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Timing and direction of faunal exchange between the Nearctic and the Palaearctic in Odonata

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Abstract

Aim: Species have different distribution patterns across the globe and among biogeographical regions. The Nearctic and Palaearctic regions share lineages because of their parallel biogeographic histories and ecological conditions. As the number of phylogenetic studies increases, there are more insights into past exchange events between these two regions and their effects on the current distribution of diversity. However, several groups have not been tested and an overall generalization is still missing. Here, we analyse the biogeographic history across multiple genera of odonates to elucidate a general process of species exchange, vicariance and species divergence between these two regions.

Location: The Holarctic, including the entire Nearctic and the East and West Palaearctic.

Taxon: 14 genera of Odonata (Insecta).

Methods: We reconstructed a time-calibrated phylogenetic tree for each genus to determine species relationships and divergence time using 3614 COI sequences of 259 species. Biogeographic ancestral range estimation was inferred for each phylogeny using BioGeoBEARS. Preferred habitat (lotic versus lentic) was established for each species.

Results: Exchange events were not restricted in time, direction or either lentic habitat or lotic habitat. Most genera crossed between both regions only once, and it was mainly across the Beringia, while three diverse anisopteran genera revealed multiple exchanges. Recent exchanges during the Pleistocene were associated with cold-dwelling and lentic species.

Main Conclusions: Our finding reveals the absence of a generalizable pattern of species exchange and divergence between the Nearctic and Palaearctic regions; instead, we found lineage-specific biogeographic patterns. This finding highlights the complexity of drivers and functional traits that shaped current diversity patterns. Moreover, it emphasizes that general conclusions cannot be formulated based on one single clade.

Cesc Múrria and Vincent J. Kalkman contributed equally to this work.

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KEYWORDS

biogeography, climate change, damselflies, dragonflies, Holarctic

1 | INTRODUCTION

Biodiversity is not equally distributed across the globe, and the accumulated diversity differs among biogeographical regions. For instance, the tropical areas have accumulated a higher number of species, which decreases towards the poles (Gaston, 2000; Hillebrand, 2004). As a result, different ecoregions can be recognized based on the species composition and the similarity of communities (Olson et al., 2001). In the Northern Hemisphere, the Palaearctic and Nearctic regions share some biomes such as taiga, tundra and temperate broadleaf forest, which form a band running in a longitudinal direction (Moncrieff et al., 2015). Their proximity and geographic history favour a high percentage of shared lineages compared to the Southern Hemisphere regions where long-term geographic isolation has resulted in higher phylogenetic uniqueness (Barber-James et al., 2008; Liu et al., 2023). While global regionalizations based on different taxa and taxonomic levels might draw different biogeographic regions (Liu et al., 2023), the similarity between the Nearctic and Palaearctic flora and fauna is among the highest when compared to other biogeographical regions (Holt et al., 2013).

Across biogeographical regions, close-related species can be geographically separated, and these disjunct distributions can be explained by long-distance dispersal and ancient vicariance when a new geographical barrier divides the populations (de Queiroz, 2005; Sanmartín et al., 2001). The phylogenetic relationships and current species distributions across regions are commonly analysed for elucidating their biogeographical history and testing different biogeographic models (García-Verdugo et al., 2019; Standring et al., 2022). Therefore, understanding species movement and vicariance events is critical for revealing evolutionary trajectories of species complexes (de Queiroz, 2005).

During the last millions of years, various land connections have existed between the Palaearctic and the Nearctic. The North Atlantic land bridges connected West Europe with Eastern North America until at least 55 Mya (Brikiatis, 2014). On the other side of the Palaearctic, the Beringian Land Bridge (BLB) connected Eastern Asia with Western North America, which remained open until ~5 Mya (Marincovich & Gladenkov, 1999). During the Pleistocene, the BLB was restored periodically due to lowered sea level through glaciations, when the BLB was covered by tundra shrub vegetation (Elias & Crocker, 2008; Sanmartín et al., 2001). As a result, the BLB has been reported to play a significant role in the biota exchange and the biogeography of numerous taxa, such as plants (Elias & Crocker, 2008; Liu et al., 2021; Maguilla et al., 2018) and insects (Branstetter et al., 2021; Maresova et al., 2021; Pisanty et al., 2022; Rubinoff & Doorenweerd, 2020; Schär et al., 2018).

