Ecology

Range geographies, not functional traits, explain convergent range and phenology shifts under climate change

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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.

eLife Assessment

This article presents **valuable** 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 combined analysis of temporal trends in phenology and distribution and their potential drivers. The support for the findings is **solid**, though additional clarification regarding the methods and alternative sensitivity analyses would strengthen the conclusions.

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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; 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 (**Figure 1**; Chen et al., 2011; 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 be driven by 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 (Kerr et al., 2015; Stephens et al., 2016), but potential relationships between phenological and geographic responses have not yet been investigated at continental scales.

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 generalize poorly taxonomically and geographically, and cross-continental tests have not been attempted (Angert et al., 2011; Buckley and Kingsolver, 2012; Estrada et al., 2016; MacLean and Beissinger, 2017).

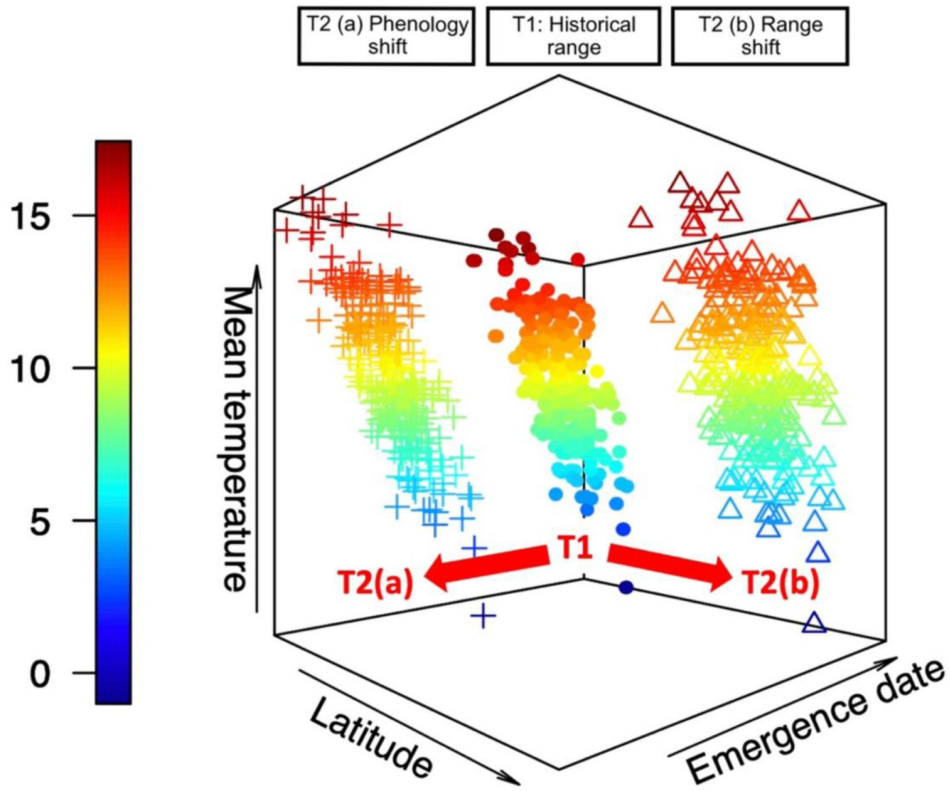


Figure 1

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. **(A)** Points represent historical observations, triangle symbols show observations following a shift towards higher latitudes, and plus signs show observations following a shift towards earlier emergence dates, necessary to maintain temperatures to which species were exposed historically, after temperatures warmed across the species' range. Warm and cool colors show hot and cold temperatures, respectively. **(B)** Grey points represent historical observations, and the colored points show observations after warming without allowing shifts through time or space. In this scenario, we assumed that the hottest temperature tolerated by the species corresponds to the hottest temperature experienced in its historical niche. In this case, individuals are exposed to hotter temperatures overall while declining in areas outside species' thermal tolerances after warming.

Geographic locations and environmental characteristics of species' ranges may also predict range shifts, as species with high latitude ranges have been shown to exhibit smaller range shifts (MacLean and Beissinger, 2017), 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 opportunities to answer new questions (Kalkman et al., 2018). Dragonflies and damselflies respond rapidly to climate change, both spatially (Ball-Damerow et al., 2015; Grewe et al., 2013; Hickling et al., 2005; Powney et al., 2015; Rapacciuolo et al., 2017; Sirois-Delisle and Kerr, 2022) and temporally (Hassall, 2015; Hassall et al., 2007; McCauley et al., 2018), making them an excellent indicator species (Hassall, 2015). 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; Fritz et al., 2009; Suhonen et al., 2022), and rates of decline and expansion within limited geographic scopes (Powney et al., 2015; Rapacciuolo et al., 2017). 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, lentic species (i.e. species breeding in slow moving water like lakes or ponds) tend to have larger ranges and higher dispersal capacities than lotic species (i.e. fast moving water-dwelling species), and may track their climate niches more closely (Grewe et al., 2013; Hof et al., 2006). Lotic habitat may be more difficult to reach, and lotic species may face stronger anthropogenic pressures in places where their diversity is high (Kalkman et al., 2018), affecting species abilities to track changes in climatic seasonal timing. Lentic species have been shown to expand their range boundaries more than lotic species, but only among species with more southern distributions (Grewe et al., 2013). Abundances of European odonates with ranges extending south from sample landscapes have been found to respond more positively to climate change than species with ranges extending north from sample locations, due to their geographic position and thermal tolerance (Powney et al., 2015). Species previously limited by tolerance to low temperatures could expand their ranges following warming (Devictor et al., 2008).

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 biological 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 generalist species would shift their phenologies and geographies, 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); in contrast, we expect specialists to fail to shift in both space and time, making them more vulnerable to extirpation and extinction. 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, 2010a; Zattara and Aizen, 2021a). 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. In the event that the same species was found in both Europe and North America, we selected records from the continent containing the largest number of observations (Supplementary Information).

We assigned species presences to 100 × 100 km quadrats 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 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).

