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Range geography and temperature variability explain cross-continental convergence in range and phenology shifts in a model insect taxon

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eLife Assessment

The article presents **important** findings on the impact of climate change on odonates, integrating phenological and range shifts to broaden our understanding of biodiversity change. The study leverages extensive natural history data, offering a **convincing** analysis of temporal trends in phenology and range limit and their potential drivers.

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Abstract

Climate change may introduce conditions beyond species' tolerances; to survive, species must avoid these extremes. Phenological shifts are one strategy, as species move their activity or life history events in time to avoid extreme conditions. Species may also shift in space, moving their ranges poleward to escape extremes. However, whether species are more likely to exhibit one or both strategies, and whether this can be predicted based on a species' functional traits, is unknown. Using a powerful macroecological dataset of European and North American odonate observations, we assessed range and phenology shifts between two time periods (1980-2002 and 2008-2018) to measure the strength and direction of the association between responses. Species with the greatest poleward range shifts also showed the largest phenological shifts toward earlier annual activity periods, with half of all species shifting in both space and time. This response was consistent across continents, despite highly divergent land use and biogeographical histories in these regions. Surprisingly, species' range and phenology shifts were not related to functional traits; rather, southern species shifted their range limits more strongly, while increasing temperature variability hindered range shifts. By reducing risk through phenological shifts, the resulting larger populations may be more likely to disperse and expand species' ranges. While species shifting in both space and time may be more resilient to extreme conditions, we identified a small number of species (approximately 10%) that failed to shift at all; these species are likely to be particularly vulnerable to climate change, and should be prioritized for conservation intervention.

Introduction

Climate change alters climatic means and increases the frequency of extreme weather events, exposing species to conditions outside of their tolerances, and often leading to population declines (Goulson, 2019; IPCC, 2021). Species may avoid extreme conditions by dispersing to new areas where conditions pose fewer weather-related challenges, often leading to poleward range expansion (Davis et al., 2005; Lawlor et al., 2024). Species' biological timing could also shift, through adaptation or phenotypic plasticity, with earlier warming advancing the timing of early-season activities and life-history events (Davis et al., 2005; Hällfors et al., 2024; Novella-Fernandez et al., 2023; Parmesan and Yohe, 2003). Both species' geographical ranges and seasonal timing depend strongly on climate and habitat conditions, with shifts in space and time permitting species to remain within the limits of their ecological niches (Chen et al., 2011; Engelhardt et al., 2022; Grewe et al., 2013; Menzel et al., 2006; Parmesan and Yohe, 2003). This allows populations to grow, despite changing environments, and reduces the risk of climate debt and extinction (Devictor et al., 2012; Franks et al., 2018; Lustenhouwer et al., 2018; Saino et al., 2010; Souza et al., 2023; Urban, 2015).

Positive population trends can be stronger in species that shift both their range and phenology (Hällfors et al., 2024). Greater phenological plasticity under warmer spring temperatures may increase reproductive success, leading to greater population growth and range expansions (Macgregor et al., 2019), as positive or stable trends in species abundance and habitat availability are essential for range shifts (Mair et al., 2014; Platts et al., 2019). However, there could also be a trade-off between phenological and geographical shifts (Amano et al., 2014; Hassall, 2015; Socolar et al., 2017). Species with greater dispersal abilities may have less need for phenological shifts as they track their climatic niche through space, while weaker dispersers may be confronted with greater selective pressure to shift phenology within their range (Amano et al., 2014; Hassall, 2015; Socolar et al., 2017). Since range shifts can also result from extirpations at species' trailing range edge (Parmesan et al., 1999), greater phenological shifts may mitigate the need for range shifts, as species better tolerate new climatic conditions. Cross continental studies report converging effects of climate change on species' range shifts and abundances (Neate-Clegg et al., 2024; Stephens et al., 2016), including among insects (Kerr et al., 2015; Neate-Clegg et al., 2024; Pinkert et al., 2022), but potential relationships between phenological and geographic responses have not yet been investigated at continental scales. Functional traits, such as dispersal, may determine species' spatial and temporal responses to climate change (Chen et al., 2011; Kharouba et al., 2009; Schuetz et al., 2019; Zografou et al., 2021). However, these relationships are inconsistent across taxa and regions, and cross-continental tests have not been attempted (Angert et al., 2011; Buckley and Kingsolver, 2012; Estrada et al., 2016; MacLean and Beissinger, 2017). Geographic locations and environmental characteristics of species' ranges may also predict range shifts, as animal species with high latitude ranges have been shown to exhibit smaller range shifts (MacLean and Beissinger, 2017; Pinkert et al., 2022), while increasing local temperature and loss of natural landcover may drive range retractions (Pacifici et al., 2020). However, exposure to extreme climate events (e.g. drought, heat waves, or storms) within species ranges may disrupt species' dispersal abilities and capacities to tolerate new conditions (Kerr, 2020; Román-Palacios and Wiens, 2020). Exposure to thermal anomalies can rapidly change entire communities and create shifts towards new ecosystems, sometimes leading to local declines (Day et al., 2018; Grant et al., 2017; Harris et al., 2018; Román-Palacios and Wiens, 2020).

While global change research on insects often emphasizes butterfly and bee taxa, recently assembled databases of odonate observations provide a rare opportunity to investigate species' spatiotemporal responses at larger taxonomic and spatial scales, particularly as most work has been done at national scales (Córdoba-Aguilar et al., 2023; Kalkman et al., 2018; Sandall et al.,

2022). Due to their use of aquatic and terrestrial habitat across life different stages, dragonflies and damselflies are also considered indicator species for both terrestrial and aquatic insect responses to changing climates (Hassall, 2015; Pinkert et al., 2022; Šigutová et al., 2025), giving the study of these species broad relevance for conservation. There is some evidence that functional traits relate to odonates' interspecific variation in range shifts (Angert et al., 2011; Grewe et al., 2013), phenology shifts (Diamond et al., 2011; Gutiérrez and Wilson, 2021; Zografou et al., 2021), extinction risks (Cardillo et al., 2008; Cooper et al., 2008; Rocha-Ortega et al., 2022; Suhonen et al., 2022), and rates of decline and expansion within limited geographic scopes (Powney et al., 2015; Rapacciuolo et al., 2017; Rocha-Ortega et al., 2020). While relationships between morphological traits and range boundaries have been shown for some groups (i.e. Rundle et al., 2007), these may depend on species' geographic context. For example, differences in habitat connectivity and dispersal ability may constrain range shifts for lentic species (those species that breed in slow moving water like lakes or ponds) and lotic species (those living in fast moving-water) in different ways (Kalkman et al., 2018). More southerly lentic species may expand their range boundaries more than lotic species, as species accustomed to ephemeral lentic habitats better dispersers (Grewe et al., 2013), yet lotic species have also been found to expand their ranges more often than lentic species, potentially due to the loss of lentic habitat in some areas (Bowler et al., 2021). While warm-adapted species with more equatorial distributions could expand their ranges poleward following warming (Devictor et al., 2008), they could also increase in abundance in this new range area relative to species that historically occupied those areas and are less heat-tolerant (Powney et al., 2015).

In this study, we tested whether species with stronger geographical range shifts also advanced their emergence phenologies, or if one response offsets the need for the other. We also asked whether functional traits, range geography (i.e. southerly vs. northerly), or temperature variability predict range shifts at species' northern range limits, and whether these factors can also predict shifts in species emergence phenology. We predicted that species would exhibit shifts in both geography and phenology, as we expect species shifting in phenology to have larger populations, increasing likelihood of dispersal and successful range shifts. We predicted that species able to use both lentic and lotic habitats would shift their phenologies and geographies more than those able to use just one habitat type, as generalists outperform specialists as climate and land uses change (Ball-Damerow et al., 2015, 2014; Hassall and Thompson, 2008; Powney et al., 2015; Rapacciuolo et al., 2017). Alternatively, species might respond to rapid climate changes in ways that reflect their geographical position, indicating that where they are found is a better predictor of their conservation risk from global change than their intrinsic biological characteristics.

Methods

Biological records

We assembled ~2 million observations records for North American and European odonate species collected between 1980 and 2018. Data sources included online dataset aggregators GBIF (*http://gbif.org/*) and Canadensys (*http://www.canadensys.net/*), Odonata Central (Abbott, 2020), and other institutions (see Acknowledgments). While odonates were sampled opportunistically, biases associated with data that are not systematically collected are less likely to affect trends at large spatial and temporal scales, particularly if data are obtained from multiple independent sources (Pyke and Ehrlich, 2010; Zattara and Aizen, 2021). We removed records with incomplete or missing species identification, year, or locality information. We selected unique observations for species, location, year, and Julian day of collection, and restricted the data to continental North America and Europe. We mapped species-specific observations using ArcGIS software (ESRI, 2019), and qualitatively verified species ranges. If a species was found on both continents, we only retained observations from the continent that was the most densely sampled. If we merged data for one species found on both continents, we could not perform a cross-continental

comparison. However, if the same species on different continents was treated as different species, this would lead to uninterpretable outcomes (and the creation of pseudo-replication) in the context of phylogenetic analyses. In addition, species found on both continents did not have sufficient data to meet criteria for the phenology analysis.

We followed widely accepted methods to determine species range boundaries (Devictor et al., 2012, 2008; Kerr et al., 2015), although other methods exist that are appropriate for different data types and research questions i.e. (Ni and Vellend, 2021). We assigned species presences to 100×100 km quadrats, a scale that is large enough to maintain adequate sampling intensity but still relevant to conservation and policy (Soroye et al., 2020), to identify the best sampled species. We excluded species found in fewer than 50 quadrats to increase the likelihood of accurately predicting the position of species' northern range boundaries. We retained ~1,100,000 records from Canada, the United States, and Northern Mexico, comprising 76 species (**Figure 2**). Observation records were separated into two time periods, to compare species' recent phenologies and northern range limits (2008 to 2018) to conditions in a historical time period (1980 to 2002).

Temperature Variability

Temperature variability during a species' flight season may impact its ability to establish in new locations, or shift its emergence timing the following year. We downloaded a high-resolution gridded dataset for monthly average daily maximum temperature from the Climatic Research Unit (New et al., 2002). We extracted average values per 100×100 km quadrat across the months of April to October, covering the main flight period for odonates in this study, for each year included in the historical and recent periods. We calculated the coefficient of variation per quadrat for each time period and averaged these values per species and time period to measure interannual temperature variability during species' flight season across their range. We used the difference between recent and historical measures as an estimate of change in temperature variability.

Spatial and temporal change metrics

To limit potential effects of temporal and spatial biases, we generated range and phenology shift metrics with specific criteria for quadrats and species selection (Bartomeus et al., 2018; Gaiji et al., 2013; García-Roselló et al., 2015); we retained 76 species for range shift estimates (Supplementary Information). Species' northern range boundaries were calculated using the mean of the 10 most northern points of each species range in both the historic (1980 – 2002) and recent (2008 – 2018) time periods, measured in kilometers from the equator (as in Kerr et al., 2015). We used the difference between range limit positions in the historic recent time periods to estimate species' northern range limit shifts.

Since spatiotemporal biases sometimes inflate range shift measurements (Kujala et al., 2013), we used null models to test whether observed range shift estimates were robust, and the extent to which those responses differed from expectations arising because of rising sampling intensity over time. 1000 randomized datasets were created with the same number of species-specific geographical points per time period as the number of actual observations. Maximum and minimum latitude and longitude values were held constant relative to observed values. Northern range limit shifts were calculated as the difference in the mean of the 10 most northern points between the historic and recent time periods. We used generalized linear models (GLMs; glm command in R) to test whether species-specific range limit shifts in each iteration predicted range shifts measured from the observation data (**Figure S1**, **S2**). We found that observed northern range limit shifts are not consistent with expectations derived from changes in sampling intensity.

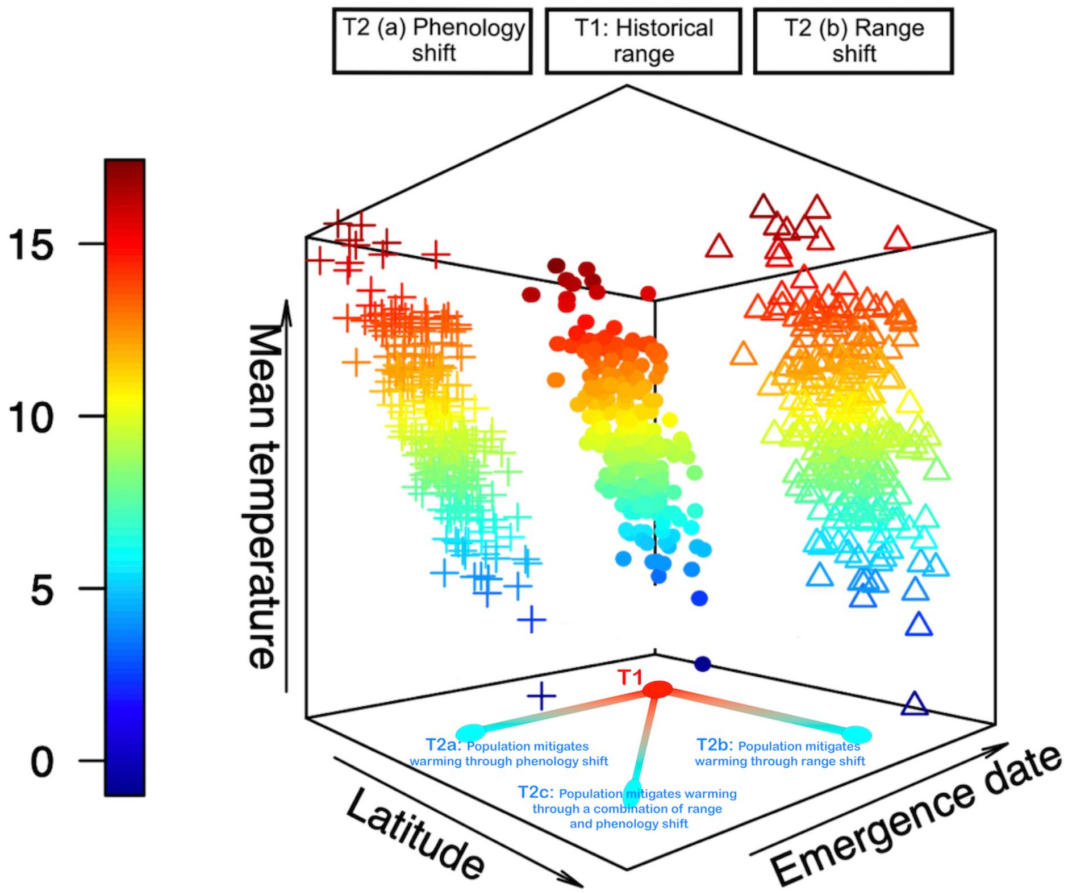


Figure 1

Representation of temporal and geographical limits characterising the ecological niche of a hypothetical odonate species.

Points show 250 individuals according to their Julian day of emergence, latitudinal position, and temperatures to which each individual is exposed. Points represent historical observations (T1), plus signs show observations following a shift towards earlier emergence dates after warming. (T2a) triangle symbols show observations following a shift towards higher latitudes after warming (T2b). Species could also shift both range and phenology in response to warming (T2c). Warm and cool colors show hot and cold temperatures, respectively.

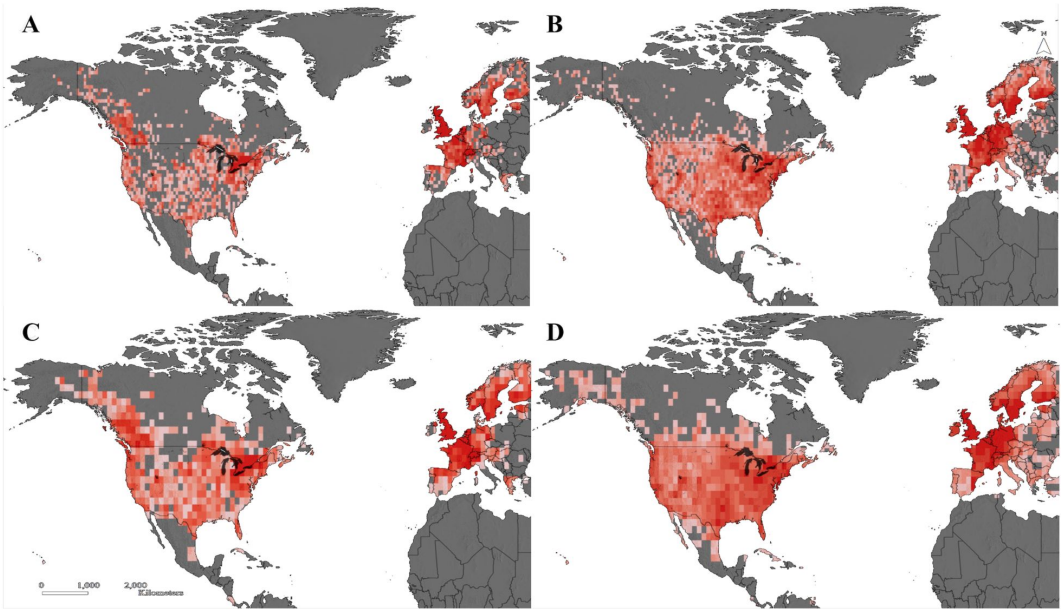


Figure 2

Richness of 76 odonate species sampled in North America and Europe in the historic period (1980-2002; panes A and C) and the recent period (2008-2018; panes B and D).

Species richness per 100 × 100 km quadrat is shown in panes A and B, while panes C and D show species richness per 200 × 200 km quadrat. Dark red indicates high species richness, while light pink indicates low species richness.

We estimated species-specific emergence phenology for each time period in 200×200 km quadrats; using larger quadrats increases probabilities of detecting signals of emergence phenology, which may otherwise be lost due to gaps in data density. We retained quadrats that contained at least 25 observations for a given species in both time periods. To estimate phenology per area, we used the *weib.limit* function of the *WeibullR* R package (Pearse et al., 2017). This function uses the Weibull distribution to estimate the Julian day of a species' first appearance, and is especially useful to measure the timing of phenological events in sparsely sampled datasets. Techniques such as using the average of the nth first observations of phenological events, or the nth percentile flight dates (Brooks et al., 2014; Robbirt et al., 2011), tend to overestimate the timing of biological events due to temporal bias towards later days in the species' active period (Pearse et al., 2017). We retained emergence estimates between March 1st and September 1st, as well as species and quadrats that showed a difference in emergence phenology of −25 to 25 days, −30 to 30 days, or −35 to 35 days between both time periods, to include only phenology shifts that could be biologically meaningful to environmental climate change. 68 species found across 63 quadrats met these criteria. Large changes in phenology are likely explained by other anthropogenic or natural factors, or could occur due to noise in the data, since these phenology calculations per region are extremely data intensive. We calculated the difference in the day of emergence per quadrat between both time periods, as well as mean phenology change across all quadrats for each species. The number of quadrats per species used to calculate their mean phenological shift varied between 2 and 46.

We used null models to assess whether our approach to estimating phenology shifts was robust, as potential issues may arise due to spatiotemporal biases in the underlying data (Kujala et al., 2013). We constructed 1000 randomized datasets of species' hypothetical days of occurrence, using the same number of quadrats, and observations within quadrats, as in each time period of the observation records. We assigned the maximum and minimum Julian day of occurrence from the observation records to limit values in the randomized datasets. We applied the same method and criteria of inclusion to the randomized datasets as we did to measure phenology shifts from the observation data. GLMs were built to test whether phenology shifts calculated using 1000 random datasets predicted the phenology shifts that we measured. No discernable pattern emerged, indicating that observed shifts in phenology are not consistent with expectations derived from differences in sampling intensity over time (**Figure S3**, **S4**).

Range geographies and functional traits

To assemble trait data for the 76 species in the database, we used field guides (Cannings, 2002; Jones et al., 2008; Paulson, 2012) and existing trait databases (Powney et al., 2014; Waller et al., 2019). We considered any evolved morphological, physiological, behavioural, or life history characteristic as a functional trait (Beissinger and Riddell, 2021). Geographic range and associated climatic characteristics are often considered ecological traits, as they are consequences of functional traits and their interactions with geographic features (Bried and Rocha-Ortega, 2023; Chichorro et al., 2019). Such ecological variables may predict species' responses to climate change, and can add significant value to predictive models (MacLean and Beissinger, 2017). We identified whether species' ranges were more northern, southern, or both northern and southern (both), and determined the range size of each species by counting the number of quadrats occupied by that species in the historical time period.