Despite the efforts for studying the importance of the BLB, there are few studies on freshwater insects and a generalization of its

importance on current distribution patterns of diversity is still lacking. Odonata (dragonflies and damselflies) is a group of freshwater insects that have terrestrial flying adults and aquatic nymphs. Importantly, they are one of the most ancient flying insects with an origin that dates back to the Carboniferous (Kohli, Letsch, et al., 2021). The highest species diversity is found in the tropics (Sandall et al., 2022), whereas in the Holarctic realm, the Nearctic has a higher diversity than larger parts of the Palaearctic (Kalkman et al., 2008). Previous studies suggested that the lower species richness of the Palaearctic is the result of the Pleistocene glacial periods having a much stronger negative impact due to the generally east-west oriented barriers (Abbott et al., 2022; Kalkman et al., 2022). For instance, the successive mountain ranges from the Caspian Sea to the Chukotka Peninsula in Asia (Dumont et al., 2021), and the Pyrenees, Alps and Balkans in the Mediterranean region (Grigoropoulou et al., 2022) reduce the possibilities to retract southwards during a glacial period. However, the role of the BLB in this pattern of diversity across the Holarctic is still unknown and there is little fossil evidence to support a general model (Garrouste & Nel, 2019).

There are 29 genera of Odonata shared between these two biogeographic regions. Some species are widely distributed, and their distribution is likely the result of long-range dispersal (e.g., *Pantala flavescens*, Troast et al., 2016). Other lineages show mainly a tropical distribution with some species reaching higher latitudes along the Holarctic such as *Gynacantha*, *Macrodiplax*, *Tholymis* and *Tramea* (Kalkman et al., 2008). From the 29 shared genera, 14 genera from different families and suborders have a distribution mostly restricted to the Holarctic: *Aeshna* Fabricius, 1775; *Calopteryx* Leach in Brewster, 1815; *Coenagrion* Kirby, 1890; *Cordulegaster* Leach in Brewster, 1815; *Cordulia* Leach in Brewster, 1815; *Enallagma* Charpentier, 1840; *Epithea* Charpentier, 1840; *Ladona* Needham, 1897; *Leucorrhinia* Brittinger, 1850; *Libellula* Linnaeus, 1758; *Nehalennia* Selys, 1850; *Ophiogomphus* Selys, 1854; *Somatochlora* Selys, 1871; and *Sympetrum* Newman, 1833 (Dijkstra & Kalkman, 2012).

In the Holarctic, odonate species are generally restricted to either the Palaearctic or the Nearctic; however, there are some species that are found across both regions (Abbott et al., 2022; Kalkman et al., 2022). Previous studies in the population structure and phylogeography of five widespread species (*Aeshna juncea*, *A. subarctica*, *Libellula quadrimaculata*, *Somatochlora sahlbergi* and *Sympetrum danae*) found similar patterns in the haplotype networks splitting the Palaearctic and Nearctic populations, except for the circumpolar *S. sahlbergi*, which revealed extremely low genetic diversity and panmixia (Kohli, Djernæs, et al., 2021; Kohli et al., 2018). Moreover, individuals from the Beringian region clustered together with the Nearctic or Palaearctic individuals depending on each species, which suggests that the regions close to the BLB have served as refugia and corridors (Kohli, Djernæs, et al., 2021; Kohli et al., 2018). For instance,

a more extensive dataset showed *A. juncea* from the East Palaearctic closer to the Nearctic populations (Schneider et al., 2023). To determine the effects of the BLB on odonates, findings using a few numbers of unrelated species were insufficient, and further analyses across lineages are needed to understand the process underlying the current distribution patterns of odonates across the Holarctic.

According to their habitat preference, odonates can be classified as lotic, those largely restricted to running waters, or lentic, those mainly occurring in standing waters. Lentic species are thought to have a higher dispersal capacity and therefore larger range sizes because lentic habitats are less stable through geological time (e.g., habitat loss associated with sediment buildup) (Grewe et al., 2013; Hof et al., 2006; Ribera & Vogler, 2000). For instance, lentic species track climate changes faster than their lotic counterparts, and the proportion of lentic species increases towards the north (Hof et al., 2008, 2012). Despite these evidences, some lentic lineages have shown high levels of speciation (Letsch et al., 2016), which contradicts the original hypothesis of lentic species having genetically unstructured populations (Papadopoulou et al., 2009; Ribera & Vogler, 2000). This might be because more broad distributions in lentic species may favour the appearance of genetic barriers such as mountains or different microhabitats, which can translate into speciation (Letsch et al., 2016). At the genus level, Swaegers et al. (2014) did not find relationships between *Coenagrion* species that colonized the Nearctic and their range size or dispersal capacity.