Climate data

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 flight period for odonates in this study, for each year included in the historical and recent periods. We calculated the standard deviation 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

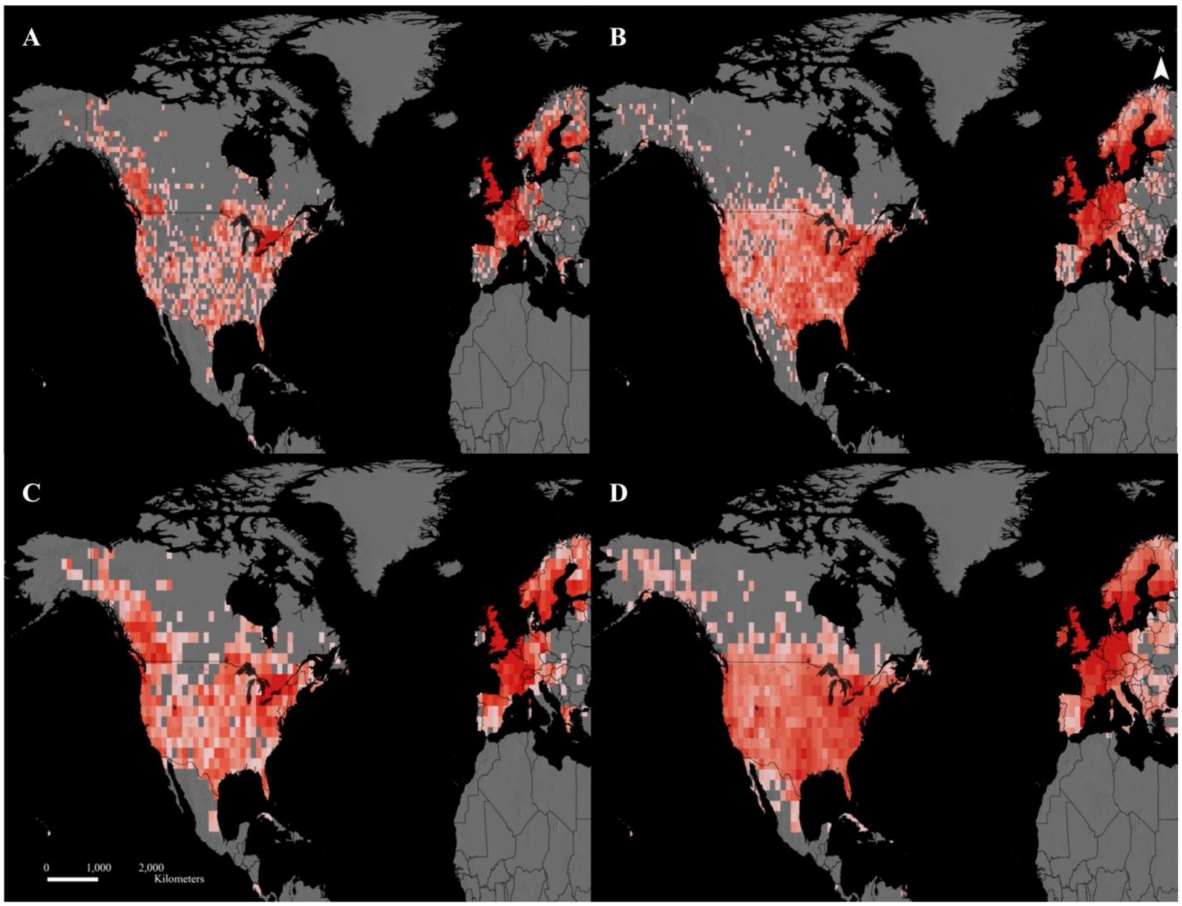


Figure 2

Richness of 76 odonate species sampled in North America and Europe between 1980 and 2018 per 100 × 100 km quadrat. Dark red indicates high species richness, while light pink indicates low species richness.

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) 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.

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 n^{th} first observations of phenological events, or the n^{th} 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 1^{st} and September 1^{st}, 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**).

Ecological traits

To assemble trait data for the 76 species in the database, we used field guides (R.A. Cannings, 2002; C.D. Jones et al., 2008; D. Paulson, 2012) and existing trait databases (G. D. Powney et al., 2014; Waller et al., 2019a). We considered any evolved morphological, physiological, behavioural, or life history characteristic as a trait (Beissinger and Riddell, 2021). Geographic or climatic characteristics (e.g. range size, geographic position of species' ranges, climatic conditions of the range) were not considered traits, as they are not products of evolution, but rather consequences of environmental, ecological, biogeographical, or evolutionary patterns linked to range shifting mechanisms (Beissinger and Riddell, 2021). Such variables may predict species' responses to climate change nonetheless, and can add significant value to predictive models (MacLean and Beissinger, 2017).

Along with two geographic and climatic attributes, including temperature variability and distribution region (northern, southern, or widespread), we selected four 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. 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. 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 nearly all 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. We used a by-species GLM and a Markov chain Monte Carlo generalized linear mixed model (MCMCglmm; Hadfield, 2010); we compared frequentist and Bayesian approaches 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 phylogenetic tree published by the Odonate Phenotypic Database (Waller et al., 2019a), which was generated using a combination of DNA-sequences and species' taxonomy based on morphology (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 biological 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. We included species traits, species range geography, and temperature variability experienced by species as predictor variables. 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 (69% of those included) 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 (**Figure S5**). Some species showed range retractions (i.e. *Libeullula luctuosa*); small range retractions may result from sampling variability or stochastic population fluctuations along the northern range edge. Most species (60% of assessed species) maintained or advanced their emergence phenology (mean of −2.71 days in emergence phenology shifts among all species;

Figure S6). 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. Species that did not respond to climate change temporally or spatially 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).

Species that shifted their northern range limits to higher latitudes also showed stronger advances in their emergence phenology (**Figure 3**), a result that was consistent in GLM and Bayesian analyses ($p < 0.05$; **Table 1**; R^2 = 17% and 15%, for GLM and MCMCglmm models, respectively). This trend converged across continents, and is consistent among both dragonflies and damselflies, although there is 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 (**Table 1**).

Drivers of range and phenology shifts

Range geography and climate variability, rather than ecological traits, predicted range shifts in both North America and Europe, with range geography consistently the strongest predictor. Species' ecological traits did not relate to the extent of observed phenological or 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 and widespread species ($p < 0.05$; **Table 2**; R^2 = 23% and 20%, for GLM and MCMCglmm models, respectively). Species experiencing smaller changes in interannual temperature variability also had a higher likelihood of northern range limit shifts ($p < 0.05$). Results from the GLM and MCMCglmm models were qualitatively similar, however a smaller amount of model variance was explained when phylogeny was accounted for. Neither range geography nor climate variability predicted emergence phenology shifts. Even though both 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**), despite pronounced recent warming. Adding a phylogeny term to the MCMCglmm models also failed to produce a pattern different to the GLMs, and model performance was not improved when accounting 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, not ecological 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.