Along with the geographic and climatic attributes, temperature variability and distribution, we selected four functional traits likely to be biologically relevant to spatial and temporal responses to climate change: flight duration, breeding habitat type (lotic, lentic, or both), egg laying habitat (exophytic vs. endophytic), and body size (Cannings, 2002; Jones et al., 2008; Paulson 2012; Powney et al., 2014; Waller et al., 2019). Species' flight period was measured as the total number of days of the flight period, estimated from the approximate time of the month of average first and last appearances. Breeding habitat was assigned according to a species' uses of lotic, lentic, or both habitat types. Egg laying habitat was assigned according to whether species use

exophytic egg-laying habitat (i.e. eggs laid in water or on land, relatively larger in number), or endophytic egg-laying habitat (i.e. eggs laid inside plants, usually fewer in number); species using exophytic habitats are associated with greater northward range limit shifts (Angert et al., 2011). Body size corresponded to the mean length of the abdomen of each species. We excluded overwintering stage and range size from our analysis as data were incomplete for many species, and excluded migratory behavior as the vast majority of species included in the study were non-migratory.

We tested for correlations amongst all predictors by calculating the Predictive Power Statistic (PPS) and Pearson correlations among traits (van der Laken, 2021): we found no evidence of correlation.

Statistical analyses

We conducted statistical analyses using R Statistical Software (R Core Team, 2019). All continuous variables were transformed into Z-scores using the *scale* function in R. First, we investigated whether there was a relationship between species' range and phenological shifts by modelling phenology shift as the dependent variable, and range shift and continent as independent variables. We used both species-level frequentist (GLM; glm function in R) and Bayesian (Markov Chain Monte Carlo generalized linear mixed model, MCMCglmm; Hadfield, 2010) models to improve the robustness of the results. We included a term to account for phylogeny in the MCMCglmm model, as species that are closely related are likely to have similar traits. We used the molecular phylogenetic tree published by the Odonate Phenotypic Database (Waller et al., 2019), which used a morphological and taxonomic phylogeny as the backbone tree, allowing species to move within their named genera or families according to molecular evidence (Waller and Svensson, 2017). Trace and density plots for the MCMCglmm model revealed no issues with autocorrelation or model convergence (**Figure S7**).

Next, we investigated whether functional traits, range geography, or temperature variability predicted range shifts at species' northern range limits, and whether the same predictors explaining range expansions could also predict shifts in species emergence phenology. We constructed two sets of GLMs, in addition to two sets of MCMCglmms accounting for phylogeny; one of each with changes in species' northern range limits as the response variable, and the other with changes in emergence phenology as the response variable. Non-significant variables, specifically all functional traits, were removed from the final geographic range shift model. No effects were significant in the model of phenology shifts. Trace and density plots for the MCMCglmm models did not indicate limitations related to autocorrelation or model convergence (**Figure S8**).

In addition to the inclusion of phylogeny in statistical models to account for potential data non-independence, we measured the phylogenetic signal in range and phenological shifts. We used the *phylosig* function of the *Phytools* package version 0.7-70 (Revell, 2012), which calculates phylogenetic signal using Pagel's lambda and Blomberg's K.

Results

Relationship between range and phenology shifts

Most species (52 of 76) expanded their northern range limits toward higher latitudes (mean range expansions of 180 km). The average range expansion across all species was 63 km northward, although some species showed range retractions (**Figure 4**). Most species (41 of 66) maintained or advanced their emergence phenology (mean of −2.71 days in emergence phenology shifts among all species; **Figure 4**). Fewer species were included in phenology analyses than analyses of range shifts due to the data intensity required to capture phenology shifts at a study site (N=66

vs. N = 76). Many species (50%) showed both advancing emergence phenology and range expansions, while 10% of species showed neither range nor phenological shifts relative to historical baselines.

The effect of species' range shifts on phenology range shifts was significant in our model investigating the relationship between these responses, indicating that species shifting their northern range limits to higher latitudes also showed stronger advances in their emergence phenology (**Figure 3**). This result that was consistent in GLM and Bayesian analyses ($p < 0.01$; **Table 1**), and was maintained across North America and Europe, with no effect of continent in the model. This trend was consistent among both dragonflies and damselflies, although there was considerable interspecific variation in the magnitude of spatial and temporal shifts. Accounting for phylogeny did not improve model predictions and did not explain greater model variance (R^2 = 17% and 15%, for GLM and MCMCglmm models, respectively).

Drivers of range and phenology shifts

Range geography and climate variability, rather than functional traits, predicted range shifts in both North America and Europe, with range geography being consistently the strongest predictor. Species' functional traits did not relate to the extent of observed geographical range shifts in tests using GLM and MCMCglmm models. Species with more southern distributions shifted their northern range limits towards higher latitudes more than northern species or species present in both the north and south (**Table 2**; $p = 0.002$ and 0.004, model R^2 = 26.6% and 23.7%, for GLM and MCMCglmm models, respectively), with no effect of range size on range shifts. Species experiencing smaller changes in interannual temperature variability also had a higher likelihood of northern range limit shifts ($p = 0.0005$ for GLM, $p = 0.002$ for MCMCglmm). Results from the GLM and MCMCglmm models were qualitatively similar, however, a smaller amount of model variance was explained when phylogeny was accounted for. Emergence phenology shifts were not affected by species' traits, range geography, nor climate variability; due to this, model results are not displayed here. While range and phenology response types are related, this suggests that the mechanisms underlying phenological shifts are different than those underlying range shifts.

A phylogenetic signal may indicate that there are traits that determine species' spatial and temporal responses to changing climate that were not measured in this study. Yet we detected no phylogenetic signal using Pagel's lambda or Blomberg's K in either geographical range or phenological responses (**Table 2**). Adding a phylogeny term to the MCMCglmm models also failed to produce a pattern different to the GLMs, and model performance did not improve when we accounted for phylogeny in our assessment of northern range shifts.

Discussion

In one of the first studies to investigate both shifts of phenology and range at a continental scale, we find that dragonfly and damselfly species show pronounced geographical and phenological shifts that converged across Europe and North America. Species expanding their ranges poleward also emerged earlier in the spring on both continents (**Figure 3**), with shifts predicted by range geography and climate variability, but not functional traits. These results suggest that some species are 'universal winners' with respect to climate change: they demonstrate the flexibility to respond both temporally and spatially to the onset of rapid climate change. Conversely, species that show neither geographic nor phenological shifts may be particularly vulnerable to climate change.

We found no evidence for a tradeoff between range and phenology shifts; instead, half of species shifted both range and phenology. Earlier seasonal timing allows species to stay within their climatic limits. This may lead to higher local population growth (Macgregor et al., 2019),

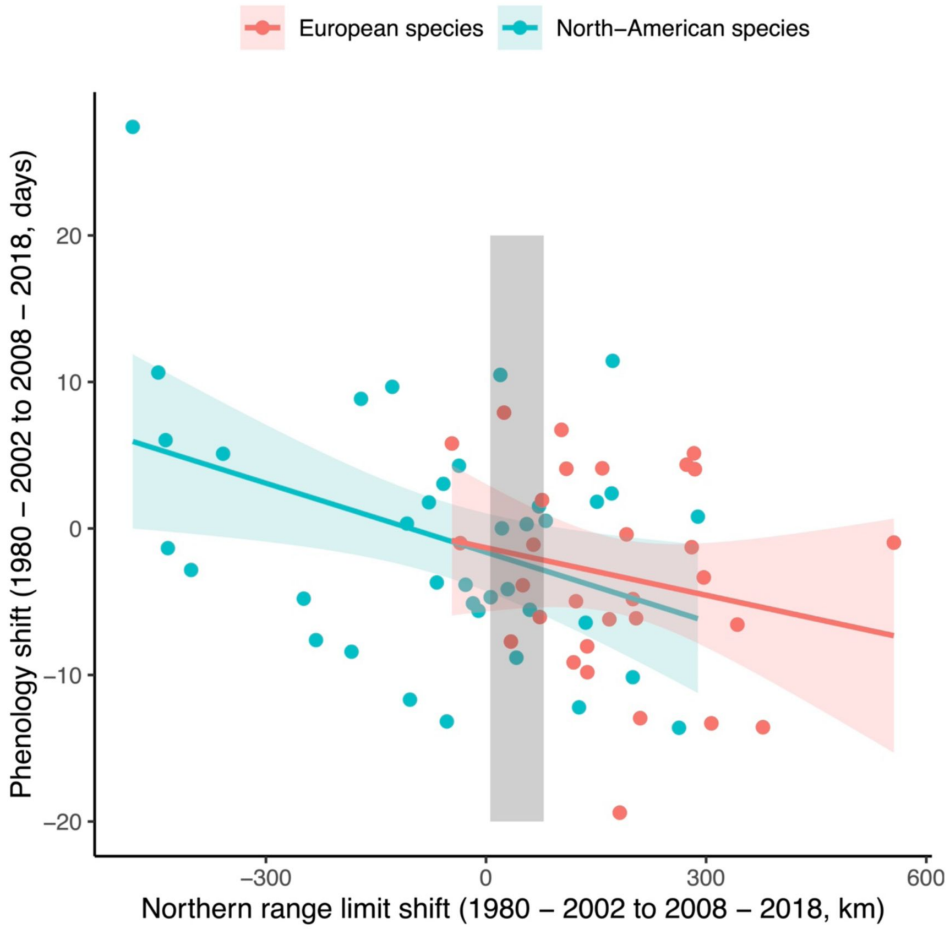


Figure 3

Relationship between range shifts and emergence phenology shifts among North American and European odonate species (N = 66; model R^2 = 17.08 for glm, 14.9% for MCMCglmm).

For reference, the shaded area shows mean latitudinal range shifts of terrestrial taxa as reported by Lenoir et al. (calculated as the yearly mean dispersal rate of 1.11 +/– 0.96 km per year over 38 years).

Table 1

Fixed effects estimates and associated statistics from the generalized linear model and generalized mixed effects model (accounting for phylogeny; for credible intervals, see Table S4) of the relationship between range shifts and emergence phenology change.

The continent term shows effects of the North American continent compared to the European continent as the reference level. N gives the number of species involved in the model, and an asterisk indicates statistical significance of the variable in question (p-value < 0.05). The pseudo R^2 type is Nagelkerke (Nagelkerke, 1991).

	Phenology shift (N = 66)			
	GLM		MCMCglmm	
Predictors	**Est.**	**p**	**Post.m**	**p**
(intercept)	0.12	0.53	0.12	-0.49
Range shift	-0.45	<0.01*	-0.45	<0.01*
Continent	-0.22	0.44	-0.22	0.42
Model evaluation				
AIC/DIC	185.39		185.43	
Null model	193.13		193.12	
Pseudo R^2	17.08%		14.90%	

Table 2

Fixed effects estimates and associated statistics from the generalized linear model and generalized mixed effects model (accounting for phylogeny; for credible intervals, see Table S4) of drivers of odonate range shifts.

N indicates the number of modelled species, an asterisk indicates statistical significance of the variable in question, and a dash symbol shows that the variable was excluded from the final model. The pseudo R^2 type is Nagelkerke (Nagelkerke, 1991). For the categorical variables breeding habitat type and range geography, we used lotic habitat type and Northern range as reference levels, respectively.

	Range shift (N = 76)			
	GLM		MCMCglmm	
Predictors	**Est.**	**p**	**Post.m**	**p**
(intercept)	-0.65	0.018	-0.65	0.022
Widespread distribution	0.34	0.32	0.34	0.31
Southern distribution	0.95	0.002	0.95	0.004
T ° variability	-0.38	0.0005	-0.38	0.002
Model evaluation				
AIC/DIC	202.8		202.9	
Null model	218.7		218.7	
Pseudo R^2	26.60%		23.70%	
Phylogenetic signal				
Pagel's lambda (p)	0.0057 (0.89)			
Blomberg's K (p)	0.11 (0.47)			

although earlier emergence could expose individuals to early season weather extremes (McCauley et al., 2018). As only a small proportion of odonate adults undertake long range dispersal (Conrad et al., 1999), greater local population sizes should contribute to higher dispersal rates (Mair et al., 2014), facilitating range shifts (Kerr, 2020; Leroux et al., 2013). This is consistent with results from other taxa: among British butterflies, early emergence increased population growth and facilitated range shifts for species with multiple generations per year (Macgregor et al., 2019); Finnish butterfly species with the greatest population growth rates shifted both their phenology and ranges (Hällfors et al., 2021). Such population growth or maintenance, and therefore the potential for range shifts, is only possible if habitat is available (Mair et al., 2014). Future work should consider habitat availability alongside range and phenology shifts, as it may help explain why some species are able to shift their phenology but not their range.

Southern species were more likely to expand their ranges northward than northern species or species present in both the north and south. Species' ability to maintain large populations may be impaired in northern latitudes, where rates of climate change are high (IPCC, 2021), hindering dispersal and colonization that are precursors to range expansions (Mair et al., 2014). Further mechanistic understanding of these processes requires abundance data. Southern species may have narrower niche breadths than widespread or northern species, and may respond more rapidly to climate change to track this narrower niche (Hällfors et al., 2024). Emerging mean conditions in areas adjacent to the ranges of southern species may offer opportunities for range expansions of these relative climate specialists, which can then tolerate climate warming in areas of range expansion better than more cool-adapted historical occupants (Day et al., 2018). Adaptive evolution and plasticity may enable higher population growth rates in newly-colonized areas (Angert et al., 2020; Usui et al., 2023), but this possibility can only be directly tested with long term population trend data. While some species experienced range retractions, these may result from sampling variability or stochastic population fluctuations along the northern range edge.

Increasing frequency and severity of extreme weather limited species' geographical range responses (**Table 2**). This trend was independent of functional traits that are mechanistically linked to species' climate change responses, such as dispersal ability or habitat preference. Extreme temperatures can reduce population sizes, leading to local extinctions (Román-Palacios and Wiens, 2020), and reducing the likelihood of range expansions (Mair et al., 2014). In odonates, experimental evidence has demonstrated that larval mortality rises with short-term extreme weather (McCauley et al., 2015). Individuals that shift phenologies earlier in the season to avoid climate extremes could still be exposed to harmful conditions (Iler et al., 2021); for example, odonate populations that respond to unusually warm spring temperatures may experience high mortality if temperatures return to seasonal conditions. Species that experience extreme conditions may then be unable to successfully shift in time, reducing population sizes, and reducing the likelihood of range shifts.

In contrast to previous work demonstrating that range and phenology shifts are at least partially determined by species traits (i.e. Sunday et al., 2015; Zografou et al., 2021), no functional trait, or combination of traits, explained these shifts in North American and European Odonata. While we could not capture all functional traits in this analysis, our results are consistent with other work that identifies climate velocity and sensitivity as the best predictors of range shifts and thermal preferences tracking in marine systems (Pinsky et al., 2013; Schuetz et al., 2019). Species' tolerances to increasingly variable temperatures also helps to predict extinction risk during climate change (Kerr, 2020; Rocha-Ortega et al., 2020). The extent to which species' traits actually determine rates of range and phenological shifts, rather than occasionally correlated with them, is worth considering further, but functional traits do not systematically drive patterns in these shifts among Odonates in North America and Europe.

The geographic positions of species' ranges determine the local pressures and environmental factors to which they are exposed (MacLean and Beissinger, 2017; Pacifici et al., 2020), potentially masking the effects of traits (Schuetz et al., 2019). This process could cause trait-related trends to differ across levels of biological organization (Srivastava et al., 2021), from local populations (where traits might be critical) to biogeographical extents (where traits might be unrelated to range or phenological shifts; Grewe et al., 2013; Gutiérrez and Wilson, 2021; Sunday et al., 2015; Zografou et al., 2021).

Given that species' functional traits did not predict temporal or geographic responses, it is unsurprising that species' responses were also independent of phylogenetic history (Franke et al., 2022). The phylogenetic approach did not improve model predictions in any model that we tested, and there was no phylogenetic signal in either response according to Pagel's lambda and Blomberg's K (**Table 2**). These results are consistent with previous work that found no phylogenetic trend in local odonate population extinctions (Suhonen et al., 2022). There may be strong variation in thermal niches among closely related species: species that are geographically isolated adapt to different local climates, while species that co-occur may experience divergent selection within their climate tolerances (Schuetz et al., 2019).

It remains unclear if range and phenology shifts relate to trends in abundance, but our results suggest that there are clear 'winners' and 'losers' under climate change (**Figure 4**). Climate 'winners', species that are shifting in space and time, may require more limited conservation intervention. Species expanding their ranges could be better supported if habitat area and connectivity are conserved, facilitating climate-driven range shifts (Littlefield et al., 2019). Species only shifting their phenologies may require further study, as phenology shifts may have positive or negative impacts on abundance (Iler et al., 2021). Climate 'losers', species that are failing to shift in both space and time, may require more direct conservation intervention, such as managed relocation (Richardson et al., 2009). Species that did not shift their ranges northwards or advance their phenology included *Coenagrion mercuriale*, a European species that is listed as near threatened by the IUCN Red List (IUCN, 2021), and is projected to lose 68% of its range by 2035 (Jaeschke et al., 2013). This group also includes *Coenagrion resolutum*, a common North American damselfly (Swaegers et al., 2014), for which we could not find evidence of decline. This may be due in part to the greater area of intact habitat available in North American compared to Europe, enabling *C. resolutum* to maintain larger populations that are less vulnerable to stochastic climate events. Still, this and other species failing to shift in range or phenology should be assessed for population health, as this species could be carrying an unobserved extinction debt. Our analysis of phenology and range shifts should be repeated in other taxa, as it may offer a method of identifying conservation actions among species groups.

Understanding how range and phenology shifts vary across species, and what drives this variation, is increasingly urgent as climate change alters local and regional environmental conditions. Here, we showed that odonate species exhibit convergent responses of range and phenology shifts across continents. While species with southern distributions were more likely to shift their ranges, increasing temperature variation limited geographical range responses among species in both Europe and North America. Climate change is associated with increasing variability as well as shifting mean conditions, contributing to species decline and even local extinction risks (Duffy et al., 2022). In this study, where species are found (i.e. their range geographies) determines whether they are exposed and respond to such negative pressures. Simultaneous consideration of shifts in range and phenology is a powerful and necessary approach to test aspects of species' vulnerabilities to rapid global changes. By considering both the seasonal and range dynamics of species, emergent and convergent climate change responses across continents become clear for this well-studied group of predatory insects.

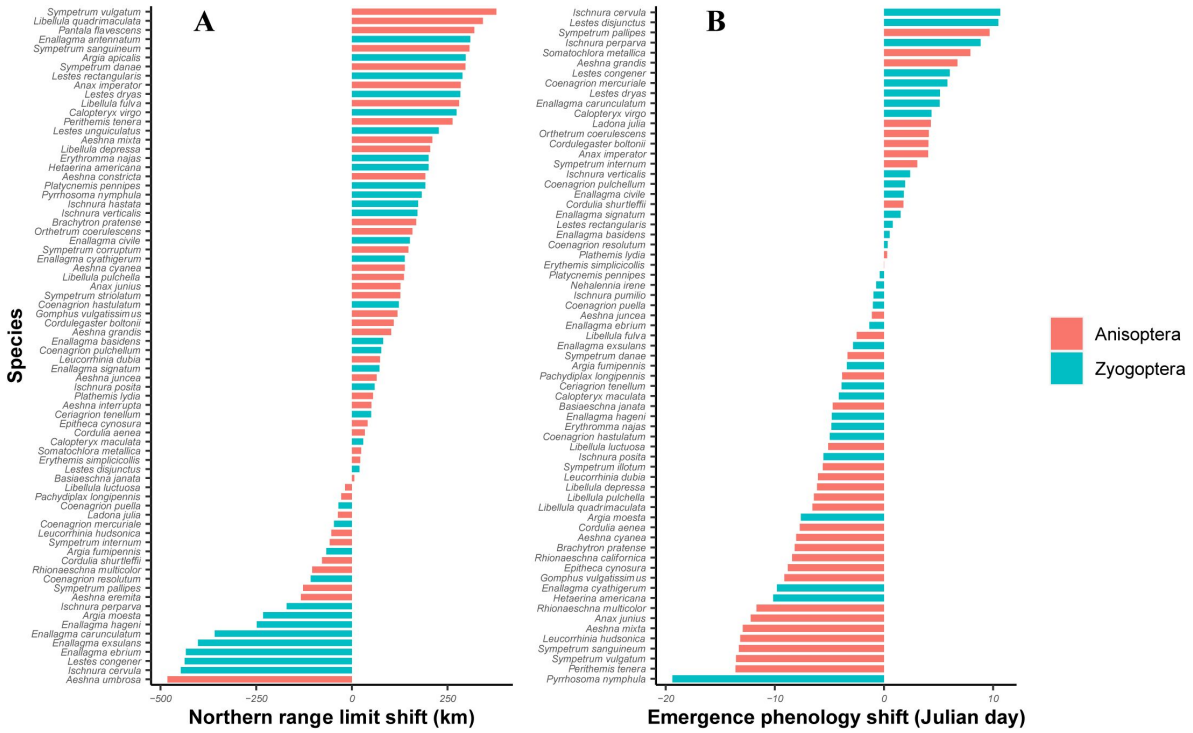


Figure 4

Distribution of Northern range limit shifts (Panel A, kilometers) and emergence phenology shift (Panel B, Julian day) of 76 European and North American odonate species between a recent time period (2008 - 2018) and a historical time period (1980 - 2002).