Here, we build a time-calibrated phylogenetic tree reconstructed from the popular animal DNA barcode marker, mitochondrial COI gene fragment, for the 14 genera distributed across the Holarctic in order to determine the number, direction and timing of exchange events between the Nearctic and the Palaearctic. Based on previous studies supporting the importance of the BLB for faunal exchange (Kohli, Djernæs, et al., 2021) and the higher diversity in the Nearctic compared to that of the Palaearctic (Abbott et al., 2022; Kalkman et al., 2022), we expect (1) exchange to be limited to the Pleistocene during which several land bridges in Beringia connected both regions; (2) exchange to be predominantly through the BLB and rarely through the North Atlantic land bridge; (3) a higher number of exchange events from the species-rich Nearctic to the relative species-poor Palaearctic than vice versa; and (4) a predominance of lentic species in exchange events since they have wider distributions and higher dispersal capacity than lotic species. However, neither of these expectations came true from our analysis.

2 | MATERIALS AND METHODS

2.1 | Sequence mining and dataset assembling

Molecular data were assembled for the 14 genera that are currently distributed across the Palaearctic and the Nearctic whose distribution is largely restricted to the Holarctic. To infer the phylogenetic relationships between all species within those genera, we used the animal DNA barcode fragment of the mitochondrial cytochrome

oxidase C subunit I (COI or *cox1*) gene. We downloaded sequences from the public repositories BOLD Systems and GenBank (see BOLD IDs and accession numbers in Table S1). We also downloaded sequences for the genera *Anotogaster* and *Neallogaster* because these species seem to be closely related to *Cordulegaster*. Regarding *Libellula depressa* and *L. fulva*, previous morphological and molecular studies found these species to be more closely related to *Ladona* than to *Libellula* (Artiss et al., 2001; Carle & Kjer, 2002), and for this reason, they were included in the analyses of *Ladona*. Only sequences of COI longer than 400bp were selected, except for *Cordulia* as most of the sequences available were shorter. Moreover, we excluded BOLD sequences labelled as 'Contaminants', 'Records with Stop Codons' and 'Flagged as Misidentifications'. Additionally, we used new sequences provided by the Naturalis Biodiversity Center and the Alabama Museum of Natural History. For some species, the entire mitochondrial genome was available, and we performed an automatic annotation through MITOS2 (Donath et al., 2019) to extract the COI fragment.

Sequences were aligned using the online version of MAFFT with default options (Kato et al., 2019), and tails were trimmed manually using BioEdit (Hall, 1999). The alignment was visually inspected for quality control. In order to identify possible sequencing errors and taxonomic misidentifications, we used both maximum likelihood (ML) and Bayesian inference (BI) to estimate phylogenetic trees for each genus and to explore the coherence of the tree topology. We ran BLAST searches at the NCBI website (Johnson et al., 2008) for checking the taxonomy of sequences that had a dubious position in the tree to ensure they were not the result of contamination. If available, the identification was confirmed or corrected using the images in BOLD Systems. Identical sequences were collapsed into haplotypes using DNACollapser (Villesen, 2007).

2.2 | Phylogenetic analysis

For improving the support of the phylogenetic analyses, PartitionFinder (Guindon et al., 2010; Lanfear et al., 2017) was used to search for the best-fit partition scheme and models of molecular evolution. The criteria for selecting the scheme were based on Bayesian information criteria (BIC). For each lineage, both ML and BI phylogenetic trees were built.

ML trees were inferred using IQ-Tree web server (Nguyen et al., 2015). For this analysis, the best evolutionary model was estimated for each codon position using ModelFinder (Kalyaanamoorthy et al., 2017) as implemented in IQ-Tree. We performed 1000 replicates of ultrafast bootstrap (Hoang et al., 2018).

For BI, we used MrBayes 3.2.7a (Ronquist et al., 2012). We ran two runs of four independent chains for 20 million generations with a sample frequency of 1000 using model parameters reported by PartitionFinder (nst=6 and rates=invgamma for COI_1; nst=1 and rates=invgamma for COI_2; nst=6 and rates=gamma for COI_3). The analysis was run on CIPRES Science Gateway (Miller et al., 2010). We assessed phylogenetic convergence by looking at the effective

sample size (ESS), which was established above 200 for all parameters using Tracer 1.7.2 (Rambaut et al., 2018) after a burn-in of 10%.