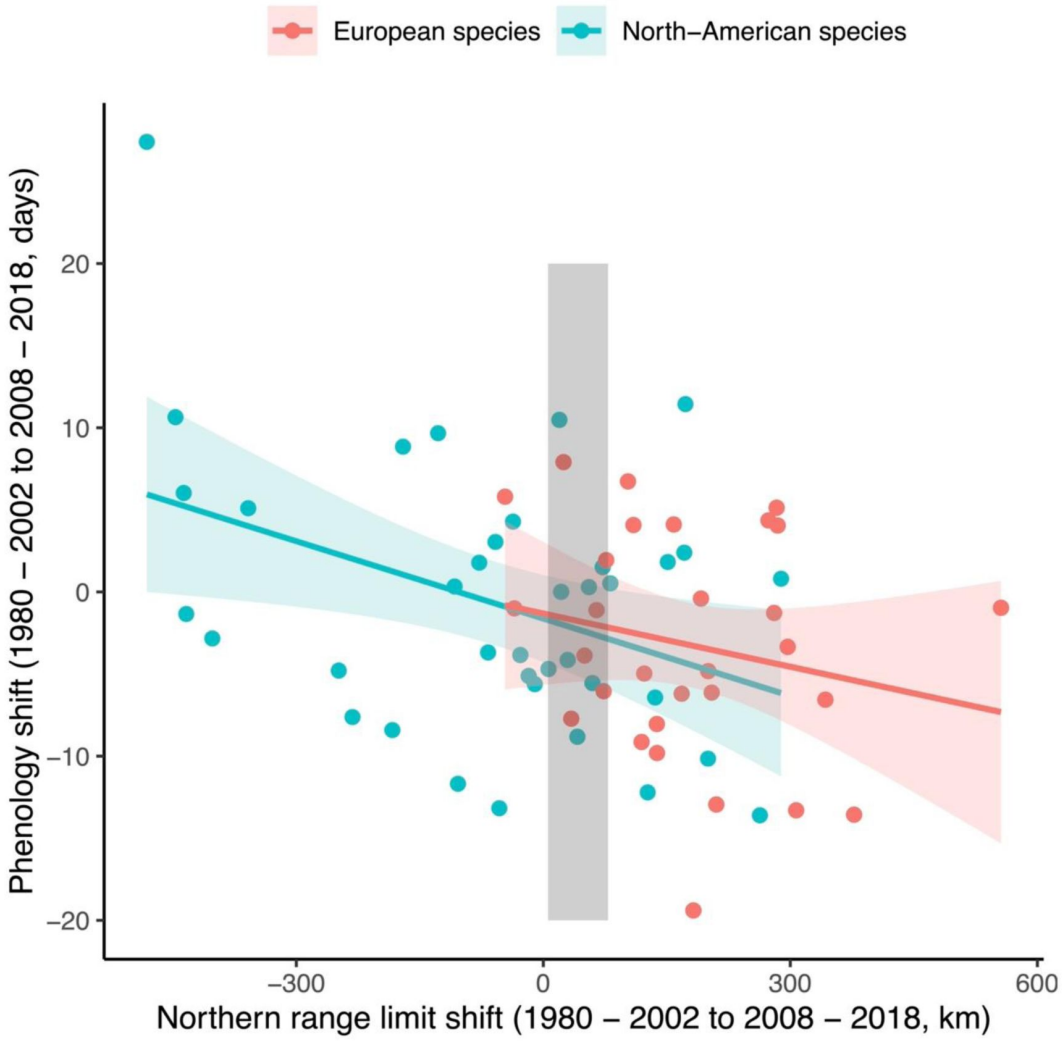


Figure 3

Relationship between range shifts and emergence phenology shifts among North American and European odonate species (N = 66). The shaded area shows mean latitudinal range shifts of terrestrial taxa (Lenoir et al., 2020), 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 S3**) 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 S3**) 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. Phenology shifts were unrelated to any of the predictor variables that we tested.

	Range shift (N = 76)			
	GLM		MCMCglmm	
Predictors	**Est.**	**p**	**Post.m**	**p**
(intercept)	-0.61	0.03*	-0.62	0.04*
Southern range	0.90	<0.01*	0.91	<0.01*
Widespread	0.32	0.34	0.32	0.36
T ° variability	-0.34	<0.01*	-0.34	<0.01*
Both hab. Types	-	-	-	-
Lentic habitat	-	-	-	-
Flight duration	-	-	-	-
Oviposition	-	-	-	-
Body size	-	-	-	-
Model evaluation				
AIC/DIC	208.99		209.08	
Null model	221.51		221.49	
Pseudo R^2	22.72%		20.18%	
Phylogenetic signal				
Pagel's lambda (p)	0.02 (0.63)			
Blomberg's K (p)	0.08 (0.77)			

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), 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 or widespread species. 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 necessary for range expansions (Mair et al., 2014). 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). As more southern species expand northwards they may be better able to tolerate local temperature extremes due to their warmer thermal niches, and should be better able to maintain populations than species with northern distributions (Day et al., 2018), facilitating further range shifts.

Increasing frequency and severity of extreme weather limited species' geographical range responses (**Table 2**). This trend was independent of 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 species' shifts. 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, rather than traits, also help predict extinction risk during climate change (Kerr, 2020). More work is needed to determine if traits consistently fail to predict range shifts, particularly at large spatial scales, although reliable observations at these scales are often lacking. Detailed mechanistic models that incorporate multiple independent processes may help untangle these patterns, although challenges with parameterization remain (Urban et al., 2022).

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). Tests of local adaptation in critical traits, like thermal tolerances among larval life stages, would be valuable.

Given that species' traits did not predict temporal or geographic responses, it is unsurprising that species' responses were also independent of phylogenetic history. 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 populations that coexist may experience divergent selection within their climate tolerances (Schuetz et al., 2019).

While more work is needed to determine if the range and phenology shifts reported here are associated with increases in species' abundances, our results suggest that there are clear 'winners' and 'losers' under climate change. 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). 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.

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. Simultaneous consideration of shifts in range and phenology is a powerful and necessary approach to measure species' apparent vulnerability to rapid global changes. 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. This study gives us new insight into patterns of range and phenology shifts, as well as suggesting processes behind the patterns, offering a valuable method of understanding species' vulnerability to change that should be explored in other taxa.

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).

