ranges have changed on a continental scale. Even though they are expert-drawn maps, one drawback of outline range maps is that species do not occur uniformly within their range [56], so that these maps can include false absences or presences [57]. Consequently, because of ignorance about the internal range structure [58], such maps may overestimate species occurrence [59], as has been addressed in the macroecological literature (e.g., Graham and Hijmans [36] and Hurlbert and White [60]). Moreover, a common critique is that outline maps represent only knowledge about the distribution that the respective authors have, rather than giving the true species distribution. If so, any analysis based on these maps could reflect changes in what the authors know rather than the true range patterns. Nevertheless, they represent the best currently available data on European dragonflies for addressing macroecological questions such as ours and multiple comparisons of outline distributions to find differences in species ranges or species richness have been published on various taxonomic groups within plants, vertebrates, and invertebrates (e.g., Hawkins et al. [61] and references therein), including macroecological studies on European dragonflies similar to ours (e.g., Olsen et al. [22], Grewe et al. [62], Hof et al. [63], Hof et al. [64], and Kalkman et al. [65]. Furthermore, of the 85 reviewed analyses of species richness in Hawkins et al. [61], 69% were based on range maps. We acknowledge that our maps represent rough approximations of the distribution of European dragonflies, but as Hurlbert and Jetz [66] demonstrated, using a sufficiently large grid resolution can surmount these problems.

Even though dragonflies are among the taxa with the best data record in space and time across Europe [5,65,67], an important concern about studies focusing on range shift is that expansions could simply be the outcome of a higher number of records. Although there will be some sampling heterogeneity on continental scale [65], the most significant northern range border shifts we found were for species that colonized Central Europe from the Mediterranean or extended their previous northern range border in Central Europe northwards into areas know to be well studied historically [34,67]. We found no general indication that the ranges shifts have been caused by false expansions due to an increase of knowledge. Hence, we assume that a lower sampling intensity in parts of Europe did not affect the observed range shifts on a 100 × 100 km grid level. Moreover, a bias in the distribution estimates should matter only if there were strong differences in mapping accuracy between damselflies and true dragonflies or among the four biogeographic groups. Finally, studies relying on true observations of range shifts rather than outcomes based on range maps yield results that support our findings on range shift in European dragonfly species, both on a more local scale (e.g., Hickling et al. [19], Knijf and Anselin [20], Ott [21], Suhling et al. [37], Hassall and Thompson [48], Riservato et al. [68], and Termaat et al. [69]), and continental scale (e.g., Kalkman et al. [65] and Boudot and Kalkman [67].

Because our geographic scope is Europe, the eastern border does not follow natural boundaries as the other range margins do. We will therefore have underestimated any shift eastwards for species distributed along the eastern border of the study area. As long as the bias causes underestimation rather than overestimation, however, we argue that we still obtained biologically meaningful and valuable information on range shift directionality by including the eastern margin.

### *4.2. Are Increases in Ranges of True Dragonflies Greater Than Those of Damselflies?*

Compared with damselflies, the true dragonflies were more prone to overall range increases independent of biogeographic origin. The geographic differences between poorly dispersing damselflies and easily dispersing true dragonflies revealed that distribution pattern and ranges seemed to be regulated differently between the two suborders. Moreover, range expansion and successful establishment are subject to physical constraints. Despite the relatively weak dispersal ability of damselflies, their passive flight across land areas should still be sufficient to confer on them sufficient geographic plasticity to keep pace with shifts in climatic envelope and resources, but they have less ability to cross wide physical barriers such as the Mediterranean Sea or the North Sea. For dispersing species, distance between suitable habitats is important with regard to their chances of tracking climate and environmental change. If suitable dispersal corridors are absent, species responses to climate change may not be realized [6,22,70]. For tropical species, which currently are represented only by true dragonflies, it is reasonable to believe that the Sahara and the Mediterranean Sea together constitute a barrier preventing Afro-Tropical damselfly species from colonizing southern Europe or at least causing them to fall behind true dragonflies. Of the four species identified as new for Europe since 1988, the three tropical species (*Orthetrum sabina*, *Orthetrum taeniolatum* and *Trithemis kirbyi*) are true dragonflies, whereas only the Mediterranean species, *Ischnura fountaineae*, which arrived from North Africa to the Italian island Panteleria southwest of Sicily, is a damselfly [50]. With regard to damselfly species, which may not be able to keep up with the dispersal capacity of tropical true dragonflies, the latitudinal range centers of damselfly and true dragonfly species within the Mediterranean group did not differ significantly in 1988 ($p > 0.05$). In contrast, in the Eurasian and Boreo-alpine groups, true dragonflies on average showed a more northerly located range center. We cannot rule out that the difference in some species could have been caused by true dragonflies being able re-colonize Europe faster after the last glaciations than some damselflies, and we have not been able to find any studies supporting directly that damselflies exhibit postglacial dispersal limitation to the present day. However, because body size and the ability to vibrate thoracic muscles to heat their body matters for survival in a colder environment, we suggest that this difference in range center could also have resulted from a synergistic effect of the larger size, thermoregulation abilities and better flight capacity of true dragonflies being generally more robust and physically strong than the thermoconform damselflies.