2.3 | Divergence time estimation

To estimate divergence time among species, BEAST 1.10.4 (Suchard et al., 2018) was used as implemented in CIPRES Science Gateway (Miller et al., 2010). For this analysis, each tip of the phylogeny should be one sequence per species. Our criterion for selecting the sequence was the longest read sequence per species in order to minimize the missing data. However, we made several exceptions to this criterion, which are summarized in the appendix (Table S2). For instance, the most common exception was when COI failed to clearly delimitate between two or more morphological species; in this case, only one sequence for all mixed species was used (Futahashi, 2018; Galimberti et al., 2021; Kohli et al., 2018; Pilgrim & Von Dohlen, 2007; Sawabe et al., 2004; Ware et al., 2017). Another exception was for species which were not retrieved as monophyletic and/or have been suggested to be identified as two morphological species in the literature (Ferreira et al., 2016; Geiger et al., 2021; Kohli, Djernæs, et al., 2021; Kohli et al., 2018). In this case, one sequence per each of the tentative species was used. ML and BI tree reconstructions were built following the parameters explained above, but the number of generations was increased to 50 million. We pruned the tree for each lineage containing only the closest outgroups.

Fossils for dating odonates were not available for all genera, so we used published estimates of substitution rates for COI in insects. We used a uniform distribution for an uncorrelated lognormal relaxed molecular clock using a high (0.0168 substitution/sites/MY) (Papadopolou et al., 2010) and a low (0.0115 substitution/sites/MY) (Brower, 1994) substitution rate as limits. A Yule speciation was set as tree prior, and we ran the analysis for 20 million generations. All the logs were checked in Tracer 1.7.2 (Rambaut et al., 2018) after a burn-in of 10% of generations. We computed the maximum clade credibility tree, the median ages and the 95% credibility interval at each node using TreeAnnotator 1.10.4 (Drummond & Rambaut, 2007).

2.4 | Biogeographical analysis

We performed an ancestral range estimation (ARE) through time using the package BioGeoBEARS v1.1.3 (Matzke, 2013) in R 4.3.0 (R Core Team, 2023). Five areas were established: West Palearctic (W), East Palearctic (E), Nearctic (N), Neotropical (T) and Afrotropical (A). We divided the Palearctic into W and E based on the West Siberian Lowland as it is suggested to be a transition zone (Kosterin, 2005). The maximum range size was set to three regions based on the current distribution of the studied odonates, and non-adjacent area combinations were disallowed. Species distribution models from Abbott et al. (2022) and Kalkman et al. (2022) were used to assign the geographic range of each species.

Each genus was analysed separately, and it was limited to the ingroup. We tested five different models: dispersal, extinction, cladogenesis [DEC] (Ree & Smith, 2008; Ree et al., 2005), a ML version of the dispersal–vicariance [DIVALIKE] (Ronquist, 1997) and a ML version of the Bayesian analysis of biogeography [BAYAREALIKE] (Landis et al., 2013). Each of these models was tested with and without the founder-event speciation (+J). Additionally, we reran all analyses by adding a matrix of dispersal multipliers based on Condamine et al. (2013), which consists of 0.5 for dispersal between adjacent areas connected by land; 0.25 for adjacent areas connected by sea; and 0.125 for non-adjacent areas. We chose the best-fitting biogeographical model based on the lowest AICc value.

2.5 | Ancestral state estimation

Three genera (*Coenagrion*, *Enallagma* and *Somatochlora*) have both lentic and lotic species. To test whether the ancestor preferred lentic or lotic habitats, a stochastic character mapping (Huelsenbeck et al., 2003) with 1000 simulations was run for each genus using the package phytools (Revell, 2012) in R 4.3.0 (R Core Team, 2023). We previously tested equal rates, all different rates, 01 and 10 models and selected equal rates because it was the most robust across the three genera based on the lowest AIC value.

3 | RESULTS

After cleaning the COI sequence dataset, we obtained 3614 sequences belonging to 259 species and 14 genera. All these sequences collapsed in 1876 unique COI haplotypes (Table S1). Sequence coverage within a genus ranged from 46% of the species in *Enallagma* up to 100% in *Epitheca* and *Cordulia*, with an average of 80% of coverage of species across the 14 Holarctic genera (Table 1).

Most of the genera were recovered as monophyletic with high support values across the different phylogenetic approaches implemented (Figures S1 and S2), except for *Aeshna*, *Sympetrum* and *Cordulegaster*. The genus *Cordulegaster* was found to be monophyletic when *Anotogaster* and *Neallogaster* were included, which indicates that further effort is needed to resolve this inconsistency. The phylogenies at genus level using all haplotypes showed most species as monophyletic or as a clear paraphyletic residuum, which occurs when a species includes a descendant lineage accepted as a species. Nevertheless, 38 identical haplotypes were labelled in the public repositories using different taxonomic names (Table S1). All these haplotypes were used in further analyses within the species that were clustered in the genus-level phylogeny. This affected a total of 41 morphological species, some of which are known to hybridize (Tables S1 and S2). In addition, some species were difficult to differentiate as species using the COI haplotype trees, 40% of Nearctic species and 10.5% of Palearctic species (Table S2). Intraspecific delimitation affected three Palearctic species and one with a Holarctic distribution (Table S2).