If a species was found on both continents, we only kept observations from the continent that was the most densely sampled. This simplified analyses in terms of calculating range and phenology shifts. It would not be logical to perform a cross-continental comparison when data points for a single species exist in both places and are merged together to create a single measurement of

range shifts or location-specific measures of phenological change. This problem cannot be solved by treating species as different units because that leads to uninterpretable outcomes (and creation of pseudo-replication) in the context of phylogenetic analyses. Most importantly, it was not possible to calculate phenology shifts for both continents in these species because of the data intensity needed to make the calculations and the strict criteria we set for inclusion of species and quadrats in the analysis. Future work may focus on species found on both continents if the data and statistical analyses permit.

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

76 species sampled across North America and Europe 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 equator. 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 × 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)	-1.13	-0.07
Southern range	0.33	1.50
Widespread	-0.32	0.96
T ° variability	-0.53	-0.12
Both hab. Types	-	-
Lentic habitat	-	-
Flight duration	-	-
Oviposition	-	-
Body size	-	-

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.

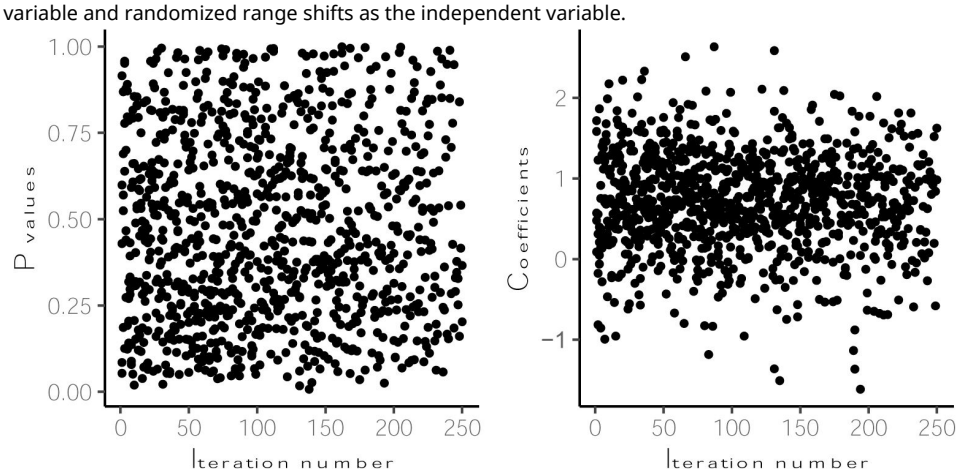


Figure S2

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.

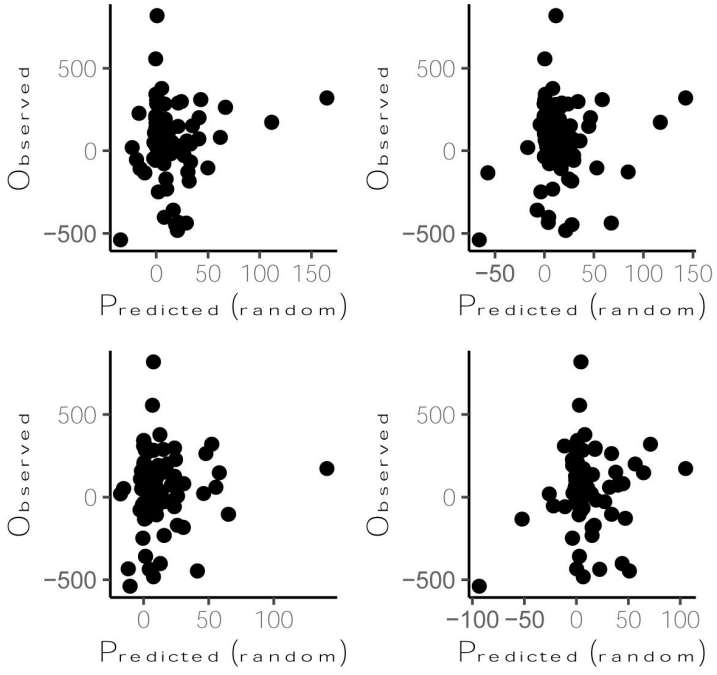


Figure S3

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.

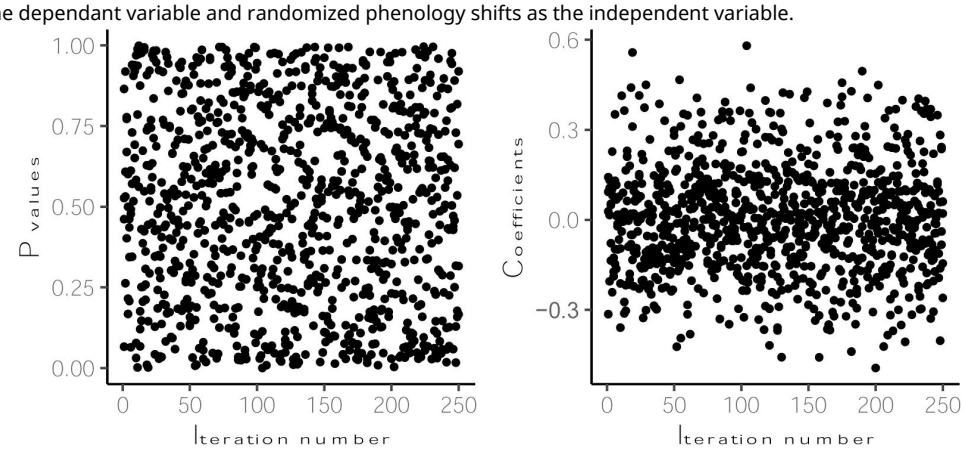
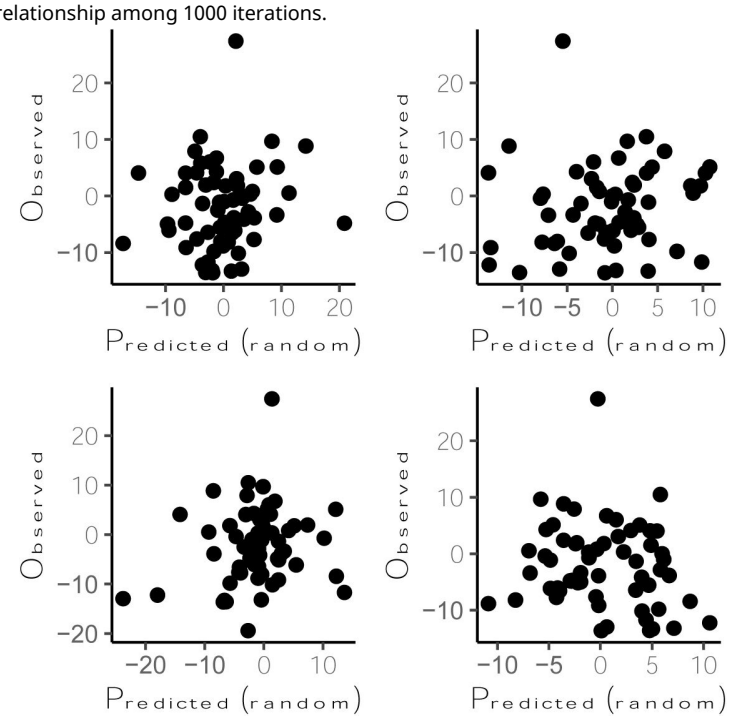


Figure S4

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.