Anisoptera (dragonflies) are shown in pink, Zygoptera (damselflies) are shown in blue.

Supplementary Information

Odonate data

The full raw dataset includes ~2 million Odonata occurrence records. We first removed inadequate records from our primary dataset. Inadequate records were identified as those with incomplete information for species identification, year, or locality, inaccurate georeferenced points, and duplicate records. We retained ~1,100,000 unique species-location-date observations. There are 452,929 records in the first time period (1980 – 2002) and 641,590 observations in the second time period (2008 – 2018).

Phenology and range position estimates

We have not tried to interpret noise in phenology shift estimates, which could occur due to sampling issues, or to another biologically meaningful eco-evolutionary response. Our methods do not enable tests of those ideas, however. For example, *Aeshna umbrosa* has a surprisingly high phenology shift (>25 days) but a very strong range retraction (<-300 km). For this species, we retained 8 quadrats to calculate mean phenology shift estimate. It is possible that a section of the range was lost in which emergence was especially early, compared to other regions, due to local adaptations. This pattern may affect results where species appear to shift emergence dates earlier/later, but phenology shifts are affected by parts of the range that remain occupied.

We put in place criteria to make sure to include species with range shifts likely to result from climate change effects, rather than from sampling issues or to other anthropogenic pressures such as land use change, or sudden land use intensification. *Nehalennia irene* was thus removed, as its range positions were highly unusual, and likely due to other factors than global change (>800 km). *Libellula quadrimaculata* was removed due to sampling intensity discrepancies between time periods, having over 10,000 extra points in the second period compared to the first.

Temporal and spatial bias are likely to be present in opportunistic data, but they are less likely to impact long term factors of species' distributions if including data from as many sources as possible, and that span across large geographic and temporal scopes (Pyke and Ehrlich, 2010; Zattara and Aizen, 2021). Here, we put in place several criteria in careful interpretation of results, as described in the Methods section of the main text. Further, among preliminary examinations of the data, we test for the effect of sampling onto our phenology and range shift estimates. We found no effect of sampling on range of phenology responses that we calculated here. We tested a linear mixed model with species as a random effect that assesses whether sampling intensity change per quadrat (where sampling intensity corresponds to sampling per species/quadrat) predicts species' phenology change per quadrat. The p-value of the predictor variable, sampling intensity change, was not significant. Secondly, we built a Generalized Linear Model to assess whether greater sampling overall (measured as the number of quadrats in which each species is sampled) predicts species' range shifts that we computed. The p-value of the predictor variable, sampling change per species, was not significant. If spatial bias was present here, we may expect the number of quadrats in which species are found to increase the position of species' northern range boundaries.

Model information and statements

We report the full model statements below as executed with the *MCMCglmm* R package, including the priors, and the model of trait evolution to account for phylogeny. Prior structure followed standard practice according to continuous or binary response variable. The family "gaussian" or "threshold" was selected depending on the continuous or binary nature of the data, respectively.

The number of iterations, burnin, and thinning parameters were tested and confirmed with a visual assessment of model convergence using the trace and density plots. It is common practice for the burnin parameter to correspond to 10% of the number of iterations.

Model 1

- Aphylo ← vcv(phylogeny, model = “Brownian”, corr = T)
- Ainv ← inverseA(phylogeny, nodes = “TIPS”, scale = F)$Ainv
- prior ← list(R=list(V=1,nu=0.002))
- MCMCglmm(Phenological shifts ∼ Range shifts + Continent, ginverse = list(species = Ainv), family = “gaussian”, prior = prior, DIC = T, nitt = 150,000, thin = 100, burnin = 15,000, data)

Model 2

- Aphylo ← vcv(phylogeny, model = “Brownian”, corr = T)
- Ainv ← inverseA(phylogeny, nodes = “TIPS”, scale = F)$Ainv
- prior ← list(R=list(V=1,nu=0.002, fix = 1))
- MCMCglmm(Range shifts ∼ Breeding habitat type + Distribution region + Flight duration + Egg laying habitat + Body size + Temperature variability, ginverse = list(species = Ainv), family = “threshold”, prior = prior, DIC = T, nitt = 150,000, thin = 100, burnin = 15,000, data)

Model 3

- Aphylo ← vcv(phylogeny, model = “Brownian”, corr = T)
- Ainv ← inverseA(phylogeny, nodes = “TIPS”, scale = F)$Ainv
- prior ← list(R=list(V=1,nu=0.002))
- MCMCglmm(Phenology shift ∼ Breeding habitat type + Distribution region + Flight duration + Egg laying habitat + Body size + Temperature variability, ginverse = list(species = Ainv), family = “gaussian”, prior = prior, DIC = T, nitt = 150,000, thin = 100, burnin = 15,000, data)

Species	Continent	NRL (1980 - 2002)	NRL (2008 - 2018)	NRL shift
Aeshna constricta	North-America	5500.81	5692.6	191.79
Aeshna cyanea	Europe	6880.39	7018.26	137.87
Aeshna eremita	North-America	7527.81	7394.66	-133.16
Aeshna grandis	Europe	7504.84	7607.68	102.83
Aeshna interrupta	North-America	7235.65	7286.83	51.18
Aeshna juncea	Europe	7747.56	7812.16	64.6
Aeshna mixta	Europe	6566.18	6776.3	210.12
Aeshna umbrosa	North-America	6691.19	6209.63	-481.55
Anax imperator	Europe	6263.92	6548.57	284.65
Anax junius	North-America	5539.31	5666.11	126.8
Argia apicalis	North-America	4922.17	5219.38	297.22
Argia fumipennis	North-America	5235.2	5168.12	-67.08
Argia moesta	North-America	5533.74	5301.98	-231.77
Basiaeschna janata	North-America	5649.43	5655.77	6.34
Brachytron pratense	Europe	6737.42	6905.46	168.04
Calopteryx maculata	North-America	5329.56	5359.13	29.57
Calopteryx virgo	Europe	7275.9	7549.35	273.45
Ceriagrion tenellum	Europe	5900.55	5950.63	50.08
Coenagrion hastulatum	Europe	7528.94	7651.51	122.57
Coenagrion mercuriale	Europe	5913.57	5867.06	-46.52
Coenagrion puella	Europe	6904.7	6869.58	-35.12
Coenagrion pulchellum	Europe	7076.45	7152.81	76.36
Coenagrion resolutum	North-America	7516.44	7408.7	-107.73
Cordulegaster boltonii	Europe	7237.43	7346.93	109.49
Cordulia aenea	Europe	7400.12	7434.02	33.9
Cordulia shurtleffii	North-America	7499.82	7421.98	-77.84
Enallagma antennatum	North-America	5037.73	5347.01	309.28

Table S1

Samples of 76 North American and European odonate species from between 1980 and 2018 followed our criteria for quality observation records for inclusion in our analysis of geographical shifts.

Species Northern Range Limits (NRL) are shown in this table, as well as range limit shifts. All range limit values are shown in kilometers from the equ10ator. We used the 10 most northern points of sampling in each time period to identify species' NRL, as detailed in the Methods section of the main text.

Enallagma basidens	North-America	4768.61	4850.05	81.44
Enallagma carunculatum	North-America	5950.86	5592.47	-358.38
Enallagma civile	North-America	5322.59	5473.78	151.19
Enallagma cyathigerum	Europe	7594.97	7733.06	138.09
Enallagma ebrium	North-America	6341.31	5907.69	-433.62
Enallagma exsulans	North-America	5655.94	5253.94	-402
Enallagma hageni	North-America	6113.97	5865.52	-248.45
Enallagma signatum	North-America	5208.92	5281.09	72.17
Epitheca cynosura	North-America	5541.19	5582.56	41.37
Erythemis simplicicollis	North-America	5271	5292.65	21.65
Erythromma najas	Europe	7171.87	7372.13	200.25
Gomphus vulgatissimus	Europe	6890.76	7010.12	119.37
Hetaerina americana	North-America	5044.41	5244.49	200.08
Ischnura cervula	North-America	5973.57	5526.83	-446.74
Ischnura hastata	North-America	4725.07	4897.71	172.65
Ischnura perparva	North-America	5608.92	5438.53	-170.4
Ischnura posita	North-America	5084.08	5143.79	59.71
Ischnura pumilio	Europe	6213.77	6769.62	555.85
Ischnura verticalis	North-America	5579.68	5750.9	171.22
Ladona julia	North-America	5908.68	5871.84	-36.83
Lestes congener	North-America	6240.48	5803.75	-436.74
Lestes disjunctus	North-America	7294.75	7314.26	19.51
Lestes dryas	Europe	6824.89	7108.33	283.44
Lestes rectangularis	North-America	5263.85	5552.64	288.79
Lestes unguiculatus	North-America	5803.91	6030.62	226.71
Leucorrhinia dubia	Europe	7675.72	7749.01	73.29
Leucorrhinia hudsonica	North-America	7500.27	7446.85	-53.42
Libellula depressa	Europe	6810.85	7015.37	204.52
Libellula fulva	Europe	6602.18	6882.5	280.32
Libellula luctuosa	North-America	5337.86	5320.1	-17.76
Libellula pulchella	North-America	5556.31	5692.14	135.83
Orthetrum coerulescens	Europe	6744.55	6903.01	158.46
Pachydiplax longipennis	North-America	5495.02	5467.11	-27.92
Pantala flavescens	North-America	5190.25	5510.15	319.9
Perithemis tenera	North-America	4929.38	5192.47	263.09
Plathemis lydia	North-America	5539.41	5594.8	55.38
Platycnemis pennipes	Europe	6934.22	7125.72	191.5
Pyrrhosoma nymphula	Europe	7131.07	7313.37	182.3
Rhionaeschna californica	North-America	5641.53	5458.21	-183.32
Rhionaeschna multicolor	North-America	5581	5477.34	-103.66

Table S1 (continued)

Somatochlora metallica	Europe	7718.67	7743.21	24.54
Somatochlora semicircularis	North-America	6533.02	5994.13	-538.89
Sympetrum corruptum	North-America	5585.68	5733.2	147.52
Sympetrum danae	Europe	7268.54	7565.29	296.75
Sympetrum internum	North-America	7179.45	7121.38	-58.07
Sympetrum pallipes	North-America	5655.65	5527.84	-127.8
Sympetrum sanguineum	Europe	6663.43	6970.56	307.13
Sympetrum striolatum	Europe	6972.22	7098.74	126.52
Sympetrum vulgatum	Europe	6897.33	7274.78	377.45

Table S1 (continued)

Species	Number of quadrats	Mean PS
Aeshna cyanea	37	-8.05
Aeshna grandis	43	6.73
Aeshna juncea	34	-1.11
Aeshna mixta	22	-12.95
Aeshna umbrosa	8	27.42
Anax imperator	27	4.05
Anax junius	19	-12.21
Argia fumipennis	8	-3.39
Argia moesta	11	-7.62
Basiaeschna janata	2	-4.69
Brachytron pratense	24	-8.18
Calopteryx maculata	15	-4.14
Calopteryx virgo	41	4.35
Ceriagrion tenellum	14	-3.88
Coenagrion hastulatum	20	-4.97
Coenagrion mercuriale	11	5.80
Coenagrion puella	33	-1.00
Coenagrion pulchellum	29	1.94
Coenagrion resolutum	2	0.33
Cordulegaster boltonii	34	4.08
Cordulia aenea	31	-7.72
Cordulia shurtleffii	4	1.78
Enallagma basidens	2	0.52
Enallagma carunculatum	8	5.10
Enallagma civile	11	1.82
Enallagma cyathigerum	46	-9.81
Enallagma ebrium	7	-1.34
Enallagma exsulans	8	-2.83
Enallagma hageni	5	-4.79
Enallagma signatum	6	1.51

Table S2

66 species sampled across North America and Europe between 1980 and 2018 followed our criteria for quality observation records for inclusion in our analysis of emergence phenology shifts.

Mean phenological shifts (PS) is measured in the number of Julian days comparing both time periods, as estimated using the Weibull distribution (See Methods). We also report the number of 200 X 200 quadrats used to calculate phenology estimates per species.

Epitheca cynosura	4	-8.82
Erythemis simplicicollis	15	0.01
Erythromma najas	35	-4.82
Gomphus vulgatissimus	12	-9.14
Hetaerina americana	6	-10.15
Ischnura cervula	3	10.65
Ischnura perparva	2	8.85
Ischnura posita	12	-5.55
Ischnura pumilio	14	-0.97
Ischnura verticalis	16	2.39
Ladona julia	9	4.29
Lestes congener	9	6.03
Lestes disjunctus	4	10.48
Lestes dryas	6	5.13
Lestes rectangularis	12	0.81
Leucorrhinia dubia	18	-6.05
Leucorrhinia hudsonica	4	-13.17
Libellula depressa	30	-6.13
Libellula fulva	16	-2.50
Libellula luctuosa	15	-5.11
Libellula pulchella	14	-6.43
Orthetrum coerulescens	22	4.11
Pachydiplax longipennis	13	-3.84
Perithemis tenera	5	-13.60
Plathemis lydia	14	0.30
Platycnemis pennipes	30	-0.40
Pyrrhosoma nymphula	39	-19.40
Rhionaeschna californica	2	-8.41
Rhionaeschna multicolor	4	-11.68
Somatochlora metallica	31	7.91
Sympetrum danae	32	-3.34
Sympetrum internum	5	3.05
Sympetrum pallipes	3	9.67
Sympetrum sanguineum	28	-13.30
Sympetrum vulgatum	16	-13.56

Table S2 (continued)

Species	Habitat	Distribution	Flight	Oviposition	Body size
Aeshna constricta	Both	W	2.5	Endophytic	69
Aeshna cyanea	Lentic	S	3	Endophytic	71.5
Aeshna eremita	Both	N-W	3	Endophytic	72.5
Aeshna grandis	Both	N	4	Endophytic	73.5
Aeshna interrupta	Both	W	3	Endophytic	66.5
Aeshna juncea	Lentic	N	4.5	Endophytic	75.5
Aeshna mixta	Both	S	2.5	Endophytic	60
Aeshna umbrosa	Both	W	3	Endophytic	68.5
Anax imperator	Lentic	S	2.5	Endophytic	76.5
Anax junius	Both	S-W	7	Endophytic	74
Argia apicalis	Both	S-W	4	Endophytic	36.5
Argia fumipennis	Both	S-W	3.5	Endophytic	31.5
Argia moesta	Lotic	S-W	3	Endophytic	39.5
Basiaeschna janata	Both	W	1	Endophytic	59
Brachytron pratense	Lentic	S	2	Endophytic	58.5
Calopteryx maculata	Lotic	S-W	3	Endophytic	48
Calopteryx virgo	Lotic	W	3.5	Endophytic	47
Ceriagrion tenellum	Both	S	3	Endophytic	30
Coenagrion hastulatum	Lentic	N	2.5	Endophytic	32
Coenagrion mercuriale	Lotic	S	2.5	Endophytic	29.5
Coenagrion puella	Lentic	S	3.5	Endophytic	34

Table S3

Ecological and geographical traits of 76 North American and European odonate species used in this work.

Field guides (Cannings, 2002; Jones et al., 2008; Paulson, 2012) and existing trait databases (Powney et al., 2014; Waller et al., 2019) were used to build this dataset. Habitat type represents species' breeding habitat, and can have a value of lentic, lotic, or both types. Distribution shows the general geographic position of each species' range, which can be widespread (W), southern (S), northern (N), southern and widespread (SW), or northern and widespread (NW). Oviposition type corresponds to egg laying inside plants (endophytic) as opposed to directly in water or on plants (exophytic). Body size is measured as body length in mm. In the case that body length was given as a maximum and minimum value, we used the average of both values.

Coenagrion pulchellum	Both	S	2	Endophytic	36
Coenagrion resolutum	Lentic	N-W	2.5	Endophytic	30
Cordulegaster boltonii	Lotic	W	3.5	Endophytic	77
Cordulia aenea	Lentic	S	2	Exophytic	51
Cordulia shurtleffii	Both	N-W	2	Exophytic	46
Enallagma antennatum	Both	S-W	2	Endophytic	30
Enallagma basidens	Both	S-W	4.5	Endophytic	24.5
Enallagma carunculatum	Both	W	3.5	Endophytic	31.5
Enallagma civile	Both	S-W	3.5	Endophytic	33.5
Enallagma cyathigerum	Both	W	3.5	Endophytic	32
Enallagma ebrium	Both	N-W	2.5	Endophytic	31
Enallagma exsulans	Both	S-W	3.5	Endophytic	34
Enallagma hageni	Both	N-W	2.5	Endophytic	30
Enallagma signatum	Both	S-W	2.5	Endophytic	32.5
Epitheca cynosura	Both	S-W	2.5	Endophytic	40.5
Erythemis simplicicollis	Both	S-W	2.5	Endophytic	41
Erythromma najas	Both	S	3	Endophytic	33
Gomphus vulgatissimus	Lotic	S	2	Exophytic	47.5
Hetaerina americana	Lotic	S-W	5	Endophytic	42
Ischnura cervula	Both	W	6	Endophytic	27.5
Ischnura hastata	Lentic	S-W	3.5	Endophytic	24
Ischnura perparva	Both	S-W	5	Endophytic	26.5
Ischnura posita	Both	S-W	3.5	Endophytic	25
Ischnura pumilio	Lentic	S	3	Endophytic	29
Ischnura verticalis	Both	W	3.5	Endophytic	26.5
Ladona julia	Lentic	N-W	2	Endophytic	41.5
Lestes congener	Lentic	W	2.5	Endophytic	36.5
Lestes disjunctus	Both	W	2.5	Endophytic	37.5
Lestes dryas	Lentic	S	2	Endophytic	37.5
Lestes rectangularis	Both	S-W	2.5	Endophytic	45
Lestes unguiculatus	Both	W	3	Endophytic	37.5
Leucorrhinia dubia	Lentic	N	2.5	Exophytic	33.5
Leucorrhinia hudsonica	Lentic	N-W	2	Endophytic	29.5
Libellula depressa	Lentic	S	2.5	Exophytic	43.5
Libellula fulva	Lentic	S	2	Exophytic	43.5
Libellula luctuosa	Lentic	S-W	2.5	Exophytic	46
Libellula pulchella	Both	W	2.5	Endophytic	54.5
Orthetrum coerulescens	Lotic	S	3	Exophytic	40.5
Pachydiplax longipennis	Both	S-W	3	Endophytic	35.5
Pantala flavescens	Both	S	3	Exophytic	48.5

Table S3 (continued)

Table S3 (continued)

Perithemis tenera	Both	S-W	4.5	Exophytic	22.5
Plathemis lydia	Both	S-W	3	Exophytic	45
Platycnemis pennipes	Lotic	S	2.5	Endophytic	36
Pyrrhosoma nymphula	Lentic	W	1.5	Endophytic	34.5
Rhionaeschna californica	Lentic	S-W	4	Endophytic	60.5
Rhionaeschna multicolor	Both	S-W	2	Endophytic	67
Somatochlora metallica	Both	W	1.5	Exophytic	53
Somatochlora semicircularis	Lentic	W	2	Exophytic	49.5
Sympetrum corruptum	Both	S-W	5	Exophytic	40.5
Sympetrum danae	Lentic	W	2	Exophytic	31.5
Sympetrum internum	Lentic	W	4	Exophytic	33.5
Sympetrum pallipes	Both	S-W	2	Endophytic	36
Sympetrum sanguineum	Lentic	S	3.5	Exophytic	36.5
Sympetrum striolatum	Both	W	5	Exophytic	39.5
Sympetrum vulgatum	Lentic	S	2	Exophytic	37.5

Table S4

Credible intervals of all MCMCglmm models testing predictions regarding the range and phenology shifts across 66 odonate species in North America and Europe.