TABLE 1 Summary of data used.

Genus	Number of species	Number of species included	Sample coverage (%)	Number of sequences	Number of haplotypes	Number of sequences used in dated tree*
<i>Aeshna</i>	27	25	93	547	330	25
<i>Cordulegaster</i>	29	25	86	256	176	25
<i>Anotogaster</i>	15	7	47	60	47	7
<i>Neallogaster</i>	9	2	22	4	4	2
<i>Cordulia</i>	2	2	100	34	21	4
<i>Epitheca</i>	12	12	100	80	61	5
<i>Ladona</i>	7	5	71	63	30	5
<i>Leucorrhinia</i>	14	14	100	142	69	12
<i>Libellula</i>	23	22	96	176	156	19
<i>Ophiogomphus</i>	24	21	88	273	109	8
<i>Somatochlora</i>	41	31	76	230	128	26
<i>Sympetrum</i>	53	40	75	710	331	35
<i>Calopteryx</i>	16	9	56	114	47	8
<i>Coenagrion</i>	26	20	77	475	136	19
<i>Enallagma</i>	44	20	45	295	158	12
<i>Nehalennia</i>	6	4	67	155	73	4
Total	348	259	75	3614	1876	216

Note: For each genus: number of current species and species included, sample coverage and number of sequences and haplotypes. (*) refers to the number of sequences used for the dated tree after splitting or combining sequences from species with intraspecific delimitation and without interspecific delimitation.

Time-calibrated phylogenetic trees showed the most recent common ancestor (MRCA) of each genus ranged from 4.9 [1.4–15.8] Mya in *Cordulia* to 34.2 [24.3–107.1] Mya in *Calopteryx* (Table 2, Figure S3). We ran 12 models for estimating the ancestral range for each genus; the best-fit model selected by AICc for most genera was DEC or DIVALIKE with the optional dispersal multipliers matrix included. However, for complex genera such as *Sympetrum* and *Calopteryx*, the +J parameter was preferred (Table S3).

The estimated origin of the range for the MRCA was different across genera, and most of the genera have had just one exchange event (Table 2, Figures 1 and S3). MRCA between the Nearctic and Palaearctic lineages within a genus differed in age (ranging from 0.5 [0.09–1.3] Mya in *Aeshna* to 29.7 [13.9–57.2] Mya in *Calopteryx*) and estimated ranges (Table S4). Three genera showed a Nearctic origin (*Enallagma*, *Libellula* and *Nehalennia*), and the origin of another three genera was located in the Palaearctic (*Coenagrion*, *Leucorrhinia* and *Cordulegaster*). *Coenagrion* and *Cordulegaster* invaded the Nearctic twice independently from the Palaearctic. The remaining genera showed less resolved topologies; thus, the inference of the exact number of exchanges and direction had low support. There were one or two colonization events for *Calopteryx* and *Leucorrhinia* and more than two for the species-rich genera *Aeshna*, *Somatochlora* and *Sympetrum*. Overall, the data show that at least 18 to at most 27 exchange events occurred between the two regions (Figure S3). Five exchanges went with certainty from the Palaearctic to the Nearctic, whereas at least six exchanges went from the Nearctic to the Palaearctic

(Table S4). Moreover, MRCA between the Nearctic and Palaearctic lineages within a genus had an estimated distribution range more associated with the Eastern Palaearctic than with the Western Palaearctic (Table S4).

Regarding the habitat preference, 31.3% of the species analysed were lotic, whereas 68.7% of the species were lentic. According to the preferred habitat, approximately 25% of the colonizations were conducted by lotic species, whereas the remaining 75% were lentic species (Table 2). Results from the ancestral habitat preference estimation show a lentic ancestral state for *Coenagrion* and *Enallagma*, whereas *Somatochlora* has two clades: one mainly lentic and another one more lotic (Figure S4).

4 | DISCUSSION

Our findings indicate that, rather than a general pattern of biogeographical history across the 14 Holarctic genera of odonates, each genus has its own distinct story. Counter to our hypothesis, the number of exchange events was not restricted to a period of time, one direction or a higher number for lentic over lotic species. This result highlights the complexity of the historical events, evolutionary processes and ecological drivers that shape species distributions, which leads to idiosyncratic responses across genera.