### *4.3. Have the Ranges of Southern Species Increased More Than the Ranges of Continental and Northern Species?*

Distributions of southern species (Tropical and Mediterranean groups) expanded to a larger extent than those of northern species (Eurasian and Boreo-alpine groups), which is consistent with other studies, at least in the temperate part of the world (e.g., Hickling et al. [19], Knijf and Anselin [20], and Ott [21]. This finding supports the expectation that it is especially in the species adapted to a warmer climate that we see the greatest range expansions.

The northward range expansions and the Afro-Tropical species entering southern Europe indicate that the range expansion of southern dragonfly species in Europe in particular is ongoing. However, the Sahara and the Mediterranean Sea together seem to constitute a barrier that cause the initial colonization to occur at a relatively low rate and range shifts are geographically skewed, with most range expansions occurring in central and northern Europe, whereas changes in the south are fewer and smaller. Here, the only species with a relatively large change in range were the Afro-Tropical species entering Europe. For most lowland species in southern Europe, temperature is not as much the constraining factor for their range as is the occurrence of freshwater and suitable habitat [71].

### *4.4. Will Northern Species and High-Elevation Species Experience Reduced Overall Ranges as Their Realized Climatic Envelopes Shrink Because of Global Warming?*

Most Boreo-alpine species had expanded their distributional range, and we find no indications that these are false expansions due to increase of knowledge. Hence, we argue that any shifts in species range are not simply constrained by the availability of suitable habitat but may to some degree also be explained by constraints in the realized thermal niche and distributions at the range margins. The change in range centroids in Boreo-alpine species showed a mean longitudinal shift towards the west mainly into Fennoscandia and Central Europe, highlighting that turnover in species richness may be driven not only by northbound range expansions, but also by westward colonization. This pattern of longitudinal shift towards the west is counterintuitive to what we would expect for climate-driven range shift [2]. However, as the realized niche is not necessarily the same as the fundamental niche of the species, the thermal niche of some of the Boreo-alpine species could have been wider than the temperature, which used to be available in the area they are occupying, so when climate warms, they are still inside their fundamental niche and can perform better, causing the range expansion with the largest towards the west. Furthermore, it has been suggested that more dispersal (gene flow) may occur from central to peripheral populations (asymmetric migration) than the reverse [19]. If gene flow is stronger than selection along the range margins, core populations represent sources and the peripheral populations are sinks where genetic variation is continuously replenished [19]. In this way, local evolutionary adaptation at range margins may be prevented even though climate change triggers a different selective pressure than in the core range. When global warming eventually reaches the area with the genetically more diverse central populations, it may cause a shift in the species' realized niche. In response, rather than persisting only with a narrow range of habitat characteristics, the species may gradually adapt in a way that allows for the exploitation of formerly unsuitable habitats [3,4]. Following this, we suggest that some Boreo-alpine species with westward range expansion may not yet have been able to colonize all available areas and persist within their climatic envelope or may show some degree of thermal release during a climate-driven range expansion. The result could be a shift in their thermal niche, making them able to adapt to new resource conditions and exploit formerly unsuitable habitats. This pattern may explain why it was mostly Boreo-alpine species that expanded westward, especially so during the last decades, when global warming has been affecting boreal forest and taiga at increasing rates [12].

