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

Catherine Sirois-Delisle[1]*, Susan C.C. Gordon[1], Jeremy T. Kerr[1]

[1]University of Ottawa, 75 Laurier Ave E, Ottawa, ON K1N 6N5, Canada

Correspondence: sgord027@uottawa.ca

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. Species shifting in both space and time may be more resilient to extreme conditions, although further work integrating abundance data is needed. We also 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.

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 may have an advantage 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 and maintain population growth rates (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 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 high 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 or confounding the effects of traits that evolved under conditions

determined by range geography (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 may be '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.

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. doi:10.1098/rspb.2013.3017

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. doi:10.1146/annurev-ecolsys-012120-091002

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

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. doi:10.1007/s10531-014-0707-5

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. doi:10.3897/zookeys.482.8453

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. doi:10.1098/rstb.2017.0389

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

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

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

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. doi:10.1007/s00484-013-0780-6

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. doi:10.1146/annurev-ecolsys-110411-160516

Cannings RA. 2002. Introducing the Dragonflies of British Columbia and Yukon. Royal British Columbia Museum.

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. doi:10.1098/rspb.2008.0179

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.

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

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. doi:10.1111/j.1600-0587.1999.tb01282.x

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

Córdoba-Aguilar A, Beatty C, Bried JT. 2023. Dragonflies and Damselflies: Model Organisms for Ecological and Evolutionary Research. Oxford University Press.

Davis MB, Shaw RG, Etterson JR. 2005. Evolutionary responses to changing climate. *Ecology* **86**:1704–1714. doi:10.1890/03-0788

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. doi:10.1111/ddi.12753

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

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

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

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. doi:10.1111/gcb.16200

ESRI. 2019. ArcGIS (Version 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. doi:10.1016/j.tree.2015.12.014

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

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. doi:10.1111/gcb.13960

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**. doi:10.17161/bi.v8i2.4124

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. doi:10.1111/geb.12260

Goulson D. 2019. The insect apocalypse, and why it matters. *Current Biology* **29**:R967–R971. doi:10.1016/j.cub.2019.06.069

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. doi:10.1098/rstb.2016.0146

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. doi:10.1111/geb.12004

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

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

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. doi:10.1093/evlett/qrad004

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. doi:10.1111/ele.13774

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. doi:10.1038/s41558-018-0187-9

Hassall C. 2015. Odonata as candidate macroecological barometers for global climate change. *Freshwater Science* **34**:1040–1049. doi:10.1086/682210

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

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. doi:10.1146/annurev-ecolsys-011921-032939

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.

Jones CD, Kingsley A, Burke P, Holder M. 2008. Field guide to the dragonflies and damselflies of Algonquin Provincial Park and the surrounding area, 1st ed. The Friends of the Algonquin Park.

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. doi:10.1007/s10750-017-3495-6

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. doi:10.1098/rspb.2020.2061

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

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. doi:10.1890/08-1304.1

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. doi:10.1111/gcb.12042

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. doi:10.1038/s43017-024-00527-z

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. doi:10.1038/s41559-020-1198-2

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. doi:10.1890/12-1407.1

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. doi:10.1002/fee.2043

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. doi:10.1111/gcb.13947

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. doi:10.1038/s41467-019-12479-w

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. doi:10.1111/gcb.13736

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. doi:10.1038/nclimate2086

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. doi:10.1111/een.12175

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. doi:10.1002/ecs2.2151

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. doi:10.1111/j.1365-2486.2006.01193.x

Nagelkerke NJD. 1991. A Note on a General Definition of the Coefficient of Determination. *Biometrika* **78**:691–692. doi:10.2307/2337038

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. doi:10.1038/s41559-024-02536-z

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. doi:10.3354/cr021001

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. doi:10.1111/gcb.15524

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. doi:10.1038/s41467-023-44106-0

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. doi:10.1038/s41467-020-16684-w

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. doi:10.1038/21181

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

Paulson D. 2012. Dragonflies and Damselflies of the East. Princeton University Press.

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. doi:10.1038/s41559-017-0350-0

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. p. 0. doi:10.1093/oso/9780192898623.003.0027

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

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. doi:10.1038/s41598-019-51582-2

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* e1041. doi:10.3897/BDJ.2.e1041

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

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. doi:10.1111/j.1469-185X.2009.00098.x

R Core Team. 2019. R: A language and environment 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. doi:10.1007/s10531-017-1399-4

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

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.