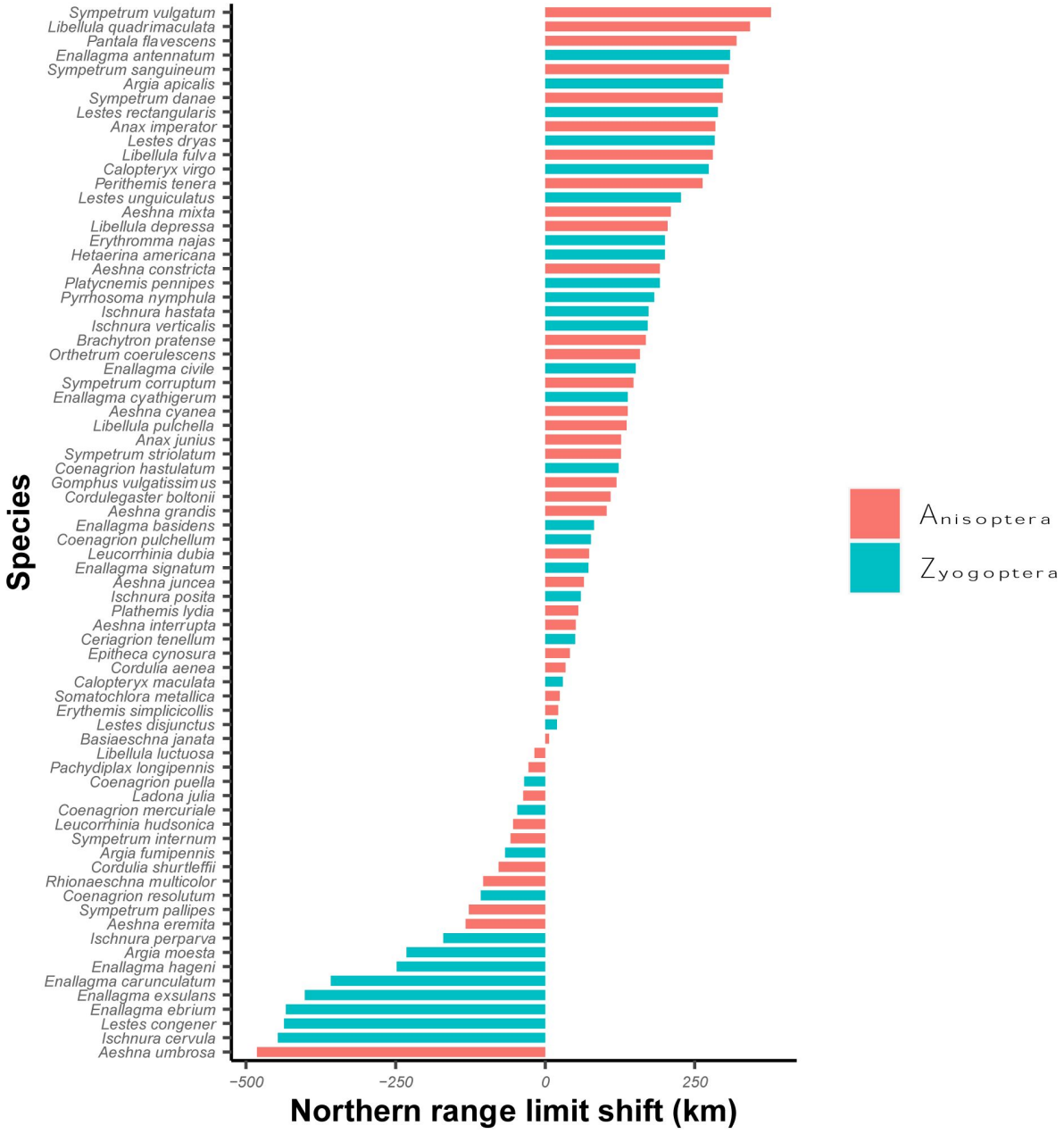


Figure S5

Distribution of values computed for range shifts of 76 European and North American species between a recent time period (2008 - 2018) and a historical time period (1980 - 2002). See Methods section of the main text for full details on data assembly, and steps undertaken to produce these preliminary results.