Evidence of a strong negative impact of climate change on dragonflies is lacking, although local examples of desiccation of bog habitats have been described [72]. We found three Boreo-alpine species that showed range contraction, namely the relatively widespread *Coenagrion lunulatum* and *Leucorrhinia albifrons* and the much rarer *Nehalennia speciosa*. We suggest that these trends could be consequences of global warming, and if so, they provide a negative signal for selection of oligotrophic freshwater species. Range contraction may not necessarily be driven by a decrease in their realized climatic envelopes as much as by habitat loss and degradation. For some dragonfly species, available habitat continues to decline because of global warming and drainage of wetland areas, but pollution and overgrowth of habitats may also threaten them [34]. Loss and degradation of habitat will cause local populations to go extinct and simultaneously escalate the degree of fragmentation. This pattern is believed to explain why *Nehalennia speciosa* is declining and has already become regionally extinct in many areas across its European range [73].

### *4.5. Are Northwards Range Shifts Greater Than Movements at Other Range Margins Reflecting a Directional Poleward Shift Rather Than Non-Directional Range Expansion?*

Even though latitudinal shift at the northern range margin was larger on average than shifts at any other margins, we expected that range shift resulting from climate warming would occur not only at the northern margins, but also as poleward shifts of southern range margins [74]. We did not find significant contraction of the southern range boundaries, which could be explained by the fact that southern boundaries of distributional ranges for most species lie outside Europe, but also to some degree because the southern limit has been historically poorly defined. Nevertheless, especially in Mediterranean species, local diversity had declined in regions on the Iberian Peninsula and along the Mediterranean Sea and the Black Sea [68,71]. This is likely due to habitat destruction and degradation, pollution, mismanagement of water bodies due to increased water demand and a lower level of precipitation due to climate change [68]. These dynamics jointly illustrate that species occurrences may decline or that species may go locally extinct without causing a current contraction in overall range [2].

Tropical species highlight the colonization corridors for Afro-Tropical species entry into southern Europe, by crossing the narrowest straits of the Mediterranean Sea through the Iberian or Italian peninsulas, by using Mediterranean islands as stepping stones, or through the Near East. Although the initial colonization of Europe occurred as northbound movement from Africa [75], it is important to note that the colonization did not immediately follow a direct northerly route. When species have crossed the Mediterranean Sea, they may occur in fragmented ranges with populations scattered along various southern latitudes. Increase in range and subsequent colonization by these subpopulations means that the direction in their range shift appears stochastic rather than following a recognizable pattern. This appearance is illustrated by the tropical species *Paragomphus genei*, which had the largest change in range centroid in a 1081-km shift westward, resulting from recent range expansion across the Iberian Peninsula, where the species has begun to reproduce in watering pools constructed for sheep [76]. This example offers a possible explanation for why, in contrast to expectations, shift patterns in range centroid and overall range were mixed. Expanding species had an overall northbound directionality in their range expansion, and we expected this trend to manifest not only at the northern range boundary but also in the direction of range centroid shifts. However, as the plots illustrate (Figure 2), there was no common directionality because of differences in habitat requirements, habitat dispersal abilities, knowledge in distribution and other factors [22]

### *4.6. Are Geographical Shifts in Species Richness Patterns Driven Mainly by Southern Species Rather Than by Species from a More Continental and Northern Origin?*