These models are detailed in *Model information and statements* of the Supplementary Information.

	Lower credible interval	Upper credible interval
Phenological shifts ~ Range shifts		
(Intercept)	-0.26	0.49
Range shifts	-0.71	-0.16
Continent	-0.75	0.30
Range shifts ~ Range geography + T ° variability		
(intercept)	-1.22	-0.12
Southern range	0.36	1.56
Widespread	-0.32	1.08
T ° variability	-0.60	-0.18

Figure S1

P-values and coefficients of 1000 GLM iterations testing whether range shifts as calculated from random datasets predict the range shifts measured in the study.

Each point shows the results of a single GLM model, with measured range shifts as the dependant variable and randomized range shifts as the independent variable.

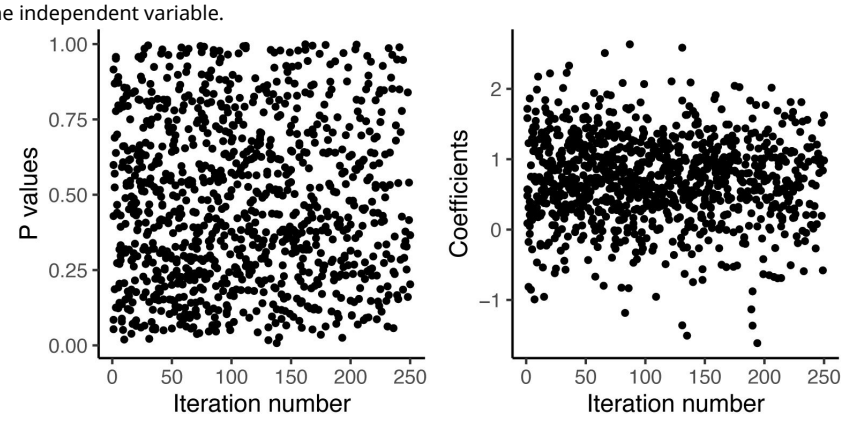


Figure S2

Observed range shifts in km from the equator, against randomized predicted values according to 4 random datasets.

Points represent species and each pane contains a different set of random data in calculations of randomized range shifts. There is no consistent relationship among 1000 iterations.

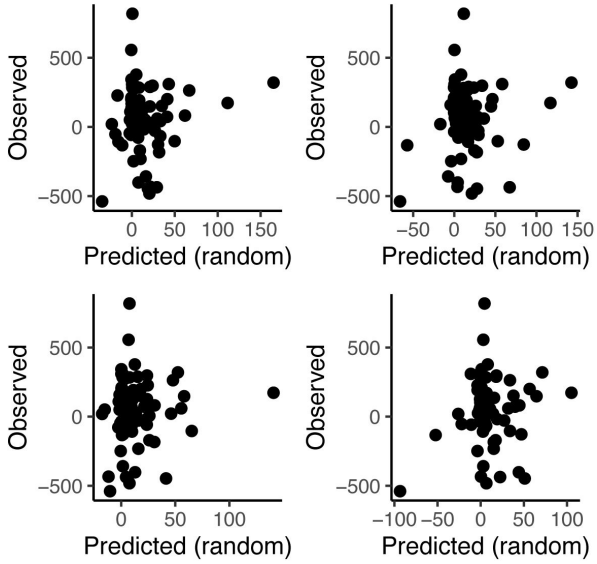


Figure S3

P-values and coefficients of 1000 GLM iterations testing whether phenology shifts as calculated from random datasets predict the phenology shifts measured in the study.

Each point shows the results of a single GLM model, with measured phenology shifts as the dependant variable and randomized phenology shifts as the independent variable.

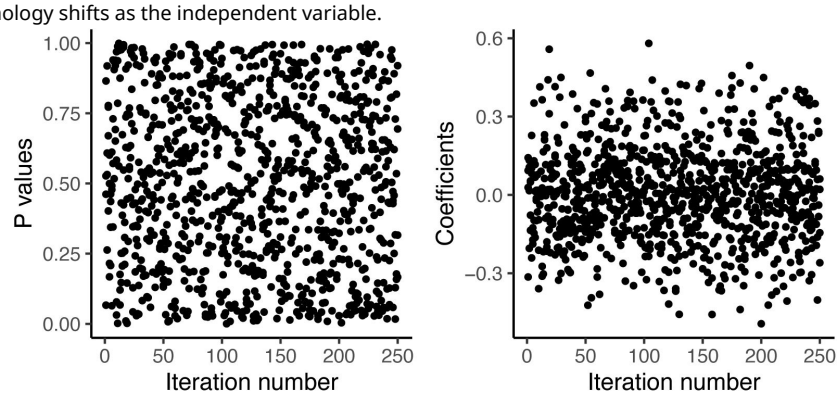
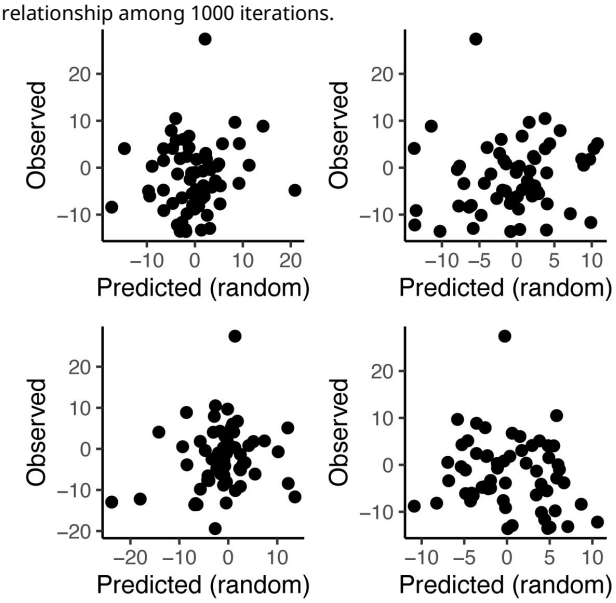


Figure S4

Observed phenology shifts in Julian day, against randomized predicted values according to 4 random datasets.

Points represent species and each pane contains a different set of random data in calculations of randomized phenology shifts. There is no consistent relationship among 1000 iterations.



A

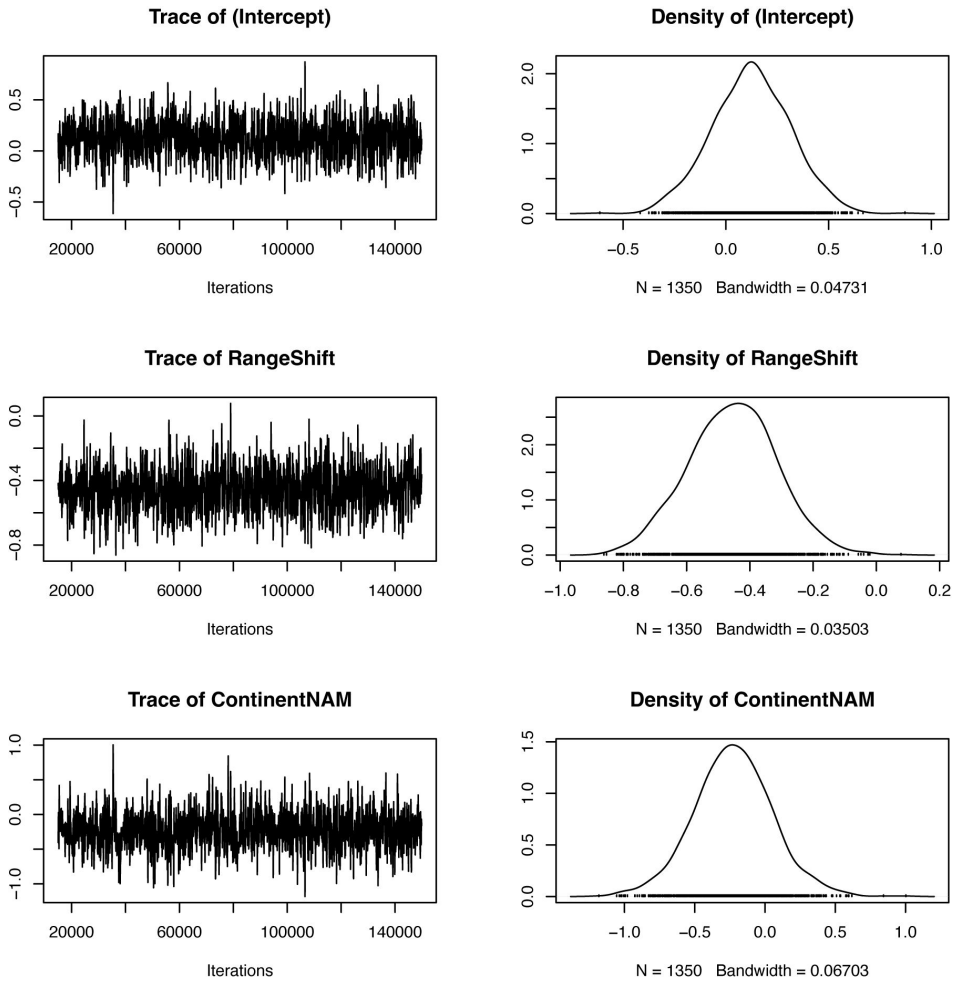


Figure S7

Panels A and B show the trace and density estimates of a phylogenetic mixed effects model exploring the relationship between range and phenology shifts in North American and European odonates (N = 66).

150,000 iterations were run to produce these results. These plots verify model convergence and absence of autocorrelation within the explanatory variables.

B

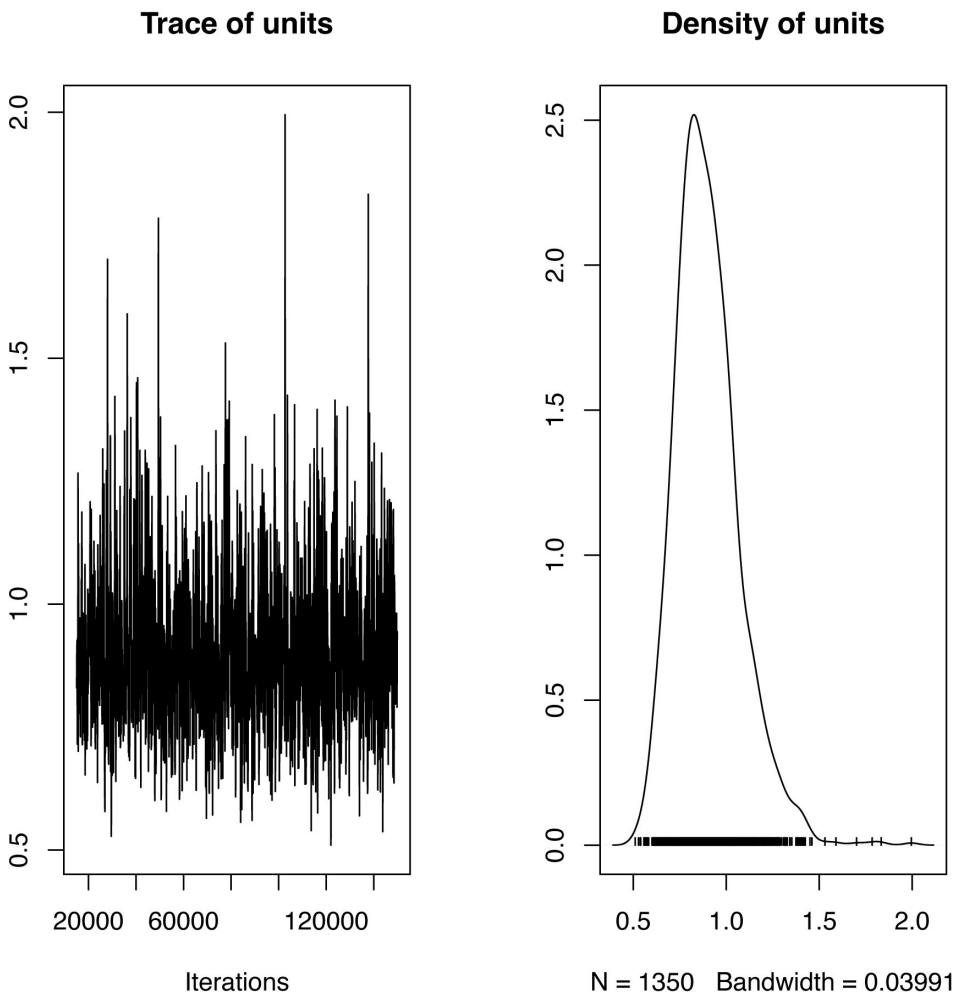


Figure S7 (continued)

A

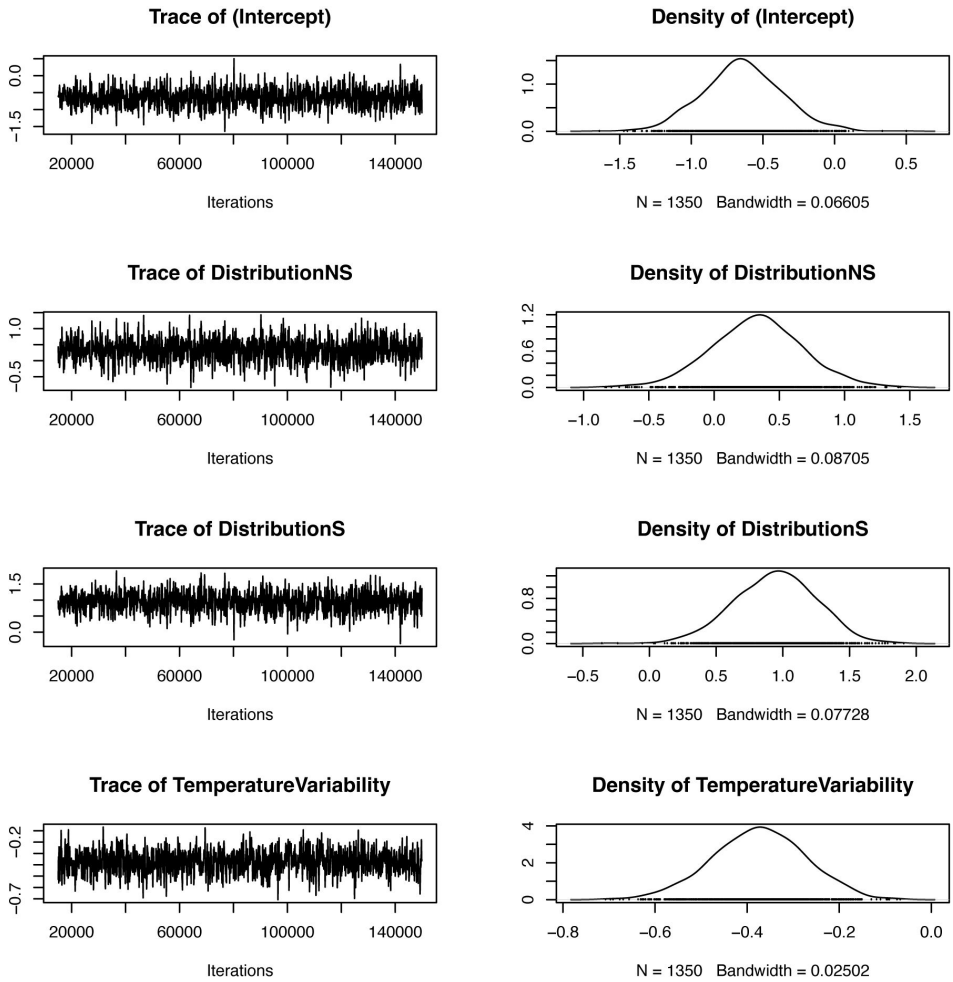


Figure S8

Panels A and B show the trace and density estimates a phylogenetic mixed effects model testing whether ecological traits, and geographic and climatic attributes predict range shifts in North American and European odonates (N = 76).

150,000 iterations were run to produce these results. Results of the best model, according to DIC, are shown here. These plots verify model convergence and absence of autocorrelation within the explanatory variables.

B

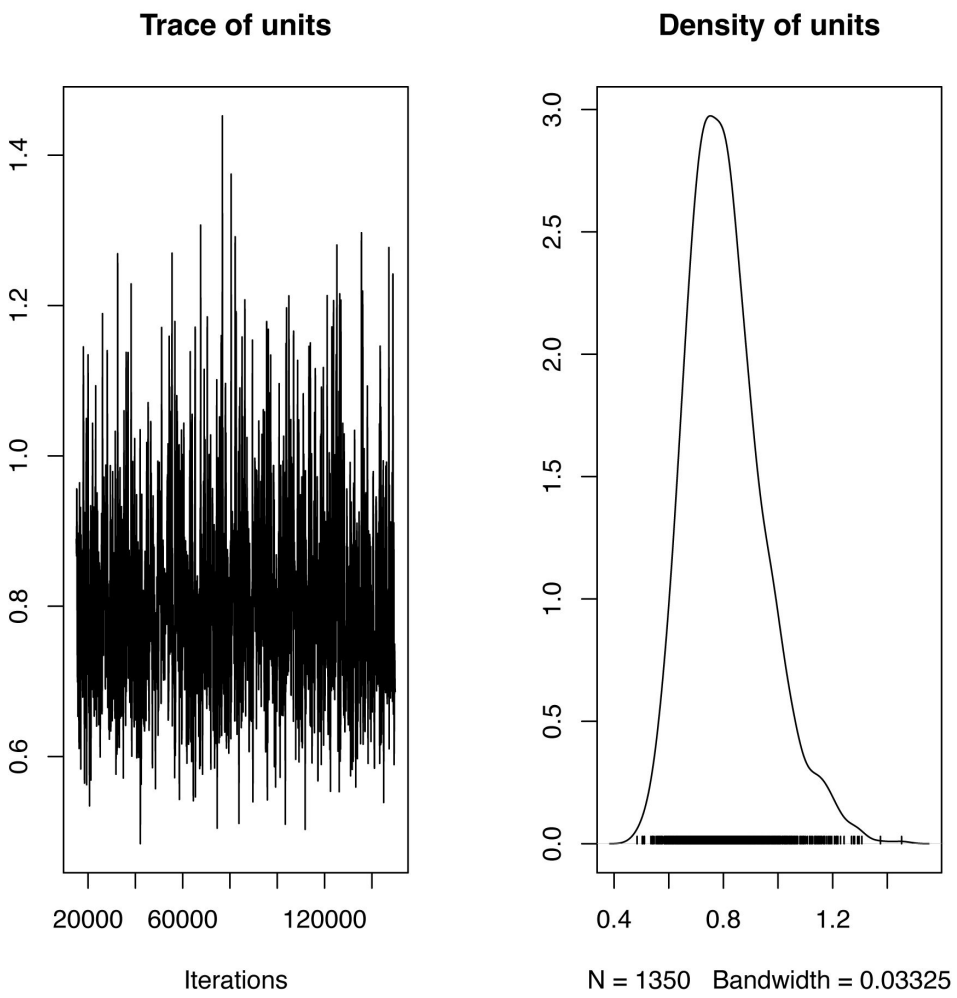


Figure S8 (continued)

Additional information

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References

Amano T, Freckleton RP, Queenborough SA, Doxford SW, Smithers RJ, Sparks TH, Sutherland WJ (2014) **Links between plant species' spatial and temporal responses to a warming climate** *Proceedings of the Royal Society B: Biological Sciences* **281**:20133017 https://doi.org/10.1098/rspb.2013.3017 | Google Scholar

Angert AL, Bontrager MG, Ågren J (2020) **What Do We Really Know About Adaptation at Range Edges?** *Annual Review of Ecology, Evolution, and Systematics* **51**:341–361 https://doi.org/10.1146/annurev-ecolsys-012120-091002 | Google Scholar

Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ, Chunco AJ (2011) **Do species' traits predict recent shifts at expanding range edges?** *Ecology Letters* **14**:677–689 https://doi.org/10.1111/j.1461-0248.2011.01620.x | Google Scholar

Ball-Damerow JE, M'Gonigle LK, Resh VH (2014) **Changes in occurrence, richness, and biological traits of dragonflies and damselflies (Odonata) in California and Nevada over the past century** *Biodivers Conserv* **23**:2107–2126 https://doi.org/10.1007/s10531-014-0707-5 | Google Scholar

Ball-Damerow JE, Oboyski PT, Resh VH (2015) **California dragonfly and damselfly (Odonata) database: temporal and spatial distribution of species records collected over the past century** *Zookeys* :67–89 https://doi.org/10.3897/zookeys.482.8453 | Google Scholar

Bartomeus I, Stavert JR, Ward D, Aguado O (2018) **Historical collections as a tool for assessing the global pollination crisis** *Philosophical Transactions of the Royal Society B: Biological Sciences* **374**:20170389 https://doi.org/10.1098/rstb.2017.0389 | Google Scholar

Beissinger SR, Riddell EA (2021) **Why Are Species' Traits Weak Predictors of Range Shifts?** *Annual Review of Ecology, Evolution, and Systematics* **52**:47–66 https://doi.org/10.1146/annurev-ecolsys-012021-092849 | Google Scholar

Bowler DE, Eichenberg D, Conze K-J, Suhling F, Baumann K, Benken T, Bönsel A, Bittner T, Drews A, Günther A, Isaac NJB, Petzold F, Seyring M, Spengler T, Trockur B, Willigalla C, Bruelheide H, Jansen F, Bonn A (2021) **Winners and losers over 35 years of dragonfly and damselfly distributional change in Germany** *Diversity and Distributions* **27**:1353–1366 https://doi.org/10.1111/ddi.13274 | Google Scholar

Bried JT, Rocha-Ortega M (2023) **Using range size to augment regional priority listing of charismatic insects** *Biological Conservation* **283**:110098 https://doi.org/10.1016/j.biocon.2023.110098 | Google Scholar

Brooks SJ, Self A, Toloni F, Sparks T (2014) **Natural history museum collections provide information on phenological change in British butterflies since the late-nineteenth century** *Int J Biometeorol* **58**:1749–1758 https://doi.org/10.1007/s00484-013-0780-6 | Google Scholar

Buckley LB, Kingsolver JG (2012) **Functional and Phylogenetic Approaches to Forecasting Species' Responses to Climate Change** *Annual Review of Ecology, Evolution, and Systematics* **43**:205–226 https://doi.org/10.1146/annurev-ecolsys-110411-160516 | Google Scholar

Cannings RA (2002) **Introducing the Dragonflies of British Columbia and Yukon** Royal British Columbia Museum Google Scholar

Cardillo M, Mace GM, Gittleman JL, Jones KE, Bielby J, Purvis A (2008) **The predictability of extinction: biological and external correlates of decline in mammals** *Proceedings of the Royal Society B: Biological Sciences* **275**:1441–1448 https://doi.org/10.1098/rspb.2008.0179 | Google Scholar

Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) **Rapid Range Shifts of Species Associated with High Levels of Climate Warming** *Science* **333**:1024–1026 Google Scholar

Chichorro F, Juslén A, Cardoso P (2019) **A review of the relation between species traits and extinction risk** *Biological Conservation* **237**:220–229 https://doi.org/10.1016/j.biocon.2019.07.001 | Google Scholar

Conrad KF, Willson KH, Harvey IF, Thomas CJ, Sherratt TN (1999) **Dispersal characteristics of seven odonate species in an agricultural landscape** *Ecography* **22**:524–531 https://doi.org/10.1111/j.1600-0587.1999.tb01282.x | Google Scholar

Cooper N, Bielby J, Thomas GH, Purvis A (2008) **Macroecology and extinction risk correlates of frogs** *Global Ecology and Biogeography* **17**:211–221 https://doi.org/10.1111/j.1466-8238.2007.00355.x | Google Scholar

Córdoba-Aguilar A, Beatty C, Bried JT (2023) **Dragonflies and Damselflies: Model Organisms for Ecological and Evolutionary Research** Oxford University Press Google Scholar

Davis MB, Shaw RG, Etterson JR (2005) **Evolutionary responses to changing climate** *Ecology* **86**:1704–1714 https://doi.org/10.1890/03-0788 | Google Scholar

Day PB, Stuart-Smith RD, Edgar GJ, Bates AE (2018) **Species' thermal ranges predict changes in reef fish community structure during 8 years of extreme temperature variation** *Diversity and Distributions* **24**:1036–1046 https://doi.org/10.1111/ddi.12753 | Google Scholar

Devictor V, Julliard R, Couvet D, Jiguet F (2008) **Birds are tracking climate warming, but not fast enough** *Proceedings of the Royal Society B: Biological Sciences* **275**:2743–2748 https://doi.org/10.1098/rspb.2008.0878 | Google Scholar

Devictor V, van Swaay C, Brereton T, Brotons L, Chamberlain D, Heliölä J, Herrando S, Julliard R, Kuussaari M, Lindström Å, Reif J, Roy DB, Schweiger O, Settele J, Stefanescu C, Van Strien A, Van Turnhout C, Vermouzek Z, WallisDeVries M, Wynhoff I, Jiguet F. (2012) **Differences in the climatic debts of birds and butterflies at a continental scale** *Nature Clim Change* **2**:121–124 https://doi.org/10.1038/nclimate1347 | Google Scholar

Diamond SE, Frame AM, Martin RA, Buckley LB (2011) **Species' traits predict phenological responses to climate change in butterflies** *Ecology* **92**:1005–1012 https://doi.org/10.1890/10-1594.1 | Google Scholar

Duffy K, Gouhier TC, Ganguly AR (2022) **Climate-mediated shifts in temperature fluctuations promote extinction risk** *Nat Clim Chang* **12**:1037–1044 https://doi.org/10.1038/s41558-022-01490-7 | Google Scholar

Engelhardt EK, Biber MF, Dolek M, Fartmann T, Hochkirch A, Leidinger J, Löffler F, Pinkert S, Poniatowski D, Voith J, Winterholler M, Zeuss D, Bowler DE, Hof C (2022) **Consistent signals of a warming climate in occupancy changes of three insect taxa over 40 years in central**

Europe *Global Change Biology* **28**:3998–4012 https://doi.org/10.1111/gcb.16200 | Google Scholar

ESRI (2019) **ArcGIS** ESRI 10.7.1

Estrada A, Morales-Castilla I, Caplat P, Early R (2016) **Usefulness of Species Traits in Predicting Range Shifts** *Trends in Ecology & Evolution* **31**:190–203 https://doi.org/10.1016/j.tree.2015.12.014 | Google Scholar

Franke S, Pinkert S, Brandl R, Thorn S (2022) **Modeling the extinction risk of European butterflies and odonates** *Ecology and Evolution* **12**:e9465 https://doi.org/10.1002/ece3.9465 | Google Scholar

Franks SE, Pearce-Higgins JW, Atkinson S, Bell JR, Botham MS, Brereton TM, Harrington R, Leech DI (2018) **The sensitivity of breeding songbirds to changes in seasonal timing is linked to population change but cannot be directly attributed to the effects of trophic asynchrony on productivity** *Global Change Biology* **24**:957–971 https://doi.org/10.1111/gcb.13960 | Google Scholar

Gaiji S, Chavan V, Ariño AH, Otegui J, Hobern D, Sood R, Robles E (2013) **Content assessment of the primary biodiversity data published through GBIF network: Status, challenges and potentials** *Biodiversity Informatics* **8** https://doi.org/10.17161/bi.v8i2.4124 | Google Scholar

García-Roselló E, Guisande C, Manjarrés-Hernández A, González-Dacosta J, Heine J, Pelayo-Villamil P, González-Vilas L, Vari RP, Vaamonde A, Granado-Lorencio C, Lobo JM (2015) **Can we derive macroecological patterns from primary Global Biodiversity Information Facility data?** *Global Ecology and Biogeography* **24**:335–347 https://doi.org/10.1111/geb.12260 | Google Scholar

Goulson D (2019) **The insect apocalypse, and why it matters** *Current Biology* **29**:R967–R971 https://doi.org/10.1016/j.cub.2019.06.069 | Google Scholar

Grant PR, Grant BR, Huey RB, Johnson MTJ, Knoll AH, Schmitt J (2017) **Evolution caused by extreme events** *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**:20160146 https://doi.org/10.1098/rstb.2016.0146 | Google Scholar

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

Gutiérrez D, Wilson RJ (2021) **Intra- and interspecific variation in the responses of insect phenology to climate** *Journal of Animal Ecology* **90**:248–259 https://doi.org/10.1111/1365-2656.13348 | Google Scholar

Hadfield JD (2010) **MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package** *Journal of Statistical Software* **33**:1–22 https://doi.org/10.18637/jss.v033.i02 | Google Scholar

Hällfors MH, Heikkinen RK, Kuussaari M, Lehikoinen A, Luoto M, Pöyry J, Virkkala R, Saastamoinen M, Kujala H (2024) **Recent range shifts of moths, butterflies, and birds are**

driven by the breadth of their climatic niche *Evolution Letters* **8**:89–100 https://doi.org/10.1093/evlett/qrad004 | Google Scholar

Hällfors MH, Pöyry J, Heliölä J, Kohonen I, Kuussaari M, Leinonen R, Schmucki R, Sihvonen P, Saastamoinen M (2021) **Combining range and phenology shifts offers a winning strategy for boreal Lepidoptera** *Ecology Letters* **24**:1619–1632 https://doi.org/10.1111/ele.13774 | Google Scholar

Harris RMB, Beaumont LJ, Vance TR, Tozer CR, Remenyi TA, Perkins-Kirkpatrick SE, Mitchell PJ, Nicotra AB, McGregor S, Andrew NR, Letnic M, Kearney MR, Wernberg T, Hutley LB, Chambers LE, Fletcher M-S, Keatley MR, Woodward CA, Williamson G, Duke NC, Bowman DMJS (2018) **Biological responses to the press and pulse of climate trends and extreme events** *Nature Clim Change* **8**:579–587 https://doi.org/10.1038/s41558-018-0187-9 | Google Scholar

Hassall C (2015) **Odonata as candidate macroecological barometers for global climate change** *Freshwater Science* **34**:1040–1049 https://doi.org/10.1086/682210 | Google Scholar

Hassall C, Thompson DJ (2008) **The effects of environmental warming on Odonata: a review** *International Journal of Odonatology* **11**:131–153 https://doi.org/10.1080/13887890.2008.9748319 | Google Scholar

Iler AM, CaraDonna PJ, Forrest JRK, Post E (2021) **Demographic Consequences of Phenological Shifts in Response to Climate Change** *Annual Review of Ecology, Evolution, and Systematics* **52**:221–245 https://doi.org/10.1146/annurev-ecolsys-011921-032939 | Google Scholar

IPCC (2021) **Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change** Cambridge University Press Google Scholar

Jones CD, Kingsley A, Burke P, Holder M (2008) **Field guide to the dragonflies and damselflies of Algonquin Provincial Park and the surrounding area** The Friends of the Algonquin Park Google Scholar

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

Kerr JT (2020) **Racing against change: understanding dispersal and persistence to improve species' conservation prospects** *Proceedings of the Royal Society B: Biological Sciences* **287**:20202061 https://doi.org/10.1098/rspb.2020.2061 | Google Scholar

Kerr JT, Pindar A, Galpern P, Packer L, Potts SG, Roberts SM, Rasmont P, Schweiger O, Colla SR, Richardson LL, Wagner DL, Gall LF, Sikes DS, Pantoja A (2015) **Climate change impacts on bumblebees converge across continents** *Science* **349**:177–180 https://doi.org/10.1126/science.aaa7031 | Google Scholar

Kharouba HM, Algar AC, Kerr JT (2009) **Historically calibrated predictions of butterfly species' range shift using global change as a pseudo-experiment** *Ecology* **90**:2213–2222 https://doi.org/10.1890/08-1304.1 | Google Scholar

Kujala H, Vepsäläinen V, Zuckerberg B, Brommer JE (2013) **Range margin shifts of birds revisited – the role of spatiotemporally varying survey effort** *Global Change Biology* **19**:420–430 https://doi.org/10.1111/gcb.12042 | Google Scholar

Lawlor JA, Comte L, Grenouillet G, Lenoir J, Baecher JA, Bandara RMWJ, Bertrand R, Chen I- C, Diamond SE, Lancaster LT, Moore N, Murienne J, Oliveira BF, Pecl GT, Pinsky ML, Rolland J, Rubenstein M, Scheffers BR, Thompson LM, van Amerom B, Villalobos F, Weiskopf SR, Sunday J. (2024) **Mechanisms, detection and impacts of species redistributions under climate change** *Nat Rev Earth Environ* **5**:351–368 https://doi.org/10.1038/s43017-024-00527-z | Google Scholar

Lenoir J, Bertrand R, Comte L, Bourgeaud L, Hattab T, Murienne J, Grenouillet G (2020) **Species better track climate warming in the oceans than on land** *Nat Ecol Evol* **4**:1044–1059 https://doi.org/10.1038/s41559-020-1198-2 | Google Scholar

Leroux SJ, Larrivée M, Boucher-Lalonde V, Hurford A, Zuloaga J, Kerr JT, Lutscher F (2013) **Mechanistic models for the spatial spread of species under climate change** *Ecological Applications* **23**:815–828 https://doi.org/10.1890/12-1407.1 | Google Scholar

Littlefield CE, Krosby M, Michalak JL, Lawler JJ (2019) **Connectivity for species on the move: supporting climate-driven range shifts** *Frontiers in Ecology and the Environment* **17**:270–278 https://doi.org/10.1002/fee.2043 | Google Scholar

Lustenhouwer N, Wilschut RA, Williams JL, van der Putten WH, Levine JM. (2018) **Rapid evolution of phenology during range expansion with recent climate change** *Global Change Biology* **24**:e534–e544 https://doi.org/10.1111/gcb.13947 | Google Scholar

Macgregor CJ, Thomas CD, Roy DB, Beaumont MA, Bell JR, Brereton T, Bridle JR, Dytham C, Fox R, Gotthard K, Hoffmann AA, Martin G, Middlebrook I, Nylin S, Platts PJ, Rasteiro R, Saccheri IJ, Villoutreix R, Wheat CW, Hill JK (2019) **Climate-induced phenology shifts linked to range expansions in species with multiple reproductive cycles per year** *Nat Commun* **10**:4455 https://doi.org/10.1038/s41467-019-12479-w | Google Scholar

MacLean SA, Beissinger SR (2017) **Species' traits as predictors of range shifts under contemporary climate change: A review and meta-analysis** *Global Change Biology* **23**:4094–4105 https://doi.org/10.1111/gcb.13736 | Google Scholar

Mair L, Hill JK, Fox R, Botham M, Brereton T, Thomas CD (2014) **Abundance changes and habitat availability drive species' responses to climate change** *Nature Clim Change* **4**:127–131 https://doi.org/10.1038/nclimate2086 | Google Scholar

McCauley SJ, Hammond JI, Frances DN, Mabry KE (2015) **Effects of experimental warming on survival, phenology, and morphology of an aquatic insect (Odonata)** *Ecological Entomology* **40**:211–220 https://doi.org/10.1111/een.12175 | Google Scholar

McCauley SJ, Hammond JI, Mabry KE (2018) **Simulated climate change increases larval mortality, alters phenology, and affects flight morphology of a dragonfly** *Ecosphere* **9**:e02151 https://doi.org/10.1002/ecs2.2151 | Google Scholar

Menzel A, Sparks TH, Estrella N, Koch E, Aasa A, Ahas R, Alm-Kübler K, Bissolli P, Braslavská O, Briede A, Chmielewski FM, Crepinsek Z, Curnel Y, Dahl Å, Defila C, Donnelly A, Filella Y, Jatczak K, Måge F, Mestre A, Nordli Ø, Peñuelas J, Pirinen P, Remišová V, Scheifinger H, Striz M, Susnik A, Van Vliet AJH, Wielgolaski F-E, Zach S, Zust A (2006) **European phenological response to climate change matches the warming pattern** *Global Change Biology* **12**:1969–1976 https://doi.org/10.1111/j.1365-2486.2006.01193.x | Google Scholar

Nagelkerke NJD (1991) **A Note on a General Definition of the Coefficient of Determination** *Biometrika* **78**:691–692 https://doi.org/10.2307/2337038 | Google Scholar

Neate-Clegg MHC, Tonelli BA, Tingley MW (2024) **Advances in breeding phenology outpace latitudinal and elevational shifts for North American birds tracking temperature** *Nat Ecol Evol* **8**:2027–2036 https://doi.org/10.1038/s41559-024-02536-z | Google Scholar

New M, Lister D, Hulme M, Makin I. (2002) **A high-resolution data set of surface climate over global land areas** *Climate Research* **21**:1–25 https://doi.org/10.3354/cr021001 | Google Scholar

Ni M, Vellend M (2021) **Space-for-time inferences about range-edge dynamics of tree species can be influenced by sampling biases** *Global Change Biology* **27**:2102–2112 https://doi.org/10.1111/gcb.15524 | Google Scholar

Novella-Fernandez R, Brandl R, Pinkert S, Zeuss D, Hof C (2023) **Seasonal variation in dragonfly assemblage colouration suggests a link between thermal melanism and phenology** *Nat Commun* **14**:8427 https://doi.org/10.1038/s41467-023-44106-0 | Google Scholar

Pacifici M, Rondinini C, Rhodes JR, Burbidge AA, Cristiano A, Watson JEM, Woinarski JCZ, Di Marco M. (2020) **Global correlates of range contractions and expansions in terrestrial mammals** *Nat Commun* **11**:2840 https://doi.org/10.1038/s41467-020-16684-w | Google Scholar

Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennent WJ, Thomas JA, Warren M (1999) **Poleward shifts in geographical ranges of butterfly species associated with regional warming** *Nature* **399**:579–583 https://doi.org/10.1038/21181 | Google Scholar

Parmesan C, Yohe G (2003) **A globally coherent fingerprint of climate change impacts across natural systems** *Nature* **421**:37–42 https://doi.org/10.1038/nature01286 | Google Scholar

Paulson D (2012) **Dragonflies and Damselflies of the East** Princeton University Press Google Scholar

Pearse WD, Davis CC, Inouye DW, Primack RB, Davies TJ (2017) **A statistical estimator for determining the limits of contemporary and historic phenology** *Nat Ecol Evol* **1**:1876–1882 https://doi.org/10.1038/s41559-017-0350-0 | Google Scholar

Pinkert S, Clausnitzer V, Acquah-Lamptey D, De Marco P, Johansson F. (2022) **Odonata as focal taxa for biological responses to climate change** In: Cordoba-Aguilar A, Beatty C, Bried J, editors. *Dragonflies and Damselflies: Model Organisms for Ecological and Evolutionary Research* Oxford University Press :0 https://doi.org/10.1093/oso/9780192898623.003.0027 | Google Scholar

Pinsky ML, Worm B, Fogarty MJ, Sarmiento JL, Levin SA (2013) **Marine Taxa Track Local Climate Velocities** *Science* **341**:1239–1242 https://doi.org/10.1126/science.1239352 | Google Scholar

Platts PJ, Mason SC, Palmer G, Hill JK, Oliver TH, Powney GD, Fox R, Thomas CD (2019) **Habitat availability explains variation in climate-driven range shifts across multiple taxonomic groups** *Sci Rep* **9**:15039 https://doi.org/10.1038/s41598-019-51582-2 | Google Scholar

Powney GD, Brooks SJ, Barwell LJ, Bowles P, Fitt RNL, Pavitt A, Spriggs RA, Isaac NJB (2014) **Morphological and Geographical Traits of the British Odonata** *Biodivers Data J e* **1041** https://doi.org/10.3897/BDJ.2.e1041 | Google Scholar

Powney GD, Cham SSA, Smallshire D, Isaac NJB (2015) **Trait correlates of distribution trends in the Odonata of Britain and Ireland** *PeerJ* **3**:e1410 https://doi.org/10.7717/peerj.1410 | Google Scholar

Pyke GH, Ehrlich PR (2010) **Biological collections and ecological/environmental research: a review, some observations and a look to the future** *Biological Reviews* **85**:247–266 https://doi.org/10.1111/j.1469-185X.2009.00098.x | Google Scholar