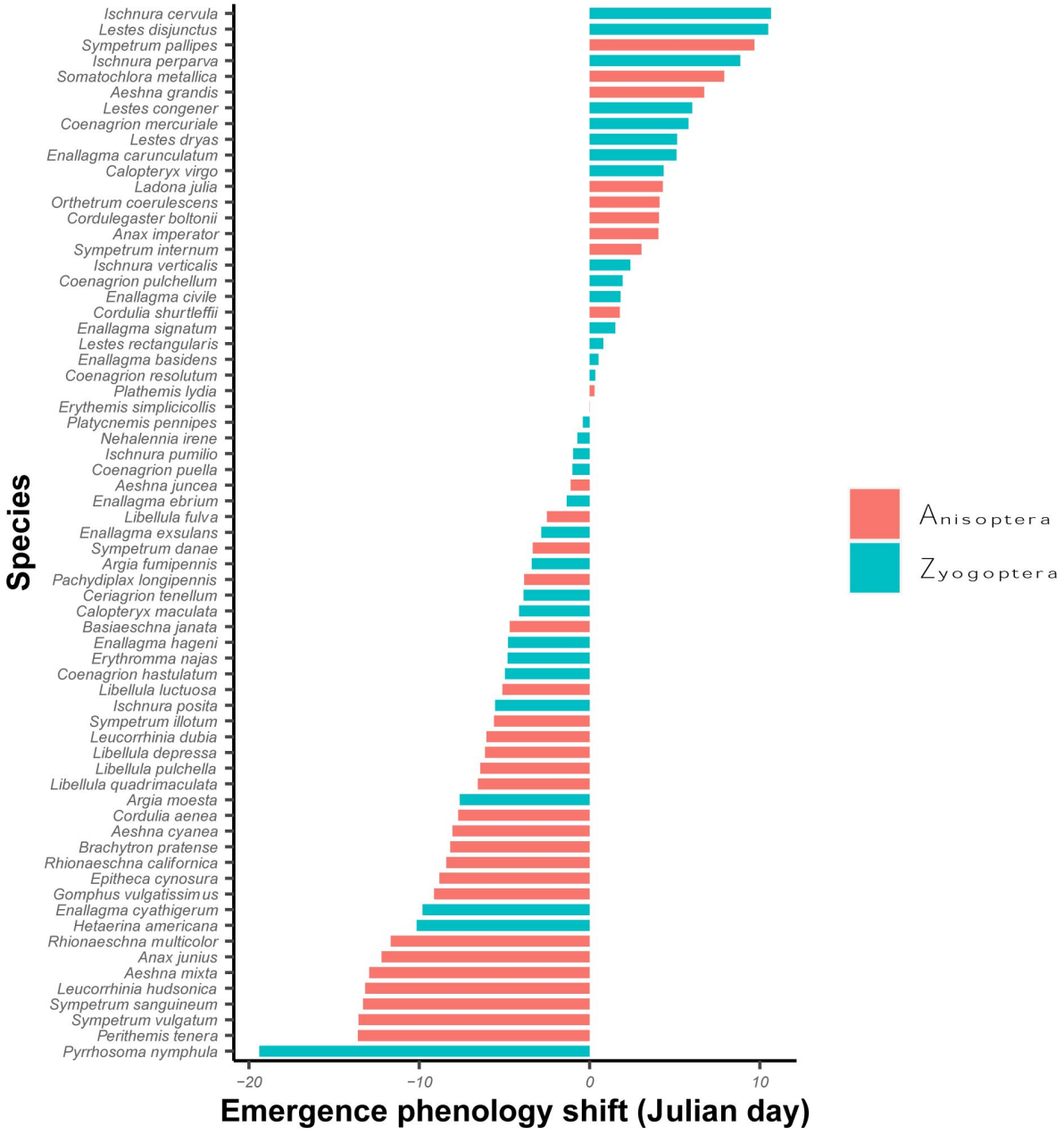


Figure S6

Distribution of values computed for phenology shifts of 66 European and North American species between a recent time period (2008 - 2018) and a historical time period (1980 - 2002). See Methods section of the main text for full details on data assembly, and steps undertaken to produce these preliminary results.