Since 1988, average range size for species in all biogeographic groups has increased, with southern species especially having expanded their ranges to the north, some increasing by hundreds of kilometers. This expansion, in turn, is driving increased overall species richness to a higher extent than expansions in continental and northern species, especially so across all of Central Europe. For tropical species, the most species-rich regions in Europe are currently situated in the southern part of the Iberian Peninsula and in southern Turkey. In contrast, local species richness of Mediterranean species has declined in southern Europe, but increased in northwestern, central, and eastern Europe, which is a general trend observed across animals and plants [7]. This overall pattern of increase in local species richness in dragonflies is mirrored almost completely by the Eurasian species, except for an additional increase in central Scandinavia and on the Balkan and Italian peninsulas. There is high diversity of Eurasian species throughout Central Europe, but with a clear decline along the northern Pyrenees, indicating that for the continental species associated with lower elevation land areas, the mountain areas may constitute physical barriers that limit range expansion from the northeast into the Iberian Peninsula. The diversity in Boreo-alpine species has increased in most of Scandinavia and in various isolated, rather fragmented parts of Central Europe, in contrast to declines in species richness north of the Black Sea.

Recent data on continental scale support that the expansion of ranges to the north, which in general was observed across all biogeographic groups between 1988 and 2010, seem to continue [67], which, in turn, drives shifts in dragonfly species richness across Europe even further [65]. We would argue that the shift in European species richness seen in our study and supported by more recent data could be accelerated further by very warm summers such as observed in the last few years.

The distribution of dragonfly species in Europe exemplifies a distinct biogeographical pattern. The lowest diversity occurs in the northern parts of mainland Europe and on islands such as Great Britain and Ireland, whereas the highest is found in Central Europe, where tropical and Mediterranean species co-occur with species from more temperate and boreal climates. As Central Europe is an area of confluence of multiple expansion routes, a higher overall diversity is to be expected. Confirmation of this region as a hotspot for dragonfly diversity underlines the high ecological importance of the Central European wetlands for water-linked species. In contrast, the Mediterranean glacial refuge areas are not as species rich as the central part of Europe. Recent studies based on plants, terrestrial vertebrates, and butterflies have demonstrated that postglacial recolonization of most of temperate Europe has come not only from the three major Pleistocene refugia on the Iberian, Italian, and Balkan peninsulas, but also from the east and from small ice age refugia in Europe north of the Alps (e.g., Simonsen and Huemer [41], Ursenbacher et al. [42], Brochmann et al. [43], Schmitt et al. [44]). Dragonflies are believed to have high dispersal capacities [33], so that changes in distribution and geographical richness pattern should mainly be driven by present-day climate warming and availability of suitable habitat [16] and only to a lesser extent by historical legacies of past climate; however, physical barriers such as high-altitude mountain ranges may prevent postglacial recolonization in certain regions. Such barriers could explain why the Mediterranean region is not as rich in species as the central part of Europe. Moreover, especially for the less mobile dragonfly species, it could indicate that assemblages of species in the westernmost peninsula of Eurasia and other geographically isolated regions such as Fennoscandia could reflect stepwise reductions in species immigration from glacial refuge regions during the postglacial recolonization process due to geographic distance [77] and physical barriers [45].

## 5. Conclusions

The results of this study demonstrate that large-scale changes in patterns of dragonfly species richness are the result of several divergent dynamics that differ for the taxonomic suborders and biogeographic groups of dragonflies. In addition to showing an overall increase in species range for the whole order, true dragonflies were more prone than damselflies to exhibit overall range expansions, independent of biogeographic origin. Consequently, true dragonflies had more local turnover than did damselflies. Even though damselflies are strong enough to keep pace with shifts in the climatic envelope by passive flight across land, they are usually not strong enough to cross wide physical barriers such as the Sahara, Mediterranean Sea, or the North Sea. Tropical and Mediterranean species had much more expanded ranges than did Eurasian and Boreo-alpine species. The greatest range expansions were found in warm-adapted species, with the most prominent diversity changes shaped by southern species. However, several Boreo-alpine species also expanded their ranges, especially westward. This pattern suggests that thermal release during climate-mediated range expansion may shift local species richness across Europe. The Central European hotspot for dragonfly diversity documents the high conservation value of the Central European wetlands for water-linked species. Local species richness declined in the Iberian Peninsula, the Mediterranean Sea, and the Black Sea areas, suggesting a negative impact of climate change on dragonfly species in warm regions. Range contractions of three Boreo-alpine habitat specialists in oligotrophic freshwater should be given special conservation attention to avoid regional extinction. This is especially true for *Nehalennia speciosa*, which face severe challenges from climate change declines.