Phylogenetic reconstructions were based on a massively sequenced single mitochondrial marker covering a large geographical and taxonomic range (3614 sequences, 259 species and 14 genera), which

TABLE 2 Summary of the main results for each genus showing the estimate of time and confidence interval to the most recent common ancestor (MRCA), the ancestral range estimation (ARE), the estimated number of exchange events and information on habitat preference and the number of estimated exchange events.

Genus	MRCA	ARE	Number of exchange events	Number of lotic species	Number of lentic species	Number of lotic events	Number of lotic events
<i>Aeshna</i>	9.4 [5.6–14.8]	WN	3		25		3
<i>Cordulegaster</i>	11.7 [7.9–16.7]	WE	2	34		2	
<i>Cordulia</i>	4.9 [1.4–15.8]	WEN	1		2		1
<i>Epitheca</i>	10.1 [5.4–18.2]	EN	1		12		1
<i>Ladona</i>	19.2 [11.1–30.5]	WN	1		5		1
<i>Leucorrhinia</i>	26.1 [14.6–41.4]	W	1		14		1
<i>Libellula</i>	25.4 [15.2–39.6]	N	1		22		1
<i>Ophiogomphus</i>	7.7 [3.9–13.9]	WN	1	21		1	
<i>Somatochlora</i>	10.2 [6.9–19.7]	WEN	3	10	21	1	2
<i>Sympetrum</i>	28 [17.2–42.4]	EN	5		40		5
<i>Calopteryx</i>	34.2 [24.3–107.1]	EN	2	9		2	
<i>Coenagrion</i>	17.7 [11.7–25.8]	W	2	5	15		2
<i>Enallagma</i>	17.1 [10.3–26.7]	N	1	2	18		1
<i>Nehalennia</i>	13.9 [7.6–25]	N	1		4		1
Total				31.27%	68.73%	24	76

allowed us to track large-scale differences in biogeographic patterns across genera. The use of different markers could provide different insights, for instance, if an ancestral polymorphism is retained causing discrepancies between gene trees and species trees (incomplete lineage sorting). However, the tree topologies were consistent between ML and BI analysis and coherent in general with previous studies using different markers (Artiss et al., 2001; Callahan & McPeck, 2016; Dumont et al., 2005; Hövmöller & Johansson, 2004; Johansson et al., 2017; Misof et al., 2000; Pilgrim & von Dohlen, 2012; Schneider et al., 2021, 2022, 2023; Ware et al., 2017; Weekers et al., 2001).

Our results indicate that exchange events took place over a long time period, which is contrary to our expectation of an interchange limited to the Pleistocene. Previous studies indicate the possible interchange of dragonflies to explain the distribution of fossil taxa found in both North America and Europe during the Paleogene (Bechly et al., 2021; Petrulėvičius et al., 2007). Our findings agree with other dated phylogenies of zygopteran genera (Callahan & McPeck, 2016; Dumont et al., 2005; Swaegers et al., 2014); however, dates are younger than in a published fossil-calibrated phylogeny of all anisopteran (Letsch et al., 2016). This result is not surprising because time-calibrated phylogenies can show different dates when fossils or molecular data are used, which raised the ‘clock versus rocks’ debate (Tiley et al., 2020). Additionally, we allowed the molecular clock to vary between branches; however, mutation rates can vary among lineages (Ho & Lo, 2013), and hence, our divergence times should be interpreted cautiously. We reported the MRCA ages between the Nearctic and Palaearctic lineages; however, the colonization ages may be younger for genera with a big time gap between the stem and the crown age of the real split and colonization time (García-Verdugo et al., 2019). Most of the exchanges

probably took place through Beringia as the Nearctic species were found to be closer to species restricted to the East Palaearctic or located across the Palaearctic rather than species restricted to the West Palaearctic. However, we cannot completely reject the North Atlantic route. For instance, in *Ophiogomphus*, the MRCA is predicted to have had a distribution spanning both the West Palaearctic and the Nearctic; however, this result might be an artefact of the lack of eastern Palaearctic representatives of this genera in our molecular dataset.