A

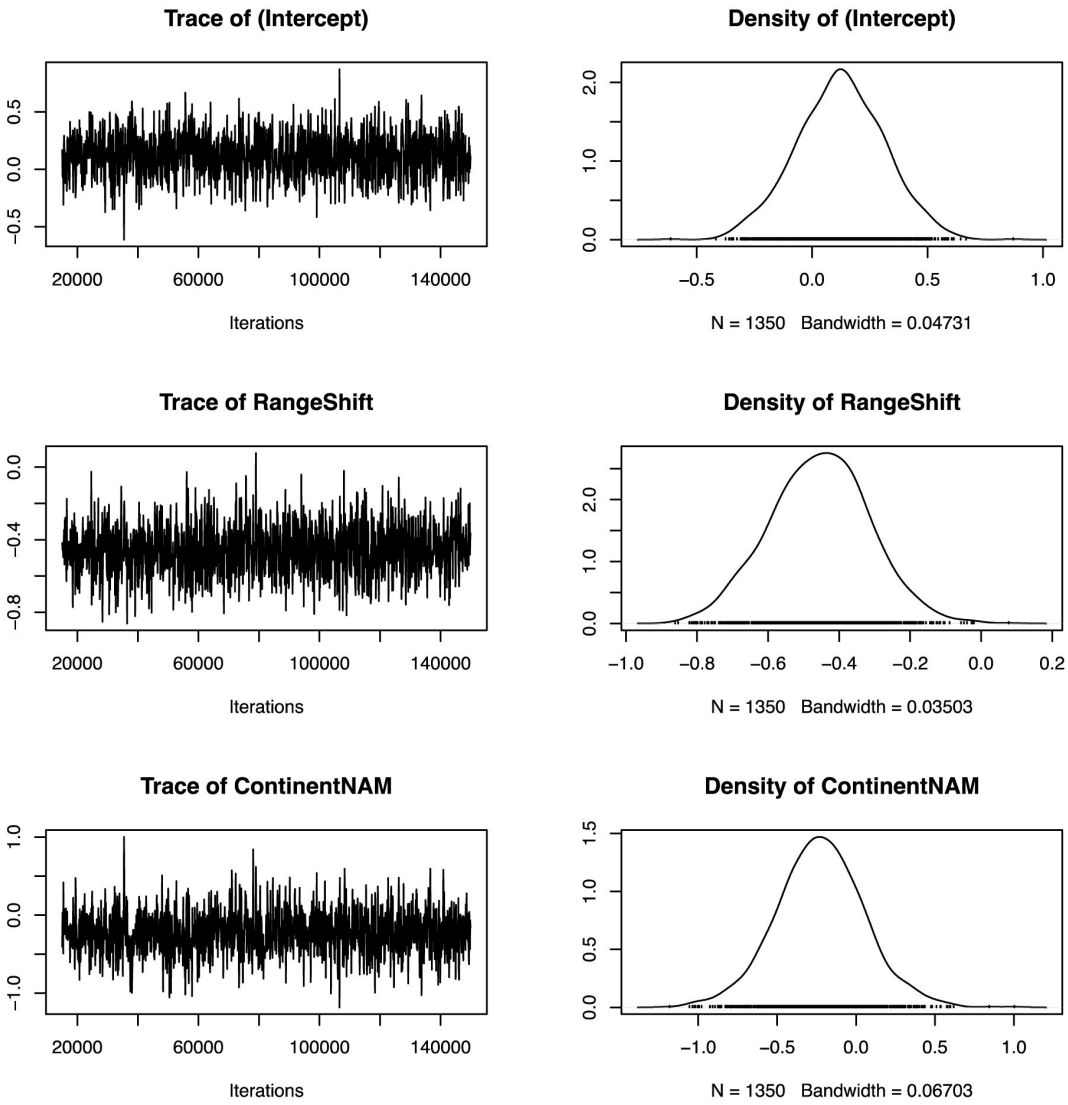


Figure S7

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

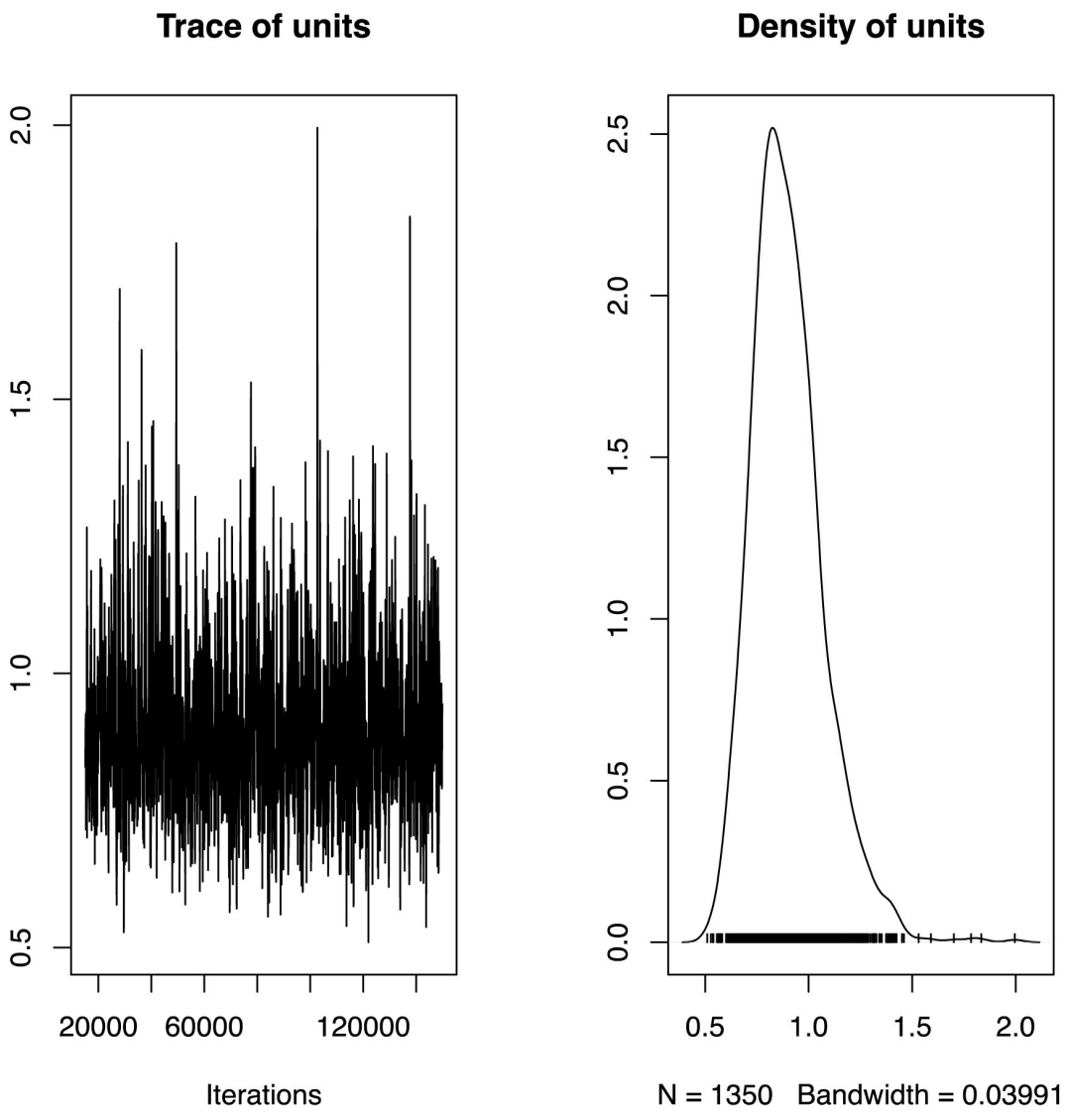


Figure S7 (continued)