We have provided an assessment on a European scale of how dragonfly species richness patterns have changed over a 22-year period. Our focus was on range shifts between groups of species with shared traits that we consider to be important drivers of changes in species richness. In this way, we document that understanding range changes and tracking changes in diversity patterns are important tools for conservation of dragonflies, and at the same time, dragonflies emerge as important first-level indicators of environmental health and conservation needs.

**Supplementary Materials:** The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d14121066/s1. Figure S1: Geographical patterns of European dragonfly (Odonata) species richness and changes by biogeographical groups; Table S1: List of European dragonfly (Odonata) species excluded from the analysis, where modifications to species range have been applied, that colonized Europe after 1988, and with taxonomic and nomenclatural changes between 1988 and 2010; Table S2: Data for the analysis of range shift in European dragonfly (Odonata) species. The list includes taxonomic suborder and scientific names of all species included in the analysis of range shift and changes in species richness 1988–2010. Also presented are the per species biogeographic group, range shift trend, relative change in range (percent change in number of occupied 100 × 100 km grid cells), distance of shift in northern, southern, eastern, and western range margins, and direction of shift in range centroid and distance of shift in range centroid; Table S3: Summary statistics of various measures of range shifts between 1988 and 2010 in European damselfly (Zygoptera) and true dragonfly (Anisoptera) species; Table S4: Summary statistics of various measures of range shifts between 1988 and 2010 in all European dragonfly (Odonata), damselfly (Zygoptera), and true dragonfly (Anisoptera) species, and species in the four biogeographical groups—Tropical, Mediterranean, Eurasian, and Boreo-alpine; and Table S5: Summary statistics of range margin shifts between 1988 and 2010 at the northern margin and the southern, eastern, and western margins combined in all European dragonfly (Odonata), damselfly (Zygoptera), and true dragonfly (Anisoptera) species, and species in the four biogeographical groups—Tropical, Mediterranean, Eurasian, and Boreo-alpine [78,79].

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## Appendix A

List of European dragonfly (Odonata) species included in the analysis of range shift and changes in species richness 1988–2010 with information on taxonomic suborder, scientific name including author and year of species description, biogeographic group, and range shift trend. * Indicate the four species that in 2010 were included as new in Europe.

**Table A1.** List of European dragonfly (Odonata) species (*n* = 123) included in the analysis of range shift and changes in species richness 1988–2010 with information on taxonomic suborder, scientific name including author and year of species description, biogeographic group, and range shift trend. * Indicate the four species that in 2010 were included as new in Europe. Nomenclature and taxonomy follow IUCN [80].