According to the climate shifting hypothesis (Jiang et al., 2019), exchange between regions through BLB is expected to favour movement from areas with high diversity to areas with lower diversity where more ecological empty spaces exist. Despite the Nearctic harbouring a higher diversity of dragonflies and damselflies compared to the Palaearctic (Abbott et al., 2022; Kalkman et al., 2022), we found an equal number of exchanges between these two regions, which is in conflict with the climate shifting hypothesis. As an alternative explanation, highly stable freshwater habitats as found in the tropics, showed higher genetic diversity and low dispersion than more unstable temperate habitats, where dispersion may be required for survival (Salinas-Ivanenko & Múrria, 2021). Therefore, based on an habitat instability perspective, species richness has been accumulated regionally over time in stable habitats by weak dispersion across streams that may explain the weak exchange from the Nearctic to the Palaearctic, rather than the expected effects of ecological empty spaces in unstable habitats. Our findings agree with other studies in which exchange between the Palaearctic and the Nearctic has been reported in both directions, in one case even within a single genus such as the giant silk moth *Saturnia* (Rubinoff & Doorenweerd, 2020).

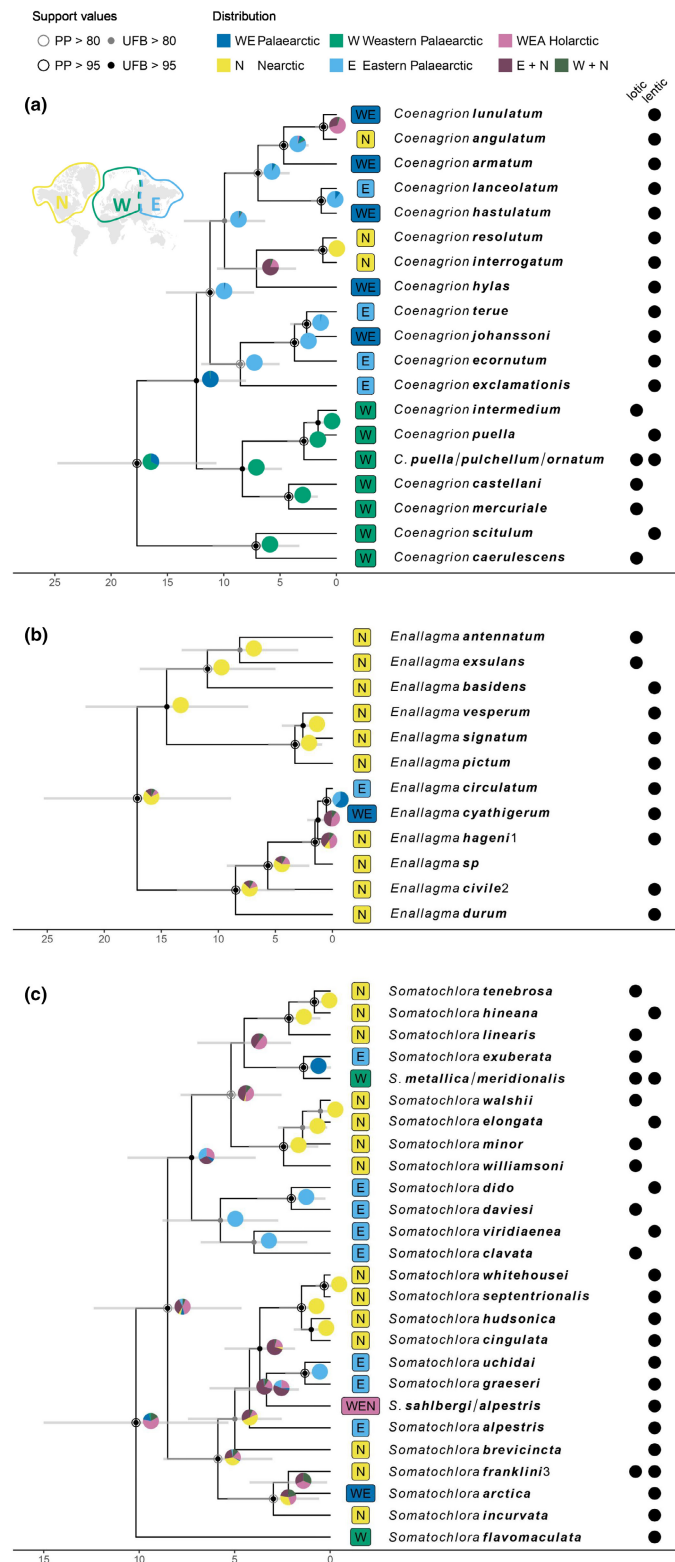


FIGURE 1 Examples of ancestral range estimations. The age is indicated on the x-axis in million years, and the bars on each node present the confidence interval of the divergence time estimation. Each tip represents a species or group of species with no interspecific delimitation with their current range distribution on the left and habitat preference on the right. Legends show support values and colours for range distribution probability for each node. (a) *Coenagrion*, as an example of a genus that invaded the Nearctic from the Palearctic twice; (b) *Enallagma*, as an example of species that invaded the Palearctic once; and (c) *Somatochlora*, as an example of a genus with a more complex pattern, where exchange events probably happened in both directions. (1) *Enallagma civile*/*E. aspersum*/*E. carunculatum*/*E. doubledayi*/*E. geminatum* (2) *Enallagma hageni*/*E. annexum*/*E. boreale*/*E. clausum*/*E. ebrium*/*E. laterale* (3) *Somatochlora franklini*/*S. forcipata*/*S. kennedy*/*S. semicircularis*.