R Core Team (2019) **R: A language and environment for statistical computing** R Foundation for Statistical Computing

Rapacciuolo G, Ball-Damerow JE, Zeilinger AR, Resh VH (2017) **Detecting long-term occupancy changes in Californian odonates from natural history and citizen science records** *Biodivers Conserv* **26**:2933–2949 https://doi.org/10.1007/s10531-017-1399-4 | Google Scholar

Revell LJ (2012) **. phytools: an R package for phylogenetic comparative biology (and other things)** *Methods in Ecology and Evolution* **3**:217–223 https://doi.org/10.1111/j.2041-210X.2011.00169.x | Google Scholar

Richardson DM, Hellmann JJ, McLachlan JS, Sax DF, Schwartz MW, Gonzalez P, Brennan EJ, Camacho A, Root TL, Sala OE, Schneider SH, Ashe DM, Clark JR, Early R, Etterson JR, Fielder ED, Gill JL, Minteer BA, Polasky S, Safford HD, Thompson AR, Vellend M, Ehrlich PR (2009) **Multidimensional Evaluation of Managed Relocation** *Proceedings of the National Academy of Sciences of the United States of America* **106**:9721–9724 Google Scholar

Robbirt KM, Davy AJ, Hutchings MJ, Roberts DL (2011) **Validation of biological collections as a source of phenological data for use in climate change studies: a case study with the orchid Ophrys sphegodes** *Journal of Ecology* **99**:235–241 https://doi.org/10.1111/j.1365-2745.2010.01727.x | Google Scholar

Rocha-Ortega M, Khelifa R, Sandall EL, Deacon C, Sánchez-Rivero X, Pinkert S, Patten MA (2022) **Linking traits to extinction risk in Odonata** In: Cordoba-Aguilar A, Beatty C, Bried J, editors. *Dragonflies and Damselflies: Model Organisms for Ecological and Evolutionary Research* Oxford University Press :0 https://doi.org/10.1093/oso/9780192898623.003.0024 | Google Scholar

Rocha-Ortega M, Rodríguez P, Bried J, Abbott J, Córdoba-Aguilar A (2020) **Why do bugs perish? Range size and local vulnerability traits as surrogates of Odonata extinction risk** *Proceedings of the Royal Society B: Biological Sciences* **287**:20192645 https://doi.org/10.1098/rspb.2019.2645 | Google Scholar

Román-Palacios C, Wiens JJ (2020) **Recent responses to climate change reveal the drivers of species extinction and survival** *Proceedings of the National Academy of Sciences* **117**:4211–4217 https://doi.org/10.1073/pnas.1913007117 | Google Scholar

Rundle SD, Bilton DT, Abbott JC, Foggo A (2007) **Range size in North American Enallagma damselflies correlates with wing size** *Freshwater Biology* **52**:471–477 https://doi.org/10.1111/j.1365-2427.2006.01712.x | Google Scholar

Saino N, Ambrosini R, Rubolini D, von Hardenberg J, Provenzale A, Hüppop K, Hüppop O, Lehikoinen A, Lehikoinen E, Rainio K, Romano M, Sokolov L. (2010) **Climate warming, ecological mismatch at arrival and population decline in migratory birds** *Proceedings of the*

Royal Society B: Biological Sciences **278**:835–842 https://doi.org/10.1098/rspb.2010.1778 | Google Scholar

Sandall EL, Pinkert S, Jetz W (2022) **Country-level checklists and occurrences for the world's Odonata (dragonflies and damselflies)** *Journal of Biogeography* **49**:1586–1598 https://doi.org/10.1111/jbi.14457 | Google Scholar

Schuetz JG, Mills KE, Allyn AJ, Stamieszkin K, Bris AL, Pershing AJ (2019) **Complex patterns of temperature sensitivity, not ecological traits, dictate diverse species responses to climate change** *Ecography* **42**:111–124 https://doi.org/10.1111/ecog.03823 | Google Scholar

Šigutová H, Pyszko P, Bílková E, Dolný A (2025) **Highly Conserved Ecosystems Facing Climate Change: Rapid Shifts in Odonata Assemblages of Central European Bogs** *Global Change Biology* **31**:e70183 https://doi.org/10.1111/gcb.70183 | Google Scholar

Socolar JB, Epanchin PN, Beissinger SR, Tingley MW (2017) **Phenological shifts conserve thermal niches in North American birds and reshape expectations for climate-driven range shifts** *Proceedings of the National Academy of Sciences* **114**:12976–12981 https://doi.org/10.1073/pnas.1705897114 | Google Scholar

Soroye P, Newbold T, Kerr J (2020) **Climate change contributes to widespread declines among bumble bees across continents** *Science* **367**:685–688 https://doi.org/10.1126/science.aax8591 | Google Scholar

Souza KS, Fortunato DS, Jardim L, Terribile LC, Lima-Ribeiro MS, Mariano CÁ, Pinto-Ledezma JN, Loyola R, Dobrovolski R, Rangel TF, Machado IF, Rocha T, Batista MG, Lorini ML, Vale MM, Navas CA, Maciel NM, Villalobos F, Olalla-Tarraga MÂ, Rodrigues JFM, Gouveia SF, Diniz-Filho JAF (2023) **Evolutionary rescue and geographic range shifts under climate change for global amphibians** *Front Ecol Evol* **11** https://doi.org/10.3389/fevo.2023.1038018 | Google Scholar

Srivastava DS, Coristine L, Angert AL, Bontrager M, Amundrud SL, Williams JL, Yeung ACY, de Zwaan DR, Thompson PL, Aitken SN, Sunday JM, O'Connor MI, Whitton J, Brown NEM, MacLeod CD, Parfrey LW, Bernhardt JR, Carrillo J, Harley CDG, Martone PT, Freeman BG, Tseng M, Donner SD. (2021) **Wildcards in climate change biology** *Ecological Monographs* **91**:e01471 https://doi.org/10.1002/ecm.1471 | Google Scholar

Stephens PA, Mason LR, Green RE, Gregory RD, Sauer JR, Alison J, Aunins A, Brotons L, Butchart SHM, Campedelli T, Chodkiewicz T, Chylarecki P, Crowe O, Elts J, Escandell V, Foppen RPB, Heldbjerg H, Herrando S, Husby M, Jiguet F, Lehikoinen A, Lindström Å, Noble DG, Paquet J-Y, Reif J, Sattler T, Szép T, Teufelbauer N, Trautmann S, van Strien AJ, van Turnhout CAM, Vorisek P, Willis SG (2016) **Consistent response of bird populations to climate change on two continents** *Science* **352**:84–87 https://doi.org/10.1126/science.aac4858 | Google Scholar

Suhonen J, Ilvonen JJ, Korkeamäki E, Nokkala C, Salmela J (2022) **Using functional traits and phylogeny to understand local extinction risk in dragonflies and damselflies (Odonata)** *Ecology and Evolution* **12**:e8648 https://doi.org/10.1002/ece3.8648 | Google Scholar

Sunday JM, Pecl GT, Frusher S, Hobday AJ, Hill N, Holbrook NJ, Edgar GJ, Stuart-Smith R, Barrett N, Wernberg T, Watson RA, Smale DA, Fulton EA, Slawinski D, Feng M, Radford BT, Thompson PA, Bates AE (2015) **Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot** *Ecology Letters* **18**:944–953 https://doi.org/10.1111/ele.12474 | Google Scholar

Swaegers J, Janssens SB, Ferreira S, Watts PC, Mergeay J, McPeek MA, Stoks R (2014) **Ecological and evolutionary drivers of range size in Coenagrion damselflies** *j evol Biol* **27**:2386–2395 https://doi.org/10.1111/jeb.12481 | Google Scholar

Urban MC (2015) **Accelerating extinction risk from climate change** *Science* **348**:571–573 https://doi.org/10.1126/science.aaa4984 | Google Scholar

Usui T, Lerner D, Eckert I, Angert AL, Garroway CJ, Hargreaves A, Lancaster LT, Lessard J-P, Riva F, Schmidt C, van der Burg K, Marshall KE. (2023) **The evolution of plasticity at geographic range edges** *Trends in Ecology & Evolution* **38**:831–842 https://doi.org/10.1016/j.tree.2023.04.004 | Google Scholar

van der Laken P. (2021) **ppsr: Predictive Power Score** *CRAN*

Waller JT, Svensson EI (2017) **Body size evolution in an old insect order: No evidence for Cope's Rule in spite of fitness benefits of large size** *Evolution* **71**:2178–2193 https://doi.org/10.1111/evo.13302 | Google Scholar

Waller JT, Willink B, Tschol M, Svensson EI (2019) **The odonate phenotypic database, a new open data resource for comparative studies of an old insect order** *Sci Data* **6**:316 https://doi.org/10.1038/s41597-019-0318-9 | Google Scholar

Zattara EE, Aizen MA (2021) **Worldwide occurrence records suggest a global decline in bee species richness** *One Earth* **4**:114–123 https://doi.org/10.1016/j.oneear.2020.12.005 | Google Scholar

Zografou K, Swartz MT, Adamidis GC, Tilden VP, McKinney EN, Sewall BJ (2021) **Species traits affect phenological responses to climate change in a butterfly community** *Sci Rep* **11**:3283 https://doi.org/10.1038/s41598-021-82723-1 | Google Scholar

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Reviewer #1 (Public review):

Summary:

This study evaluates whether species can shift geographically, temporally, or both ways in response to climate change. It also teases out the relative importance of geographic context, temperature variability, and functional traits in predicting the shifts. The study system is large occurrence datasets for dragonflies and damselflies split between two time periods and two continents. Results indicate that more species exhibited both shifts than one or the other (or neither), and that geographic context and temperature variability were more influential than traits. The results have implications for future analyses (e.g. incorporating habitat availability) and for choosing winner and loser species under climate change. The results also seem to support climate vulnerability assessments for species that rely on geographic range size and geospatial climate data layers rather than more detailed information (like demographic rates, abundances, or traits) that may not be so readily available. The methodology would be useful for other taxa and study regions with strong participatory ("citizen") science and extensive occurrence data.

Strengths:

This is an organized and well written paper that builds on a popular topic and moves it forward. It has the right idea and approach, and the results are useful answers to the predictions and for conservation planning (i.e. identifying climate winners and losers). There is technical proficiency and analytical rigor driven by an understanding of the data and its limitations.

https://doi.org/10.7554/eLife.101208.2.sa3

Reviewer #2 (Public review):

Summary:

This paper explores a highly interesting question regarding how species migration success relates to phenology shifts, and it finds a positive relationship. The findings are significant, and the strength of the evidence is solid. However, there are substantial issues with the writing, presentation, and analyses that need to be addressed. First, I disagree with the conclusion that species that don't migrate are "losers" - some species might not migrate simply because they have broad climatic niches and are less sensitive to climate change. Second, the results concerning species' southern range limits could provide valuable insights. These could be used to assess whether sampling bias has influenced the results. If species are truly migrating, we should observe northward shifts in their southern range limits. However, if this is an artifact of increased sampling over time, we would expect broader distributions both north and south. Finally, Figure 1 is missed panel B, which needs to be addressed.

Comments on revised version:

The revision has substantially improved the paper.

https://doi.org/10.7554/eLife.101208.2.sa2

Reviewer #3 (Public review):

Summary:

In their article "Range geography and temperature variability explain cross-continental convergence in range and phenology shifts in a model insect taxon" the authors rigorously investigate the spatial and temporal trends in the occurrence of odonate species and their potential drivers. Specifically, they examine whether species shift their geographic ranges poleward or alter their phenology to cope with changing conditions. Leveraging opportunistic observations of European and North American odonates, they find that species showing significant range shifts also exhibited shifts to earlier emergence. Considering a broad range of potential predictors, their results reveal that geographical factors, but not functional traits, are associated with these shifts.

Strengths:

The article addresses an important topic in ecology and conservation that is particularly timely in the face of reports of substantial insects declines in North America and Europe over the past decades. Through data integration the authors leverage the rich natural history record for odonates, broadening the taxonomic scope of analyses of temporal trends in phenology and distribution. The combination of phenological and range shifts in one framework presents an elegant way to reconcile previous findings and informs about the drivers of biodiversity loss.

Weaknesses:

To better understand whether species shifting both their ranges and phenology are more successful, or as stated here are 'clear winners', and hence whether those that do neither are more vulnerable would require integrating population trends alongside the discussed response. The ~10% species that have not shifted their distribution or phenology might have not declined in abundance, if they have rapidly adapted to local changes in climatic conditions (i.e. they might show a plastic response). These species might be the real 'winners', while species that have recently shifted their ranges or phenology may eventually reach hard limits. The authors are discussing this limitation but might want to adapt their wording, given the potential for misinterpretation. The finding that species with more northern ranges showed lesser northward shifts would speak to the fact that some species have already reached such a geographical range limit.

Achievements and impact:

The results support broad differences in the response of odonate species to climate change, and the prediction that range geography and temperature seasonality are more important predictors of these changes than functional traits. Simultaneously addressing range and phenological shifts highlights that most species exhibit coupled responses but also identifies a significant portion of species that do not respond in these ways that are of critical conservation concern. These results are important for improving forecasts of species' responses to climate change and identifying species of particularly conservation concern. Although not exhaustive regarding abundance trends, the study presents an important step towards a general framework for investigating the drivers of multifaceted species responses.

https://doi.org/10.7554/eLife.101208.2.sa1

Author response:

The following is the authors' response to the original reviews.

> ***Reviewer #1 (Public review):***
>
> *Sumary:*
>
> *This study evaluates whether species can shift geographically, temporally, or both ways in response to climate change. It also teases out the relative importance of geographic context, temperature variability, and functional traits in predicting the shifts. The study system is large occurrence datasets for dragonflies and damselflies split between two time periods and two continents. Results indicate that more species exhibited both shifts than one or the other or neither, and that geographic context and temp variability were more influential than traits. The results have implications for future analyses (e.g. incorporating habitat availability) and for choosing winner and loser species under climate change. The methodology would be useful for other taxa and study regions with strong community/citizen science and extensive occurrence data.*

We thank Reviewer 1 for their time and expertise in reviewing our study. The suggestions are very helpful and will improve the quality of our manuscript.

> *Strengths:*
>
> *This is an organized and well-written paper that builds on a popular topic and moves it forward. It has the right idea and approach, and the results are useful answers to the predictions and for conservation planning (i.e. identifying climate winners and losers). There is technical proficiency and analytical rigor driven by an understanding of the data and its limitations.*

We thank Reviewer 1 for this assessment.

> *Weaknesses:*
>
> *(1) The habitat classifications (Table S3) are often wrong. "Both" is overused. In North America, for example, Anax junius, Cordulia shurtleffii, Epitheca cynosura, Erythemis simplicicollis, Libellula pulchella, Pachydiplax longipennis, Pantala flavescens, Perithemis tenera, Ischnura posita, the Lestes species, and several Enallagma species are not lotic breeding. These species rarely occur let alone successfully reproduce at lotic sites. Other species are arguably "both", like Rhionaeschna multicolor which is mostly lentic. Not saying this would have altered the conclusions, but it may have exacerbated the weak trait effects.*

We thank the reviewer for their expertise on this topic. We obtained these habitat classifications from field guides and trait databases, and reviewed our primary sources to clarify the trait classifications. We reclassified the species according to the expertise of this reviewer and perform our analysis again; please see details below.

> *(2) The conservative spatial resolution (100 x 100 km) limits the analysis to wide- ranging and generalist species. There's no rationale given, so not sure if this was by design or necessity, but it limits the number of analyzable species and potentially changes the inference.*

It is really helpful to have the opportunity to contextualize study design decisions like this one, and we thank the reviewer for the query. Sampling intensity is always a meaningful issue in research conducted at this scale, and we addressed it head-on in this work.

Very small quadrats covering massive geographical areas will be critically and increasingly afflicted by sampling weaknesses, as well as creating a potentially large problem with

pseudoreplication. There is no simple solution to this problem. It would be possible to create interpolated predictions of species' distributions using Species Distribution Models, Joint Species Distribution Models, or various kinds of Occupancy Models. None of these approaches then leads to analyses that rely on directly observed patterns. Instead, they are extrapolations, and those extrapolations typically fail when tested, although they have still been tested (for example, papers by Lee-Yaw demonstrate that it is rare for SDMs to predict things well; occupancy models often perform less well than SDMs and do not capture how things change over time - Briscoe et al. 2021, Global Change Biology). The result of employing such techniques would certainly be to make all conclusions speculative, rather than directly observable.

Rather than employing extrapolative models, we relied on transparent techniques that are used successfully in the core macroecology literature that address spatial variation in sampling explicitly and simply. Moreover, we constructed extensive null models that show that range and phenology changes, respectively, are contrary to expectations that arise from sampling difference. 100km quadrats make for a reasonable "middle-ground" in terms of the effects of sampling, and we added a reference to the methods section to clarify this (see details below).

> *(3) The objective includes a prediction about generalists vs specialists (L99-103) yet there is no further mention of this dichotomy in the abstract, methods, results, or discussion.*

Thank you for pointing this out - it is an editing error that should have been resolved prior to submission. We replaced the terms specialist and generalist with specific predictions based on traits (see details below).

> *(4) Key references were overlooked or dismissed, like in the new edition of Dragonflies & Damselflies model organisms book, especially chapters 24 and 27.*

We thank Reviewer 1 for making us aware of this excellent reference. We have reviewed the text and include it as a reference, in addition to other references recommended by Reviewer 1 and other reviewers (see details below).

> ***Reviewer #2 (Public review):***
>
> *Summary:*
>
> *This paper explores a highly interesting question regarding how species migration success relates to phenology shifts, and it finds a positive relationship. The findings are significant, and the strength of the evidence is solid. However, there are substantial issues with the writing, presentation, and analyses that need to be addressed. First, I disagree with the conclusion that species that don't migrate are "losers" - some species might not migrate simply because they have broad climatic niches and are less sensitive to climate change. Second, the results concerning species' southern range limits could provide valuable insights. These could be used to assess whether sampling bias has influenced the results. If species are truly migrating, we should observe northward shifts in their southern range limits. However, if this is an artifact of increased sampling over time, we would expect broader distributions both north and south. Finally, Figure 1 is missed panel B, which needs to be addressed.*

We thank Reviewer 2 for their time and expertise in reviewing our study.

It is possible that some species with broad niches may not need to migrate, although in general failing to move with climate change is considered an indicator of "climate debt", signaling that a species may be of concern for conservation (ex. Duchenne et al. 2021, Ecology

Letters). We revised the discussion to acknowledge potential differences in outcomes (please see details below).

We used null models to test whether our results regarding range shifts were robust, and if they varied due to increased sampling over time. We found that observed northern range limit shifts are not consistent with expectations derived from changes in sampling intensity (Figure S1, S2).

We thank Reviewer 2 for pointing out this error in Figure 1. This conceptual figure was a challenge to construct, as it must illustrate how phenology and range shifts can occur simultaneously or uniquely to enable a hypothetic odonate to track its thermal niche over time. In a previous version of the figure, we had a second panel and we failed to remove the reference to that panel when we simplified the figure. We have updated the figure and figure caption (please see details below).

> ***Reviewer #3 (Public review):***
>
> *Summary:*
>
> *In their article "Range geographies, not functional traits, explain convergent range and phenology shifts under climate change," the authors rigorously investigate the temporal shifts in odonate species and their potential predictors. Specifically, they examine whether species shift their geographic ranges poleward or alter their phenology to avoid extreme conditions. Leveraging opportunistic observations of European and North American odonates, they find that species showing significant range shifts also exhibited earlier phenological shifts. Considering a broad range of potential predictors, their results reveal that geographical factors, but not functional traits, are associated with these shifts.*

We thank Reviewer 3 for their expertise and the time they spent reviewing our study. Their suggestions are very helpful and will improve the quality of our manuscript.

> *Strengths:*
>
> *The article addresses an important topic in ecology and conservation that is particularly timely in the face of reports of substantial insect declines in North America and Europe over the past decades. Through data integration the authors leverage the rich natural history record for odonates, broadening the taxonomic scope of analyses of temporal trends in phenology and distribution to this taxon. The combination of phenological and range shifts in one framework presents an elegant way to reconcile previous findings improving our understanding of the drivers of biodiversity loss.*

We thank Reviewer 3 for this assessment.