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. doi:10.1111/j.1365-2745.2010.01727.x

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. p. 0. doi:10.1093/oso/9780192898623.003.0024

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. doi:10.1098/rspb.2019.2645

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. doi:10.1073/pnas.1913007117

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. doi:10.1111/j.1365-2427.2006.01712.x

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. doi:10.1098/rspb.2010.1778

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. doi:10.1111/jbi.14457

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. doi:10.1111/ecog.03823

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. doi:10.1111/gcb.70183

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. doi:10.1073/pnas.1705897114

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

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**. doi:10.3389/fevo.2023.1038018

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. doi:10.1002/ecm.1471

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. doi:10.1126/science.aac4858

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. doi:10.1002/ece3.8648

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. doi:10.1111/ele.12474

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. doi:10.1111/jeb.12481

Urban MC. 2015. Accelerating extinction risk from climate change. *Science* **348**:571–573. doi:10.1126/science.aaa4984

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.
doi:10.1016/j.tree.2023.04.004
van der Laken P. 2021. ppsr: Predictive Power Score.
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.
doi:10.1111/evo.13302
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.
doi:10.1038/s41597-019-0318-9
Zattara EE, Aizen MA. 2021. Worldwide occurrence records suggest a global decline in bee
species richness. *One Earth* **4**:114–123. doi:10.1016/j.oneear.2020.12.005
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. doi:10.1038/s41598-021-82723-1

741
742

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).

764
765

Predictors	Phenology shift (N = 66)			
	GLM		MCMCglmm	
	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)			

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.

801 **Figure 2**: Richness of 76 odonate species sampled in North America and Europe in the historic

802 period (1980-2002; panes A and C) and the recent period (2008-2018; panes B and D). Species

803 richness per 100×100 km quadrat is shown in panes A and B, while panes C and D show

804 species richness per 200×200 km quadrat. Dark red indicates high species richness, while light

805 pink indicates low species richness.

810   **Figure 3**: Relationship between range shifts and emergence phenology shifts among North

811   American and European odonate species (N = 66; model R^2 = 17.08 for glm, 14.9% for

812   MCMCglmm). For reference, the shaded area shows mean latitudinal range shifts of terrestrial

813   taxa as reported by Lenoir et al. (calculated as the yearly mean dispersal rate of 1.11 +/- 0.96 km

814   per year over 38 years).

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

```
896    Aphylo ← vcv(phylogeny, model = "Brownian", corr = T)

897    Ainv ← inverseA(phylogeny, nodes = "TIPS", scale = F)$Ainv

898    prior ← list(R=list(V=1,nu=0.002))

899    MCMCglmm(Phenology shift ~ Breeding habitat type + Distribution region + Flight duration +

900    Egg laying habitat + Body size + Temperature variability, ginverse = list(species = Ainv), family

901    = "gaussian", prior = prior, DIC = T, nitt = 150,000, thin = 100, burnin = 15,000, data)
```

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.

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

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

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

909 **Table S2:** 66 species sampled across North America and Europe between 1980 and 2018

910 followed our criteria for quality observation records for inclusion in our analysis of emergence

911 phenology shifts. Mean phenological shifts (PS) is measured in the number of Julian days

912 comparing both time periods, as estimated using the Weibull distribution (See Methods). We

913 also report the number of 200 X 200 quadrats used to calculate phenology estimates per species.

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

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

914
915

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.

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

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

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

932 **Table S4**: Credible intervals of all MCMCglmm models testing predictions regarding the range

933 and phenology shifts across 66 odonate species in North America and Europe. These models are

934 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.

983
984

986 <u>Figure S7, A</u>

Trace of (Intercept)

Density of (Intercept)

Trace of RangeShift

Density of RangeShift

Trace of ContinentNAM

Density of ContinentNAM

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.

996   <u>Figure S8, A</u>

Trace of (Intercept)

Density of (Intercept)

N = 1350   Bandwidth = 0.06605

Trace of DistributionNS

Density of DistributionNS

N = 1350   Bandwidth = 0.08705

Trace of DistributionS

Density of DistributionS

N = 1350   Bandwidth = 0.07728

Trace of TemperatureVariability

Density of TemperatureVariability

N = 1350   Bandwidth = 0.02502

Trace of units

Density of units

1000

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.