A

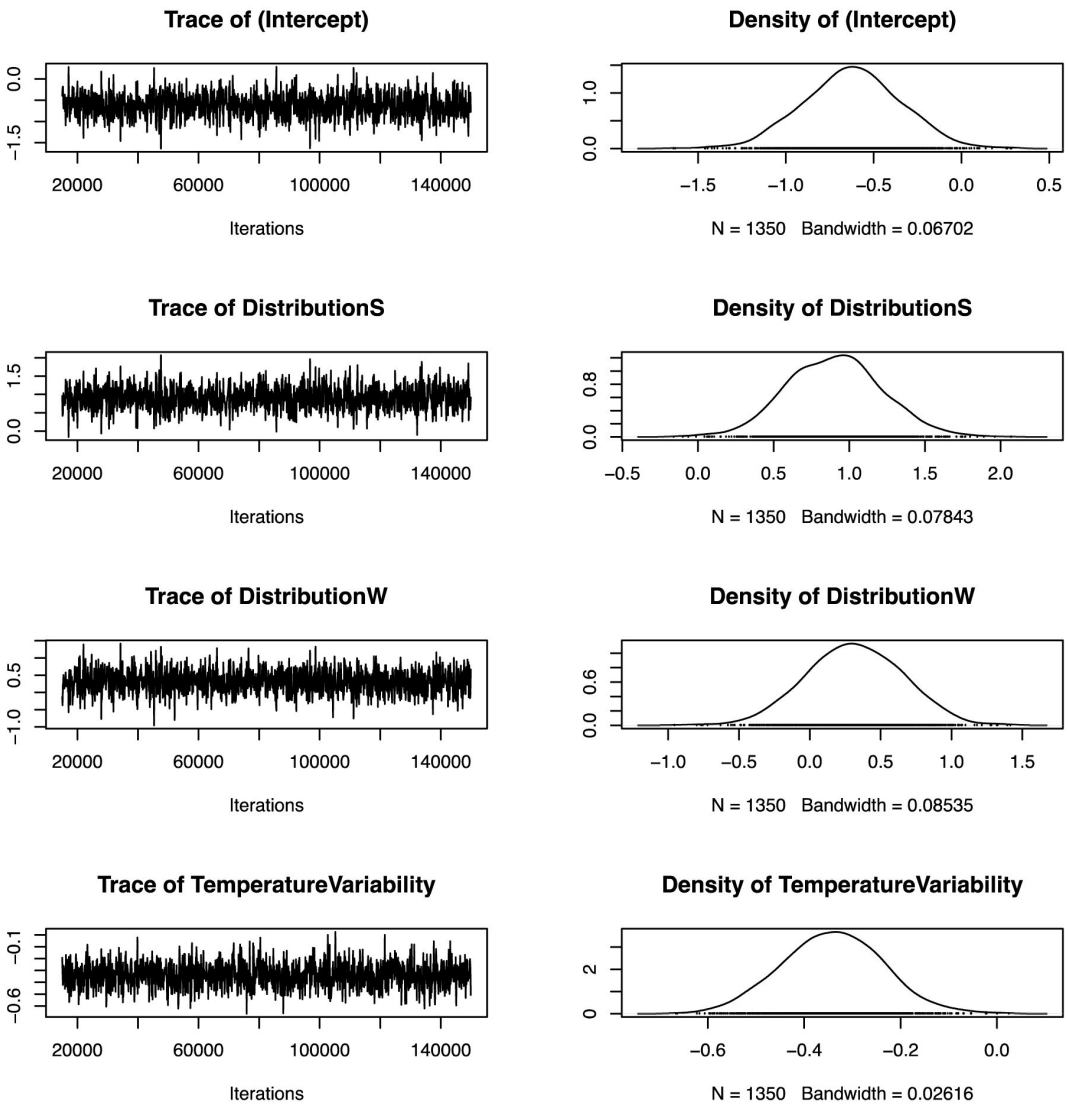


Figure S8

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

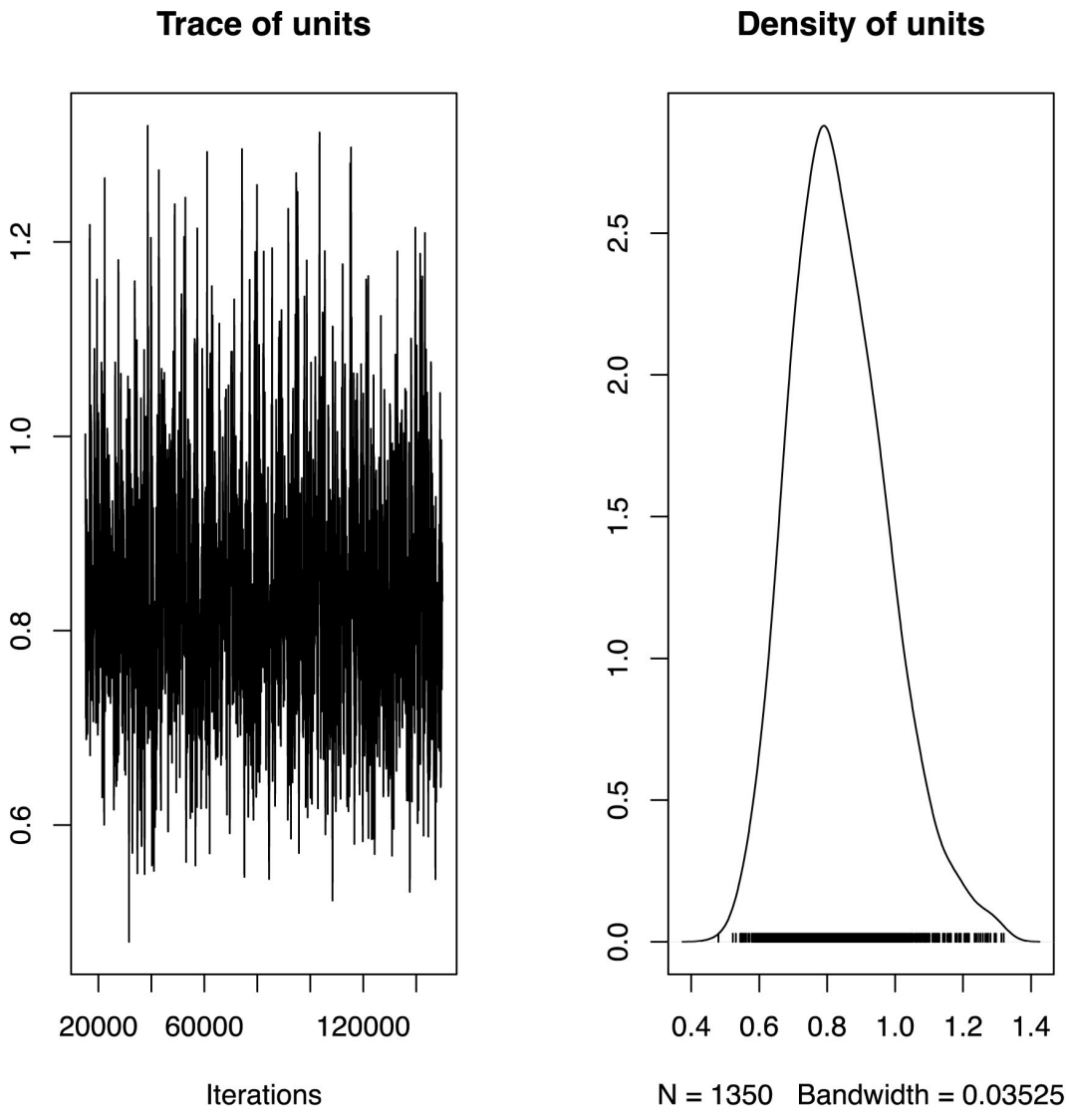


Figure S8 (continued)

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Editors

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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 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.

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.

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.

(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.

(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.

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

https://doi.org/10.7554/eLife.101208.1.sa2

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.

https://doi.org/10.7554/eLife.101208.1.sa1

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.

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.

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.

https://doi.org/10.7554/eLife.101208.1.sa0

Author response:

> ***Public Reviews:***
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> ***Reviewer #1 (Public review):***
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> *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 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 we will review our primary sources to clarify the trait classifications. We will also reclassify the species according to the expertise of this reviewer and perform our analysis again.

> *(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 will add a reference to the methods section to clarify this.

> *(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 will replace the terms specialist and generalist with specific predictions based on traits.

> *(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 will review this text and include it as a reference, in addition to other references recommended by Reviewer 1 and other reviewers.

> ***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 will revise the discussion to acknowledge potential differences in outcomes.

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.

> ***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 will revise the introduction and discussion to better contextualize species' responses to climate change and the mechanisms behind them. We will carefully review all figures and captions, and we will make changes to improve the clarity of the text and the presentation of results.

https://doi.org/10.7554/eLife.101208.1.sa4