> *Weaknesses:*
>
> *The introduction and discussion of the article would benefit from a stronger contextualization of recent studies on biological responses to climate change and the underpinning mechanism.*
>
> *The presentation of the results (particularly in figures) should be improved to address the integrative character of the work and help readers extract the main results. While the writing of the article is generally good, particularly the captions and results contain many inconsistencies and lack important detail. With the multitude of the relationships that were tested (the influence of traits) the article needs more coherence.*

We thank Reviewer 3 for these suggestions. We revised the introduction and discussion to better contextualize species' responses to climate change and the mechanisms behind them (see details below). We carefully reviewed all figures and captions, and made changes to improve the clarity of the text and the presentation of results (see details below).

> ***Reviewer #1 (Recommendations for the authors):***
>
> *Comment:*
>
> *(1) Following weakness #1 in the public review, the authors should review the habitat classifications, consult with an odonatologist, and reclassify many species from Both to Lentic and redo the analysis.*

Thank you for pointing out this disagreement among expert habitat classifications that we cited and other literature. We reclassified species' habitat preferences based on classifications by Hof et al., a source that was consistent with your suggestions, and identified additional species as Lentic that our other references had identified as Both. We performed our analysis with this new dataset and, as you suspected, our results did not change qualitatively: species habitat preferences did not predict their range shifts.

Hof, Christian, Martin Brändle, and Roland Brandl. "Lentic odonates have larger and more northern ranges than lotic species." Journal of Biogeography 33.1 (2006): 63-70.

> *Comment:*
>
> *(2) Following weakness #2, would it be worthwhile or interesting to analyze a smaller ranging group (e.g. cut the quad size in half, 50 x 50 km) to bring in more species and potentially change the inference? Or is the paper too tightly constructed to allow this, even as a secondary piece?*

Thank you for this comment, as it highlights an important consideration for macroecological analyses, and the importance of balancing multiple factors for determining quadrat size. Issues exist with identifying drivers of range boundaries among species with narrow ranges when they are analyzed separately from wide-ranging species, and examining larger quadrats can actually help clarify drivers (Szabo, Algar, and Kerr 2009). The smaller quadrats are, the higher the likelihood that the species is actually there but was never observed, or that the quadrat only covers unsuitable habitat and the species is absent from the entire (or almost entire) quadrat. Too many absences creates issues with violating model assumptions, and creates noise that makes it difficult to identify drivers of species' range and phenology shifts.

Moreover, we constructed extensive null models that show that range and phenology changes, respectively, are contrary to expectations that arise from sampling difference. 100km quadrats make for a reasonable "middle-ground", and we have included a brief explanation of this in the text: "We assigned species presences to 100×100 km quadrats, a scale that is large enough to maintain adequate sampling intensity but still relevant to conservation and policy (Soroye et al., 2020), to identify the best sampled species." (Lines 170-172).

Szabo, Nora D., Adam C. Algar, and Jeremy T. Kerr. "Reconciling topographic and climatic effects on widespread and range-restricted species richness." Global Ecology and Biogeography 18.6 (2009): 735-744.

> *Comment:*

> *(3) Following weakness #3, are specialists the ones that "failed to shift" (L18)? If so please specify. The prediction about generalists vs specialists needs to be removed or incorporated in other parts of the paper.*

Thank you for pointing this out, we intended to suggest that species with more generalist habitat requirements might be better able to shift, but ultimately found that traits did not predict species' shifts. We corrected our prediction regarding habitat generalists as follows: "We predicted that species able to use both lentic and lotic habitats would shift their phenologies and geographies more than those able to use just one habitat type, as generalists outperform specialists as climate and land uses change (Ball-Damerow et al., 2015, 2014; Hassall and Thompson, 2008; Powney et al., 2015; Rapacciuolo et al., 2017)." (Lines 128-132).

> *Comment:*
>
> *(4) Following weakness #4, cite Pinkert et al at lines 70-73 and Rocha-Ortega et al at lines 73-77 along with https://doi.org/10.1098/rspb.2019.2645. Add Sandall et al https://doi.org/10.1111/jbi.14457 to L69 references.*

Thank you for the excellent reference suggestions, we have added them as suggested (Lines 80, 86, 77).

> *Comment:*
>
> *Other comments/suggestions:*
>
> *(1) Title: consider adding temp variability 'Range geography and temperature variability, not functional traits,...'.*

Thank you for this suggestion, we have added temperature variability to the title: "Range geography and temperature variability explain cross-continental convergence in range and phenology shifts in a model insect taxon".

> *Comment:*
>
> *(2) L125: is (northern) Mexico included in North America?*

Yes, we did include observations from Northern Mexico, and have specified this in the text: "We retained ~1,100,000 records from Canada, the United States, and Northern Mexico, comprising 76 species (Figure 2)." (Lines 174-176).

> *Comment:*
>
> *(3) L128: I'd label this section 'Temperature variability' rather than 'Climate data'.*

Thank you, we agree that this is a more appropriate title for this section, and have replaced 'Climate data' with 'Temperature variability' (Line 185).

> *Comment:*
>
> *(4) Table 2: why are there no estimates for the traits?*

We apologise, this information should have been included in the main body of the manuscript, but was only explained in the Table 2 caption. We have added the following explanation: "Non-significant variables, specifically all functional traits, were excluded from the final models.". (Line 312-323).

> *Comment:*
>
> *(5) Figure 2: need to identify the A-D panels.*

We apologise for this error and have clarified the differences between panels in the figure caption:

"Figure 2: Richness of 76 odonate species sampled in North America and Europe in the historic period (1980-2002; panes A and C) and the recent period (2008-2018; panes B and D). Species richness per 100 × 100 km quadrat is shown in panes A and B, while panes C and D show species richness per 200 × 200 km quadrat. Dark red indicates high species richness, while light pink indicates low species richness." (Lines 1002-1006).

> *Comment:*
>
> *(6) L163-173: I am not familiar with this analysis but it sounds interesting and promising, I am not sure if this can be clarified further. Why the -25 to 25, and -30 to 30, doesn't the -35 to 35 cover these? And what is meant by "include only phenology shifts that could be biologically meaningful", that larger shifts would not be meaningful or tied to climate change?*

We used different cutoffs for phenology shifts to inspect for outliers that were likely to be errors, potentially do to insufficient sampling to calculate phenology. We clarified in the text as follows:

"We retained emergence estimates between March 1st and September 1st, as well as species and quadrats that showed a difference in emergence phenology of -25 to 25 days, -30 to 30 days, or -35 to 35 days between both time periods, to include only phenology shifts that could be biologically meaningful to environmental climate change (i.e. exclude errors)." (Lines 169-173).

Comment:

> *(7) L193-200: I agree but would make a distinction between ecological vs functional traits, as other studies view geographic traits as ecological manifestations of functional biology, e.g. https://doi.org/10.1016/j.biocon.2019.07.001 and https://doi.org/10.1016/j.biocon.2023.110098.*

Thank you for this suggestion, and for making us aware of the thinking around range geographies as ecological traits. We have specified throughout the manuscript that the 'traits' we are considering are 'functional traits', changed the methods subsection title to "Range geographies and functional traits" (Line 252), and added a brief discussion of ecological traits: "Geographic range and associated climatic characteristics are often considered ecological traits, as they are consequences of functional traits and their interactions with geographic features (Bried and Rocha-Ortega, 2023; Chichorro et al., 2019)." (Lines 256-259).

Comment:

> *(8) L203: What's the rationale for egg-laying habitat as "biologically relevant to spatial and temporal responses to climate change"? That one's not as obvious as the others and needs a sentence more. Also, I am wondering why other traits were not considered here, like color lightness and voltinism. And why not wing size instead of body size, or better yet the two combined (wing loading) as a proxy for dispersal ability?*

We agree that our rationale for using this trait should be better explained, and we have included the following explanation: “Egg laying habitat was assigned according to whether species use exophytic egg-laying habitat (i.e. eggs laid in water or on land, relatively larger in number), or endophytic egg-laying habitat (i.e. eggs laid inside plants, usually fewer in number); species using exophytic habitats are associated with greater northward range limit shifts (Angert et al., 2011).” (Lines 271-275).

We considered traits that have been found to be important for range and phenology shifts among odonates, as well as being key traits for expectations for species responses to climate change. Flight duration and body size are correlated with dispersal ability (Powney et al. 2015). Body size is also correlated with competitive ability (Powney et al. 2015), potentially making it an important predictor of a species’ ability to establish and maintain populations in expanding range areas. Traits correlated with range shifts also include breeding habitat type (Powney et al. 2015; Bowler et al. 2021) and egg laying habitat (Angert et al. 2011). Ideally, we would have used dispersal data from mark/release/recapture studies, but it was not available for many of the species included in this study. After finding that none of the functional traits we included were related to range shifts, there was no reason to believe that a further investigation of traits would be meaningful.

Angert AL, Crozier LG, Rissler LJ, Gilman SE, Tewksbury JJ, Chunco AJ. 2011. Do species’ traits predict recent shifts at expanding range edges? Ecology Letters 14:677–689. doi:10.1111/j.1461-0248.2011.01620.x

Bowler DE, Eichenberg D, Conze K-J, Suhling F, Baumann K, Benken T, Bönsel A, Bittner T, Drews A, Günther A, Isaac NJB, Petzold F, Seyring M, Spengler T, Trockur B, Willigalla C, Bruelheide H, Jansen F, Bonn A. 2021. Winners and losers over 35 years of dragonfly and damselfly distributional change in Germany.Diversity and Distributions 27:1353–1366. doi:10.1111/ddi.13274

Powney GD, Cham SSA, Smallshire D, Isaac NJB. 2015. Trait correlates of distribution trends in the Odonata ofBritain and Ireland. PeerJ 3:e1410. doi:10.7717/peerj.1410

> *Comment:*
>
> *(9) L210: I count at least 5 migratory species in table S3, so although maybe not enough to analyze it's misleading to say "nearly all" were non-migratory, revise to "most" or "vast majority".*

Thank you for pointing this out, we have made the suggested correction (Line 277).

> *Comment:*
>
> *(10) L252-254: save this for the Discussion and write a more generalized statement for results to avoid citations in the results.*

Thank you for this suggestion, we have moved this to the discussion (Lines 517-527).

> *Comment:*
>
> *(11) Figures S5 & S6: these are pretty important, I'd consider elevating them to the main document as one figure with two panels.*

Thank you for this suggestion, we agree these figures should be elevated to the main text, and have made them into a panel figure (Figure 4).

> *Comment:*

> *(12) L305-307: great point and recommendation!*

Thank you very much for this positive feedback!

> *Comment:*
>
> *(13) L335-336: another place to cite https://doi.org/10.1098/rspb.2019.2645 which includes a thermal sensitivity index and would add an odonate citation behind the statement.*

Thank you for this excellent suggestion, we have added this citation (line 480). (Rocha-Ortega et al. 2020)

> *Comment:*
>
> *(14) L352-353: again see also https://doi.org/10.1098/rspb.2019.2645.*

Thank you for highlighting this reference, we have added it to Line 505 as suggested.

> *Comment:*
>
> *(15) L355: revise "populations that coexist" to "species that co-occur" (big difference between population and species levels and between coexistence and co-occurrence).*

Thank you very much for pointing this out, we have made the suggested change (Line 507).

> *Comment:*
>
> *(16) L359-365: are the winners and losers depicted in Figures S5 & S6? If so reference the figure (which I suggest combining and promoting to the main text), if not create a table listing the analyzed species and their winner/loser status.*

We agree that this is an excellent place to bring up Figures S5 and S6 from the supplemental. We have moved them to the main document as one figure and referenced it at line 510.

> ***Reviewer #2 (Recommendations for the authors):***
>
> *Comment:*
>
> *(1) Line 53-55: The claim that "These relationships generalize poorly taxonomically and geographically" is valid, but the study only tests Odonata on two continents.*

Thank you for this comment – the word 'generalize' may imply that our study tries to find a general pattern across many groups. We have changed the language to: "However, these relationships are inconsistent across taxa and regions, and cross-continental tests have not been attempted (Angert et al., 2011; Buckley and Kingsolver, 2012; Estrada et al., 2016; MacLean and Beissinger, 2017)." (Lines 57-59).

> *Comment:*
>
> *(2) Line 58-59: Is this statement only true for Odonata? It does not seem to hold for plants, for example.*

Thank you for this comment – this statement references a meta-analysis of multiple animal and plant taxa, but the evidence for the importance of range location comes from animal taxa. We have specified that we are referring to animal species to clarify (Line 60).

> *Comment:*
>
> *(3) Line 87-91: This section is difficult to understand and needs clarification.*

We have clarified this section as follows: “While warm-adapted species with more equatorial distributions could expand their ranges poleward following warming (Devictor et al., 2008), they could also increase in abundance in this new range area relative to species that historically occupied those areas and are less heat-tolerant (Powney et al., 2015).” (Lines 95-121).

> *Comment:*
>
> *(4) Line 99-100: Please define "generalist" and "specialist" more clearly here (e.g., based on climate niche?).*

Thank you for pointing this out, we intended to suggest that species with more generalist habitat requirements might be better able to shift, but ultimately found that traits did not predict species’ shifts. We corrected our prediction regarding habitat generalists as follows: “We predicted that species able to use both lentic and lotic habitats would shift their phenologies and geographies more than those able to use just one habitat type, as generalists outperform specialists as climate and land uses change (Ball-Damerow et al., 2015, 2014; Hassall and Thompson, 2008; Powney et al., 2015; Rapacciuolo et al., 2017).” (Lines 128-132).

> *Comment:*
>
> *(5) Line 122: Replace the English letter "X" in "100x100 km" with the correct mathematical symbol.*

We have made the suggested replacement throughout the manuscript.

> *Comment:*
>
> *(6) Line 148: To address sampling effects, you could check the paper: https://onlinelibrary.wiley.com/doi/full/10.1111/gcb.15524. Additionally, maximum and minimum values are sensitive to extreme data points, so using 95% percentiles might be more robust.*

Thank you for sharing this paper, as it offers a valuable perspective on the study of species’ ranges. While our dataset is substantially composed of observations from adult sampling protocols, unlike the suggested paper which compares adults and juveniles, this is an interesting alternative approach.

For our purposes it is meaningful to include outliers, as otherwise we may have missed individuals at the leading edge of range expansions. Our intent here was to detect range limits, as opposed to finding the central tendency of species distributions. This approach is widely accepted in the macroecology literature (i.e. Devictor et al., 2012, 2008; Kerr et al. 2015).

We have included the following discussion of our approach in the methods section:

“We followed widely accepted methods to determine species range boundaries (Devictor et al., 2012, 2008; Kerr et al., 2015), although other methods exist that are appropriate for different data types and research questions i.e. (Ni and Vellend, 2021). We assigned species presences to 100×100 km quadrats, a scale that is large enough to maintain adequate sampling intensity but still relevant to conservation and policy (Soroye et al., 2020), to identify the best sampled species.” (Lines 168-173).

Kerr JT, Pindar A, Galpern P, Packer L, Potts SG, Roberts SM, Rasmont P, Schweiger O, Colla SR, Richardson LL,Wagner DL, Gall LF, Sikes DS, Pantoja A. 2015. Climate change impacts on bumblebees converge across continents. Science 349:177–180. doi:10.1126/science.aaa7031

Soroye P, Newbold T, Kerr J. 2020. Climate change contributes to widespread declines among bumble bees across continents. Science 367:685–688. doi:10.1126/science.aax8591

Devictor V, Julliard R, Couvet D, Jiguet F. 2008. Birds are tracking climate warming, but not fast enough.Proceedings of the Royal Society B: Biological Sciences 275:2743–2748. doi:10.1098/rspb.2008.0878

Devictor V, van Swaay C, Brereton T, Brotons L, Chamberlain D, Heliölä J, Herrando S, Julliard R, Kuussaari M,Lindström Å, Reif J, Roy DB, Schweiger O, Settele J, Stefanescu C, Van Strien A, Van Turnhout C,

Vermouzek Z, WallisDeVries M, Wynhoff I, Jiguet F. 2012. Differences in the climatic debts of birds and butterflies at a continental scale. Nature Clim Change 2:121–124. doi:10.1038/nclimate1347

> *Comment:*
>
> *(7) Line 195: The species' climate niche should also be considered a product of evolution.*

Thank you for this suggestion. To address this comment and a comment from another reviewer, we changed the text to the following: “Geographic range and associated climatic characteristics are often considered ecological traits, as they are consequences of functional traits and their interactions with geographic features (Bried and Rocha-Ortega, 2023; Chichorro et al., 2019).” (Lines 256-259).

> *Comment:*
>
> *(8) Line 244: This speculative statement belongs in the Discussion section.*

Thank you for this suggestion, we have moved this statement to the discussion (Lines 451-453).

> *Comment:*
>
> *(9) Line 252-254: The projection of Coenagrion mercuriale's range contraction is not part of your results and should be clarified or removed.*

Following this suggestion and a similar suggestion from another reviewer, we moved this text to the discussion (Line 517-527).

> *Comment:*
>
> *(10) Line 314-316: If the species can tolerate warmer temperatures better, why would they migrate?*

We apologize for the confusion, and we have reworded the section as follows: “Emerging mean conditions in areas adjacent to the ranges of southern species may offer opportunities for range expansions of these relative climate specialists, which can then tolerate climate warming in areas of range expansion better than more cool-adapted historical occupants (Day et al., 2018).” (Lines 445-448).

> *Comment:*

> *(11) Line 334-335: Species' tolerance to temperature likely depends on their traits, which were not tested in this study. This should be noted.*

We agree, and we have removed the wording “rather than traits” from this sentence (Line 479).

> ***Reviewer #3 (Recommendations for the authors):***
>
> *Comment:*
>
> *(1) Title: The title is too general not specifying that your results are on odonates only, but also stressing the implicit role of climate change to a degree the tests do not support.*

Following this comment and a suggestion from another reviewer we changed the title to the following: “Range geography and temperature variability explain cross-continental convergence in range and phenology shifts in a model insect taxon”. We wanted to emphasize our use of Odonates as a model species that we used to ask broad questions, while being more specific about the climatic variable that we examined (temperature variability).

> *Comment:*
>
> *(2) L32: consider including Novella-Fernandez et al. 2023 (NatCommun) which addresses this topic in Odonates.*

Thank you for suggesting this very interesting paper, we have added it as a citation (Line 31-32).

> *Comment:*
>
> *(3) L35: consider including Grewe et al. 2013 (GEB) and Engelhardt et al. 2022(GCB).*

Thank you for these excellent suggestions, we have added the citations (Line 35).

> *Comment:*
>
> *(4) L47: rather write 'result from' instead of 'driven by'.*

We agree this is a better characterization and have corrected the wording (Line 48-49).

> *Comment:*
>
> *(5) L49-52: There has been a recent study on this topic for birds (Neate-Clegg et al., 2024 NEE). However, specifying this to insects would make it not less relevant. This review for odonates might be helpful in this regard (Pinkert et al.. 2022, Chapter: "Odonata as focal taxa for biological responses to climate change" IN Dragonflies & Damselflies: Córdoba-Aguilar et al. (2022) Model Organisms for Ecological and Evolutionary Research.*

Thank you for again suggesting excellent references, we have added them to line 52-53, as well as adding the Pinkert citation to lines 61 and 82.

> *Comment:*
>
> *(6) L53-66: Combine into one paragraph about drivers. With traits first and the environment second. The natural land cover perspective may be too complicated in this context. Consider focusing on generalities of the impact of changes within species' ranges.*

As suggested we have combined these into one paragraph about drivers (Line 59).

> *Comment:*
>
> *(7) L67-69: The book from before would be a much stronger reference for this claim. Kalkmann et al (2018) do not address the emphasis of global change research in insects on bees and butterflies. Also, I would highlight that most of the current work is at a national scale, rather than cross-continental.*

Thank you for this suggestion, we have added the suggested reference and included that "… recently assembled databases of odonate observations provide a rare opportunity to investigate species' spatiotemporal responses at larger taxonomic and spatial scales, particularly as most work has been done at national scales." (Lines 75-77).

> *Comment:*
>
> *(8) L68: consider rephrasing this part to '..provide a rare opportunity to investigate spatiotemporal biotic responses at larger taxonomic and spatial scales'*

We appreciate this suggestion and really like the wording. We have changed the phrase to read as follows: "While global change research on insects often emphasizes butterfly and bee taxa, recently assembled databases of odonate observations provide a rare opportunity to investigate species' spatiotemporal responses at larger taxonomic and spatial scales, particularly as most work has been done at national scales." (Lines 74-77).