| Suborder | Species | Biogeographic Group | Range Shift Trend |
|---|---|---|---|
| Zygoptera | *Calopteryx haemorrhoidalis* Vander Linden, 1825 | Mediterranean | Expansion |
| Zygoptera | *Calopteryx splendens* Harris, 1780 | Eurasian | Expansion |
| Zygoptera | *Calopteryx virgo* Linnaeus, 1758 | Eurasian | Expansion |
| Zygoptera | *Calopteryx xanthostoma* Charpentier, 1825 | Mediterranean | Contraction |
| Zygoptera | *Ceriagrion georgifreyi* Schmidt, 1953 | Mediterranean | Expansion |
| Zygoptera | *Ceriagrion tenellum* De Villers, 1789 | Mediterranean | Expansion |
| Zygoptera | *Chalcolestes viridis* Vander Linden, 1825 | Mediterranean | Expansion |
| Zygoptera | *Coenagrion armatum* Charpentier, 1840 | Boreo-alpine | Expansion |
| Zygoptera | *Coenagrion caerulescens* Fonscolombe, 1838 | Mediterranean | Expansion |
| Zygoptera | *Coenagrion hastulatum* Charpentier, 1825 | Boreo-alpine | Expansion |
| Zygoptera | *Coenagrion hylas* Trybom, 1889 | Boreo-alpine | Stable |
| Zygoptera | *Coenagrion intermedium* Lohmann, 1990 | Mediterranean | Stable |
| Zygoptera | *Coenagrion johanssoni* Wallengren, 1894 | Boreo-alpine | Expansion |
| Zygoptera | *Coenagrion lunulatum* Charpentier, 1840 | Boreo-alpine | Contraction |
| Zygoptera | *Coenagrion mercuriale* Charpentier, 1840 | Mediterranean | Expansion |
| Zygoptera | *Coenagrion ornatum* Selys, 1850 | Mediterranean | Expansion |
| Zygoptera | *Coenagrion puella* Linnaeus, 1758 | Mediterranean | Expansion |
| Zygoptera | *Coenagrion pulchellum* Vander Linden, 1825 | Eurasian | Expansion |
| Zygoptera | *Coenagrion scitulum* Rambur, 1842 | Mediterranean | Expansion |
| Zygoptera | *Enallagma cyathigerum* Charpentier, 1840 | Eurasian | Expansion |
| Zygoptera | *Epallage fatime* Charpentier, 1840 | Mediterranean | Expansion |
| Zygoptera | *Erythromma lindenii* Selys, 1840 | Mediterranean | Expansion |
| Zygoptera | *Erythromma najas* Hansemann, 1823 | Eurasian | Expansion |
| Zygoptera | *Erythromma viridulum* Charpentier, 1840 | Mediterranean | Expansion |
| Zygoptera | *Ischnura elegans* Vander Linden, 1820 | Eurasian | Expansion |
| Zygoptera | *Ischnura fountaineae* * Morton, 1905 | Mediterranean | Expansion |
| Zygoptera | *Ischnura genei* Rambur, 1842 | Mediterranean | Stable |
| Zygoptera | *Ischnura graellsii* Rambur, 1842 | Mediterranean | Expansion |
| Zygoptera | *Ischnura pumilio* Charpentier, 1825 | Mediterranean | Expansion |
| Zygoptera | *Lestes barbarus* Fabricius, 1798 | Mediterranean | Expansion |
| Zygoptera | *Lestes dryas* Kirby, 1890 | Eurasian | Expansion |
| Zygoptera | *Lestes macrostigma* Eversmann, 1836 | Mediterranean | Contraction |
| Zygoptera | *Lestes sponsa* Hansemann, 1823 | Eurasian | Expansion |
| Zygoptera | *Lestes virens* Charpentier, 1825 | Eurasian | Expansion |
| Zygoptera | *Nehalennia speciosa* Charpentier, 1840 | Boreo-alpine | Contraction |
| Zygoptera | *Platycnemis acutipennis* Selys, 1841 | Mediterranean | Expansion |
| Zygoptera | *Platycnemis latipes* Rambur, 1842 | Mediterranean | Contraction |
| Zygoptera | *Platycnemis pennipes* Pallas, 1771 | Eurasian | Contraction |
| Zygoptera | *Pyrrhosoma nymphula* Sulzer, 1776 | Eurasian | Expansion |
| Zygoptera | *Sympecma fusca* Vander Linden, 1820 | Mediterranean | Contraction |
| Zygoptera | *Sympecma paedisca* Brauer, 1877 | Boreo-alpine | Expansion |
| Anisoptera | *Aeshna affinis* Vander Linden, 1820 | Mediterranean | Expansion |