Nowadays, we can appreciate species responses to climate change, such as the ongoing expansion of the African *Trithemis kirbyi* or *Crocothemis erythraea* adapted to warmer and more arid conditions reaching the European Mediterranean coast and now expanding towards Central Europe (Gil-Tapetado et al., 2023; Ott, 2010). In contrast, the exchanges that we report during the Last Glacial Maxima (e.g., *Aeshna subarctica*, *A. juncea*, *A. caerulea*, *Coenagrion angulatum*, *Cordulia shurtleffii*, *Enallagma cyathigerum*, *Libellula quadrimaculata* and *Somatochlora arctica*) were performed by lentic cold-dwelling species with geographic ranges mostly restricted to northern latitudes or high mountain ranges. During this period, BLB remained ice-free and was a suitable habitat for dragonflies, which likely favoured their exchange with the following expansion into the continent after the ice sheet regression. This process has also been reported in cold-tolerant ants (Schär et al., 2018) and butterflies that inhabit open spaces such as bogs and grasslands (Maresova et al., 2021).

Regarding the importance of functional traits, we exclusively addressed habitat preference and we found the exchange events are mainly restricted to lentic species for genera that have species inhabiting both habitat types. A higher contribution of the lentic than lotic species can be appreciated when comparing both the total number of species involved and the exchange events. Our finding is in line with the hypothesis of lentic species having a higher dispersal capacity and wider range distributions (Grewe et al., 2013; Hof et al., 2006; Ribera & Vogler, 2000), which, in this case, favours divergence processes and cladogenesis, as has been previously found (Papadopolou et al., 2009). However, despite all lotic species showing ranges restricted to one region (i.e., smaller range of lotic than lentic counterparts), we reported colonizations also in lotic genera and therefore exchange events were not exclusively limited to lentic species. Exchange between biogeographic regions has been reported in mason bees even though their biology indicates they are not good dispersers at crossing large geographic barriers (Branstetter et al., 2021). In odonates, the studies in genetic structuring of *Calopteryx splendens* indicate overland dispersal between streams by two processes, the adults flying or larval translocation due to floods (Chaput-Bardy et al., 2008), which could explain a slow but effective range expansion and colonizations of new biogeographic regions.

Some previous studies already discuss the concerns related to using COI barcode to delimitate some European dragonfly species with small interspecific genetic distances (Galimberti et al., 2021; Geiger et al., 2021). One interesting finding in our study is that species groups which cannot be delimited based on COI were clearly more frequent in the Nearctic, whereas species with two different clades spread in the phylogeny were mostly found in the Palearctic. In all these cases, a combination of molecular and morphological data is needed based on material from across the range of the species to solve these taxonomic discrepancies. Moreover, this short-term molecular divergence in the COI barcode of the Nearctic species groups may indicate that the high diversity recorded in this biogeographic

region can at least be partially explained by a recent speciation event rather than an accumulation of species over time associated with a lower extinction, as already has been suggested for *Enallagma* (Turgeon & McPeck, 2002).

Identifying past geological events and ecological drivers that have influenced current patterns of diversity is a complex task, but is needed to understand the present and future distribution of biodiversity. Our findings establish a tentative framework for future work that can be improved by adding more markers as provided by RADSeq and extensive ecological and functional trait data that may explain the differences across lineages. For instance, semivoltinism, beginning and prolongation of flight period and the preference of temporal habitats are favoured for range-shift expansions of Iberian odonates under climate change (Viza et al., 2023). Other studies showed dispersal capacity and migratory behaviours could be critical when invading and colonizing new regions (Clement et al., 2021) and can indicate high phenotypic plasticity of species to adapt to new conditions. Hence, further studies considering functional traits and phenotypic plasticity should provide insights into global trends of diversity, which can help to anticipate species responses facing ongoing climate change.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

New data are available in GenBank under the accession numbers OR823090-OR823195, PP359421-PP359422, PP379533-PP379542 and PP379544-PP379548. All sequences in this study are archived in BOLD and/or GenBank. A list of BOLD IDs and accession numbers can be found in Table S1.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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