> *Comment:*
>
> *(9) L69: This characteristic is not unique to odonates and would hamper drawing general conclusions. Honestly, I think the detailed and comprehensive data on them is the selling point.*

Thank you for this suggestion, we have edited the sentence to emphasize their use as an indicator species: "Due to their use of aquatic and terrestrial habitat across life different stages, dragonflies and damselflies are also considered indicator species for both terrestrial and aquatic insect responses to changing climates (Hassall, 2015; Pinkert et al., 2022; Šigutová et al., 2025), giving the study of these species broad relevance for conservation." (Lines 78-81)

> *Comment:*
>
> *(10) L73: Indicator for what? The first part of the sentence would suggest lesser surrogacy for responses of other taxa. Reconsider this statement. They are well- established indicators for habitat intactness and freshwater biodiversity. Darwell et al. suggested their diversity can serve as a surrogate for the diversity of both terrestrial and aquatic taxa.*

Thank you for this suggestion, we have edited the sentence to emphasize their use as an indicator species: "Due to their use of aquatic and terrestrial habitat across life different stages, dragonflies and damselflies are also considered indicator species for both terrestrial and aquatic insect responses to changing climates (Hassall, 2015; Pinkert et al., 2022; Šigutová et al., 2025), giving the study of these species broad relevance for conservation." (Lines 78-81)

> *Comment:*
>
> *(11) L76: Fritz et al., is a study on mammals, not odonates.*

Thank you for pointing out this error, the reference has been removed (Line 84-85).

> *Comment:*
>
> *(12) L84: Lotic habitats are generally better connected than lentic ones. Lentic species are considered to have a greater propensity for dispersal DUE to the lower inherent spatiotemporal stability (implying lower connectivity) compared to lotic habitats.*

Thank you for your comment, we have rewritten this section as follows: "For example, differences in habitat connectivity and dispersal ability may constrain range shifts for lentic species (those species that breed in slow moving water like lakes or ponds) and lotic species (those living in fast moving-water) in different ways (Kalkman et al., 2018). More southerly lentic species may expand their range boundaries more than lotic species, as species accustomed to ephemeral lentic habitats better dispersers (Grewe et al., 2013), yet lotic species have also been found to expand their ranges more often than lentic species, potentially due to the loss of lentic habitat in some areas (Bowler et al., 2021)." (Lines 88-95).

> *Comment:*
>
> *(13) L90: I would be cautious with this interpretation. If only part of the range is considered (here a country in the northern Hemisphere) southern species are moving more of their range into and northern species more of their range out of the study area in response to warming (implying northward shifts).*

We have clarified this section as follows: "While warm-adapted species with more equatorial distributions could expand their ranges poleward following warming (Devictor et al., 2008), they could also increase in abundance in this new range area relative to species that historically occupied those areas and are less heat-tolerant (Powney et al., 2015)." (Lines 95-121)

> *Comment:*
>
> *(14) L117: Odonata Central contains many county centroids as occurrence records. These could be an issue for your use case. I may have overlooked the steps you took to address this, but I think this requires at least more detail and possibly further removal/checks using for instance CoordinateCleaner. The functions implemented in this package allow you to filter records based on political units to avoid exactly this source of error.*

Thank you for this suggestion, we weren't aware of this issue with Odonata Central. We used the CoordinaterCleaner tool in R to filter all odonate records that we used in our analyses. Less than 1% of observations in our dataset were identified as having potential problems by the tool, so we would not expect this to affect our inferences. However, in future we will employ this tool when using similar datasets.

> *Comment:*
>
> *(15) L119: Please add a brief explanation of why this was necessary. I am ok with something along the lines in the supplement.*

We moved this information from the supplemental to the main text as follows: "If a species was found on both continents, we only retained observations from the continent that was the most densely sampled. If we merged data for one species found on both continents, we could not perform a cross-continental comparison. However, if the same species on different continents was treated as different species, this would lead to uninterpretable outcomes (and the creation of pseudo-replication) in the context of phylogenetic analyses. In addition,

species found on both continents did not have sufficient data to meet criteria for the phenology analysis." (Lines 161-167).

> *Comment:*
>
> *(16) L132: This is the letters 'X' or 'x' are not multiplier symbols! Please change to the math symbol (×), everywhere.*

Thank you for pointing out this error, we have made the correction throughout the manuscript.

> *Comment:*
>
> *(17) L133: add 'main' before 'flight period'*

Thank you for this suggestion, we have made the change. (Line 190)

> *Comment:*
>
> *(18) L135: I suggest using the coefficient of variation, as it is controlled for the mean. Otherwise, what you see is partly the signature of temperature and not of its variation. For me, it's very difficult to understand what this variation of the variation means and at least needs more explanation.*

Thank you very much for this suggestion, we agree that using the coefficient of variation is a better fit for the question that we're asking. We re-ran out analyses with the coefficient of variation as the measure of climate variability: all the results reported in the manuscript are now updated for that analysis (Line 377, Table 2), and we have also updated the methods section (Line 191). The results are qualitatively the same to our previous analysis, but we agree that they are now easier to interpret.

> *Comment:*
>
> *(19) L155: Please adequately reference all R packages (state the name, and a reference for them including the authors' names, title, and version).*

Thank you for pointing out this omission, we have added reference information for the glm function in base R (Line 298) and ensured all other packages are properly referenced.

> *Comment:*
>
> *(20) L207: Mention the literature sources here (again).*

We agree that they should be referenced here again, and we have done so (Lines 267-268).

> *Comment:*
>
> *(21) L209: You could use the number of grid cells as a proxy for range size.*

Following this excellent suggestion, we re-analysed our data using range size, calculated as the number of quadrats occupied by a species in the historical time period, as a predictor. Range size was not significant in our models, but we believe this is the best way to analyze our data, and so have updated our methods (Lines 261-263) and results (375-378).

> *Comment:*

> *(22) L218: It would be preferable to say 'species-level' instead of 'by-species'.*

Thank you for this suggestion, we agree that this is clearer and made the change (Line 298).

> *Comment:*
>
> *(23) L219-220: this is unclear. Please rephrase.*

We have clarified as follows: “We used both species-level frequentist (GLM; glm function in R) and Bayesian (Markov Chain Monte Carlo generalized linear mixed model, MCMCglmm; Hadfield, 2010) models to improve the robustness of the results.” (Lines 298-300).

> *Comment:*
>
> *(24) L224: At least for Europe there is a molecular phylogeny available, which you should preferably use (Pinkert et al. 2018, Ecography). Otherwise, I am ok with using what is available*

We apologize that the nature of the phylogeny that we used was not clear; the phylogeny that we used was built similarly to that in Pinkert et al. 2018, Ecography. It created a molecular phylogeny with a morphological/taxonomic tree as the backbone tree, so that species could only move within their named genera or families. We clarified this in the manuscript as follows:

“We used the molecular phylogenetic tree published by the Odonate Phenotypic Database (Waller et al., 2019), which used a morphological and taxonomic phylogeny as the backbone tree, allowing species to move within their named genera or families according to molecular evidence (Waller and Svensson, 2017).” (Lines 302-305).

> *Comment:*
>
> *(25) L233: You said so earlier (1st sentence of this paragraph).*

Thank you for pointing this out, we removed the repetitive sentence (Line 323).

> *Comment:*
>
> *(26) L236-238: To me, it makes more sense to test this prior to fitting the phylogenetic models.*

MCMC-GLMM is considerably less familiar to most researchers than general linear models or there derivatives/descendants, such as PGLS. We report models both with and without phylogenetic relationships included for the sake of transparency, and we are happy to acknowledge that no interpretation here changes substantially relative to these decisions. However, failing to report models that included possible (if small) effects of phylogenetic relatedness might cause some readers to question what those models might have implied. For the moment, we are opting for the most transparent reporting approach here.

> *Comment:*
>
> *(27) L241: Rather say directly XX of XX species in our data....*
>
> *(28) L245: Same here. Provide the actual numbers, please.*

Thank you for this suggestion, we made this change on Line 332 and Line 334.

> *Comment:*
>
> *(29) L247-249: Then not necessary.*

This issue highlights a challenge in the global biology literature and around the issue of biodiversity monitoring for understanding global change impacts on species. Almost no studies have been able to report simultaneous range and phenology shifts, and the literature addresses these biotic responses to global change predominantly as distinct phenomena. Differences in numbers of species for which these observations exist, even among the extremely widely-observed odonates, seems to us to be a meaningful issue to report on. If the reviewer prefers that we abbreviate or remove this sentence, we are happy to do so.

> *Comment:*
>
> *(30) L251:261: That is discussion as you interpret your results.*

Following your suggestion and the suggestion of another reviewer, we moved the following lines to the discussion section: “Species that did not shift their ranges northwards or advance their phenology included Coenagrion mercuriale, a European species that is listed as near threatened by the IUCN Red List (IUCN, 2021), and is projected to lose 68% of its range by 2035 (Jaeschke et al., 2013).” (Lines 517-527).

> *Comment:*
>
> *(31) 252: Good to mention, but why is the discussion limited to C. mercurial?*

We feel that it is important to link the broad-scale results to the specific biological characteristics of individual species, and C. mercurial is an IUCN threatened species. We are happy to expand links to natural history of this group and have added the following: “This group also includes Coenagrion resolutum, a common North American damselfly (Swaegers et al., 2014), for which we could not find evidence of decline. This may be due in part to the greater area of intact habitat available in North American compared to Europe, enabling C. resolutum to maintain larger populations that are less vulnerable to stochastic climate events. Still, this and other species failing to shift in range or phenology should be assessed for population health, as this species could be carrying an unobserved extinction debt.” (Lines 527-533).

> *Comment:*
>
> *(32) L264: Insert 'being' before 'consistently'.*

Thank you for the suggestion, we made this change (Line 373).

> *Comment:*
>
> *(33) L271: .'. However,'.*

Thank you for pointing out this grammatical error, we have corrected it (Line 382).

> *Comment:*
>
> *(34) L273: 'affected' instead of 'predicted'*

Thank you for the suggestion, we made this change (Line 383).

> *Comment:*
>
> *(35) L279: 'despite pronounced recent warming' sounds not relevant in this context.*

Thank you for this suggestion, we removed this portion of the sentence (Line 408).

> *Comment:*
>
> *(36) L281: Rather 'the model performance did not improve....'*

Thank you for the suggestion, we made this change (Line 409).

> *Comment:*
>
> *(37) L288: Add 'but' before 'not'.*

Thank you for the suggestion, we made this change (Line 416).

> *Comment:*
>
> *(38) L311-316: Reconsider the causality here. maybe rather rephrase to are associated instead. Greater dispersal ability and developmental plasticity might well lead to higher growth rates, rather than the other way around.*

We agree that plasticity/evolution at range edges is important to consider and have included it as an alternative explanation: “Adaptive evolution and plasticity may enable higher population growth rates in newly-colonized areas (Angert et al., 2020; Usui et al., 2023), but this possibility can only be directly tested with long term population trend data.” (Line 449-451).

> *Comment:*
>
> *(39) L313-316: Maybe delete the second 'should be able to'.*

This phrase has been changed in response to other reviewer comments and now reads as follows:

“Emerging mean conditions in areas adjacent to the ranges of southern species may offer opportunities for range expansions of these relative climate specialists, which can then tolerate climate warming in areas of range expansion better than more cool-adapted historical occupants (Day et al., 2018).” (Lines 445-448).

> *Comment:*
>
> *(40) L331: Limit this statement ending with 'in North American and European Odonata'.*

Thank you for this suggestion, we made this addition (Lines 475-476).

> *Comment:*
>
> *(41) L346-347: There are too many of these more-research-is-needed statements in the discussion (at least three in the last paragraphs). Please consider finishing the paragraphs rather with a significance statement.*

Thank you for this suggestion, we have changed the final sentence here to the following: “The extent to which species’ traits actually determine rates of range and phenological shifts,

rather than occasionally correlated with them, is worth considering further, but functional traits do not systematically drive patterns in these shifts among Odonates in North America and Europe." (Lines 480-483).

We also made additional changes, removing a 'more-research is needed' statement from the following paragraph (Line 443), as well as from line 499.

> *Comment:*
>
> *(42) L349: See also Franke et al. (2022, Ecology and Evolution).*

Thank you for highlighting this excellent reference! We have added it to Line 501.

> *Comment:*
>
> *(43) L363: Maybe a bit late in the text, but it is important to note that there is the third dimension 'abundance trends' or rather a common factor related to range and phenology shifts. I feel this fits better with the discussion of population growth.*

Thank you for this suggestion, we have addressed the importance of abundance trends in the following sentences: "Further mechanistic understanding of these processes requires abundance data." (Lines 442-443); "It remains unclear if range and phenology shifts relate to trends in abundance, but our results suggest that there are clear 'winners' and 'losers' under climate change." (Lines 509-510).

> *Comment:*
>
> *(44) L375-377: This last sentence is very similar to L371-373. Please reduce the redundancy. Focus more on specifically stating the process instead of vaguely saying 'new insights into patterns' and 'suggesting processes'. Rather, deliver a strong concluding message here.*

Thank you for this suggestion, we feel that we now have a much stronger concluding message: "By considering both the seasonal and range dynamics of species, emergent and convergent climate change responses across continents become clear for this well-studied group of predatory insects." (Lines 545-547).

> *Comment:*
>
> *(45) Table 1: To me, the few estimates presented here do not justify a table. rather include them in the text. OR combine them with Table 2. Also, why not include the traits as predictors (from the range shift models) in these models as well?*

We have clarified in the text that the results displayed in Table 1 are from the analysis of the relationship between range and phenology shifts: "The effect of species' range shifts on phenology range shifts was significant in our model investigating the relationship between these responses, indicating that species shifting their northern range limits to higher latitudes also showed stronger advances in their emergence phenology (Figure 3)." (Lines 341-344).

As there were no significant effects in the model of phenology change drivers, we have not shown results of this model: "Emergence phenology shifts were not affected by species' traits, range geography, nor climate variability; due to this, model results are not displayed here." (Lines 383-384).

> *Comment:*

> *(46) Table 2: L712-713: What does this mean? Are phenology shifts not used as a predictor of range shifts? (why then this comment?). Or do you want to say phenological shifts are not related to Southern range etc? Why do you present a phylosig here but not in Table 1? Why not include the traits as predictors (from the range shift models) in these models as well? Consider using the range size as a continuous predictor instead of 'Widespread'.*

We are glad the reviewer pointed this out to us. We did not emphasize this issue sufficiently. We DID evaluate traits as predictors both of geographical range and phenological shifts, and species-specific biological traits did not significantly affect models predicting either of those sets of responses. We state this on Lines 312-323, but we have also noted in the discussion (Lines 473-476) that the most commonly assessed traits, like body size, do not alter observed trends here. Instead, where species are found, rather than the characteristics of species, is the key determinant of their overall responses.

Following this excellent suggestion, we re-analysed our data using range size, calculated as the number of quadrats occupied by a species in the historical time period, as a predictor. Range size was not significant in our models, but we believe this is the best way to analyze our data, and so have updated our methods (Lines 261-263) and results (375-378).

> *Comment:*
>
> *(47) Figure 1: I don't see any grey points in the figure. Also, there is no A or B. If you are referring to the symbols then write cross and triangle instead and not use capital letters which usually refer to component plots of composite figures. Also, I highly recommend providing a similar figure based on your data (maybe each species as a dot for T1 and another symbol for T2). Given the small number of species, you could try to connect these points with arrows. For the set with only range shifts maybe play the T2-dots at the center of the 'Emergence' axis.*

Thank you for pointing out this error: a previous version of Figure 1 included grey points and multiple panels. We have removed this text from the figure caption to be consistent with the final version of the figure (Line 989).

The graphical depictions of the conceptual and empirical discoveries in this paper were challenging to create. The reviewer might be suggesting effectively decomposing Figure 3 (change in range on the y axis vs change in phenology among all species into two sets of points on the same graph, where each pair of points is a before and after value for each species. This would make for a very busy figure indeed. We have modified the conceptual Figure 1 to illustrate more clearly, we believe, that species can (in principle) remain within tolerable niche spaces by shifting their activity periods in time (phenology) or in space (geographical range) or both.

> *Comment:*
>
> *(48) Figure 2: Please add a legend. Also black is a poor background color. The maps appear to be stretched. Please check aspect ratios. Now here are capital letters without an explanation in the caption. From the context I assume the upper panel maps are for the data used to calculate range shifts at the bottom panel maps are for data used to calculate the phenological shifts.*

We apologise for the error in the figure caption and have clarified the differences between panels in the text, as well as changing the map background colour and fixing the aspect ratio:

"Figure 2: Richness of 76 odonate species sampled in North America and Europe in the historic period (1980-2002; panes A and C) and the recent period (2008-2018; panes B and D). Species richness per 100 × 100 km quadrat is shown in panes A and B, while panes C and D show species richness per 200 × 200 km quadrat. Dark red indicates high species richness, while light pink indicates low species richness." (Lines 1002-1006).

> *Comment:*
>
> *(49) Figure 3: Why this citation? Of terrestrial taxa? Please explain. Consider adding some stats here, such as the r-squared value for each of the relationships.*

We have better explained the citation in the figure caption, as well as adding r-squared values:

"Figure 3: Relationship between range shifts and emergence phenology shifts among North American and European odonate species (N = 66; model R2 = 17.08 for glm, 14.9% for MCMCglmm). For reference, the shaded area shows mean latitudinal range shifts of terrestrial taxa as reported by Lenoir et al. (2020; calculated as the yearly mean dispersal rate of 1.11 +/- 0.96 km per year over 38 years)." (Lines 679-682)

> *Comment:*
>
> *(50) L801: What are these underscored references?*

This was an issue with the reference software and has been resolved.

> *Comment:*
>
> *(51) Table S1: L848: Consider starting with 'Samples of 76 North American and European odonate species from between ...'. Please use a horizontal line to separate the content from the table header. Add a horizontal line below the last row. Same for all tables.*

Thank you for this suggestion, we have edited the caption for Figure S1 as suggested (Line 1124). We have also made the suggested line additions to Table S1, S2, and S3.

> *Comment:*
>
> *(52) Table S3: This is confusing. In Table 1 (main text) both 'southern range' and 'widespread' are used as predictors. Please explain.*

We originally included information on species range geography, including southern versus northern range, and widespread versus not, into one categorical variable. Following additional comments we re-analysed our data using range size, calculated as the number of quadrats occupied by a species in the historical time period, as a predictor. Now the methods section text (Lines 261-263) and Table 1 report results of that variable with distribution options northern, southern, or both.

> *Comment:*
>
> *(53) Figure S5 and S6: It would be more coherent if the colors refer to the continents and the suborders are indicated by shading. I would love to see a combination of the two figures with species ordered by the phylogenetic relationship and a dot matrix indicating the traits in the main text! This could really be a good starting point for a synthesis figure.*

The reviewer presents an interesting challenge for us. We have a choice, as we understand things, to present a figure showing phylogeny and traits (as requested here), or an ordered list of species relative to effect sizes in the two main responses to global change. The latter choice centers on the discoveries of the paper, while the former would be valuable for dragonfly biology but would depict information that proved to be biologically uninformative relative to our discovery. That is to say, there is no phylogenetic trend and biological traits among species did not affect results. We have gone some way toward illustrating that issue by retaining phylogeny in the MCMC-GLMM models, but we feel that a figure illustrating phylogeny and traits would (for most readers, at least) illustrate noise, rather than signal. For this reason, we have opted to take on the previous reviewer's suggestion for a modified, main-text Figure 4, which we include below.

Figure 4: Distribution of Northern range limit shifts (Panel A, kilometers) and emergence phenology shift (Panel B, Julian day) of 76 European and North American odonate species between a recent time period (2008 - 2018) and a historical time period (1980 - 2002). Anisoptera (dragonflies) are shown in pink, Zygoptera (damselflies) are shown in blue.

Change last: Figure 3: Relationship between range shifts and emergence phenology shifts among North American and European odonate species (N = 66; model R2 = 17.08 for glm, 14.9% for MCMCglmm). For reference, the shaded area shows mean latitudinal range shifts of terrestrial taxa as reported by Lenoir et al. (2020; calculated as the yearly mean dispersal rate of 1.11 +/- 0.96 km per year over 38 years).

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