**Table A1.** *Cont.*

| Suborder | Species | Biogeographic Group | Range Shift Trend |
|---|---|---|---|
| Anisoptera | *Aeshna caerulea* Ström, 1783 | Boreo-alpine | Expansion |
| Anisoptera | *Aeshna crenata* Hagen, 1856 | Boreo-alpine | Expansion |
| Anisoptera | *Aeshna cyanea* Müller, 1764 | Eurasian | Contraction |
| Anisoptera | *Aeshna grandis* Linnaeus, 1758 | Eurasian | Expansion |
| Anisoptera | *Aeshna isoceles* (Müller, 1767) | Mediterranean | Expansion |
| Anisoptera | *Aeshna juncea* Linnaeus, 1758 | Boreo-alpine | Expansion |
| Anisoptera | *Aeshna mixta* Latreille, 1805 | Mediterranean | Expansion |
| Anisoptera | *Aeshna serrata* Hagen, 1856 | Eurasian | Expansion |
| Anisoptera | *Aeshna subarctica* Walker, 1908 | Boreo-alpine | Expansion |
| Anisoptera | *Aeshna viridis* Eversmann, 1836 | Eurasian | Expansion |
| Anisoptera | *Anax imperator* Leach, 1815 | Mediterranean | Expansion |
| Anisoptera | *Anax parthenope* Selys, 1839 | Mediterranean | Expansion |
| Anisoptera | *Boyeria cretensis* Peters, 1991 | Mediterranean | Expansion |
| Anisoptera | *Boyeria irene* Fonscolombe, 1838 | Mediterranean | Expansion |
| Anisoptera | *Brachythemis impartita* Karsch, 1890 | Tropical | Expansion |
| Anisoptera | *Brachytron pratense* Müller, 1764 | Eurasian | Expansion |
| Anisoptera | *Caliaeschna microstigma* Schneider, 1845 | Mediterranean | Expansion |
| Anisoptera | *Cordulegaster bidentata* Selys, 1843 | Mediterranean | Expansion |
| Anisoptera | *Cordulegaster boltonii* Donovan, 1807 | Eurasian | Contraction |
| Anisoptera | *Cordulegaster helladica* Lohmann, 1993 | Mediterranean | Expansion |
| Anisoptera | *Cordulegaster heros* Theischinger, 1979 | Mediterranean | Expansion |
| Anisoptera | *Cordulegaster insignis* Schneider, 1845 | Mediterranean | Contraction |
| Anisoptera | *Cordulegaster picta* Selys, 1854 | Mediterranean | Expansion |
| Anisoptera | *Cordulegaster trinacriae* Waterston, 1976 | Mediterranean | Expansion |
| Anisoptera | *Cordulia aenea* Linnaeus, 1758 | Eurasian | Expansion |
| Anisoptera | *Crocothemis erythraea* Brullé, 1832 | Tropical | Expansion |
| Anisoptera | *Diplacodes lefebvrii* Rambur, 1842 | Tropical | Expansion |
| Anisoptera | *Epitheca bimaculata* Charpentier, 1825 | Eurasian | Expansion |
| Anisoptera | *Gomphus flavipes* Selys, 1837 | Eurasian | Expansion |
| Anisoptera | *Gomphus graslinii* Rambur, 1842 | Mediterranean | Expansion |
| Anisoptera | *Gomphus pulchellus* Selys, 1840 | Mediterranean | Expansion |
| Anisoptera | *Gomphus schneiderii* Selys, 1850 | Mediterranean | Expansion |
| Anisoptera | *Gomphus simillimus* Selys, 1840 | Mediterranean | Expansion |
| Anisoptera | *Gomphus vulgatissimus* Linnaeus, 1758 | Eurasian | Expansion |
| Anisoptera | *Leucorrhinia albifrons* Burmeister, 1839 | Boreo-alpine | Contraction |
| Anisoptera | *Leucorrhinia caudalis* Charpentier, 1840 | Boreo-alpine | Expansion |
| Anisoptera | *Leucorrhinia dubia* Vander Linden, 1825 | Eurasian | Expansion |
| Anisoptera | *Leucorrhinia pectoralis* Charpentier, 1825 | Eurasian | Expansion |
| Anisoptera | *Leucorrhinia rubicunda* Linnaeus, 1758 | Boreo-alpine | Expansion |
| Anisoptera | *Libellula depressa* Linnaeus, 1758 | Eurasian | Expansion |
| Anisoptera | *Libellula fulva* Müller, 1764 | Eurasian | Expansion |
| Anisoptera | *Libellula quadrimaculata* Linnaeus, 1758 | Eurasian | Expansion |
| Anisoptera | *Lindenia tetraphylla* Vander Linden, 1825 | Mediterranean | Contraction |
| Anisoptera | *Macromia splendens* Pictet, 1843 | Mediterranean | Expansion |
| Anisoptera | *Onychogomphus costae* Selys, 1885 | Mediterranean | Expansion |
| Anisoptera | *Onychogomphus forcipatus* Linnaeus, 1758 | Mediterranean | Expansion |
| Anisoptera | *Onychogomphus uncatus* Charpentier, 1840 | Mediterranean | Expansion |
| Anisoptera | *Ophiogomphus cecilia* Fourcroy, 1785 | Eurasian | Expansion |
| Anisoptera | *Orthetrum albistylum* Selys, 1848 | Mediterranean | Expansion |
| Anisoptera | *Orthetrum brunneum* Fonscolombe, 1837 | Mediterranean | Expansion |
| Anisoptera | *Orthetrum cancellatum* Linnaeus, 1758 | Mediterranean | Expansion |
| Anisoptera | *Orthetrum chrysostigma* Burmeister, 1839 | Tropical | Expansion |
| Anisoptera | *Orthetrum coerulescens* Fabricius, 1798 | Mediterranean | Expansion |
| Anisoptera | *Orthetrum nitidinerve* Selys, 1841 | Mediterranean | Expansion |

**Table A1.** *Cont.*

| Suborder | Species | Biogeographic Group | Range Shift Trend |
|---|---|---|---|
| Anisoptera | *Orthetrum sabina* * Drury, 1773 | Tropical | Expansion |
| Anisoptera | *Orthetrum taeniolatum* * Schneider, 1845 | Tropical | Expansion |
| Anisoptera | *Orthetrum trinacria* Selys, 1841 | Tropical | Expansion |
| Anisoptera | *Oxygastra curtisii* Dale, 1834 | Mediterranean | Contraction |
| Anisoptera | *Pantala flavescens* Fabricius, 1798 | Tropical | Expansion |
| Anisoptera | *Paragomphus genei* Selys, 1841 | Tropical | Expansion |
| Anisoptera | *Selysiothemis nigra* Vander Linden, 1825 | Mediterranean | Expansion |
| Anisoptera | *Somatochlora alpestris* Selys, 1840 | Boreo-alpine | Expansion |
| Anisoptera | *Somatochlora arctica* Zetterstedt, 1840 | Boreo-alpine | Expansion |
| Anisoptera | *Somatochlora flavomaculata* Vander Linden, 1825 | Eurasian | Expansion |
| Anisoptera | *Somatochlora meridionalis* Nielsen, 1935 | Mediterranean | Expansion |
| Anisoptera | *Somatochlora metallica* Vander Linden, 1825 | Eurasian | Contraction |
| Anisoptera | *Somatochlora sahlbergi* Trybom, 1889 | Boreo-alpine | Expansion |
| Anisoptera | *Sympetrum danae* Sulzer, 1776 | Eurasian | Expansion |
| Anisoptera | *Sympetrum depressiusculum* Selys, 1841 | Eurasian | Expansion |
| Anisoptera | *Sympetrum flaveolum* Linnaeus, 1758 | Eurasian | Expansion |
| Anisoptera | *Sympetrum fonscolombii* Selys, 1840 | Tropical | Expansion |
| Anisoptera | *Sympetrum meridionale* Selys, 1841 | Mediterranean | Expansion |
| Anisoptera | *Sympetrum pedemontanum* O.F.Müller, 1766 | Eurasian | Expansion |
| Anisoptera | *Sympetrum sanguineum* Müller, 1764 | Eurasian | Expansion |
| Anisoptera | *Sympetrum sinaiticum* Dumont, 1977 | Mediterranean | Expansion |
| Anisoptera | *Sympetrum striolatum* Charpentier, 1840 | Eurasian | Expansion |
| Anisoptera | *Sympetrum vulgatum* Linnaeus, 1758 | Eurasian | Expansion |
| Anisoptera | *Trithemis annulate* Palisot de Beauvois, 1807 | Tropical | Expansion |
| Anisoptera | *Trithemis festiva* Rambur, 1842 | Tropical | Expansion |
| Anisoptera | *Trithemis kirbyi* * Selys, 1891 | Tropical | Expansion |
| Anisoptera | *Zygonyx torridus* Kirby, 1889 | Tropical | Expansion |

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