Understanding how odonates respond to global change; a cross-continental analysis

Catherine Sirois-Delisle

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Department of Biology
University of Ottawa
Ottawa, Ontario, Canada

"There are so many reasons to fall in love with dragonflies. They have intriguing stories to tell us. They make our world a more beautiful place. And they are scrappy survivors."

" Chasing Dragonflies: A Natural, Cultural, and Personal History", Cindy Crosby

Abstract

Global change profoundly alters biological communities and increases species extinction rates. Recent reports show that odonate species (dragonflies and damselflies) are declining globally, however, odonates can also respond strongly to climate and land use change through shifts in range and phenology – i.e., the timing of life history events. Understanding how and when species respond to rapid environmental change is critical to address conservation risks in a timely way. I assembled a dataset of ~2 million odonate records between 1901 and 2021 and investigated a series of research questions about odonate persistence within historically occupied regions, how species respond across continents, and mechanisms leading to these responses. I discovered that non-target effects of pesticides interacted with temperature increases, leading to higher rates of odonate declines across the United States. Species with greater capacities in shifting their range northward may be more robust to impacts of global change (Chapter 2). Converging across Europe and North America, stronger range limit shifts were associated with stronger shifts in emergence phenology towards earlier spring dates, even though land use histories are highly divergent among regions. It is temperature variability and range geography, determinants of habitat conditions to which species are exposed, rather than ecological traits, that facilitated or hindered range shifts (Chapter 3). Temperature variability interacted with pesticide applications to hinder persistence or establishment in new areas that were otherwise climatically suitable, providing further evidence of impacts of extreme weather to insect declines. Tests of methods commonly used to predict species' distributions under future climate change (Species Distribution Models) revealed that species most likely to decline were also less likely to be well modeled, in terms of their temporal transferability (Chapter 4). This work deepens knowledge of spatial and temporal interspecific variation in species distributions as humans continue to reshape

the Earth's ecosystems and climatic processes. This thesis can help improve species-specific conservation planning for species that decline in the face of anthropogenic activities.

Résumé

Les changements globaux modifient profondément les communautés biologiques et augmentent le taux d'extinction des espèces. Les odonates (libellules et demoiselles) sont en déclin mondial. Cependant, les odonates peuvent répondre aux changements environnementaux en apportant des changements aux limites géographiques de leur aire de répartition et à leur phénologie, c'est-à-dire les aspects temporels des événements significatifs de leur cycle biologique. Comprendre comment et quand les espèces répondent aux changements environnementaux est essentiel pour diminuer les risques en lien à la conservation des espèces. J'ai assemblé un ensemble de données d'environ 2 millions d'observations géoréférencées d'odonates entre les années 1901 et 2021 pour étudier plusieurs questions liées à la persistance des espèces dans les régions historiquement occupées, aux réponses spatiales et temporelles des espèces à travers les continents et aux mécanismes qui mènent à ces réponses. J'ai découvert que les effets des pesticides interagissent avec l'augmentation de la température pour prédire les extinctions locales aux États-Unis. Les espèces ayant une plus grande capacité à déplacer les limites de leur aire de répartition vers le nord sont plus robustes à l'impact des changements globaux en général (Chapitre 2). Convergeant entre l'Europe et l'Amérique du Nord, les déplacements géographiques plus importants sont associés à l'avancement de la phénologie des espèces vers une émergence précoce, indépendamment des différences majeures de l'histoire de l'utilisation des terres entre ces continents. La position géographique générale des espèces et la variabilité de la température, deux facteurs déterminants des conditions auxquelles les espèces sont directement exposées, plutôt que les traits écologiques des espèces, prédisent les changements des limites de l'aire de répartition observés (Chapitre 3). La variabilité de la température interagit avec l'application de pesticides pour empêcher la persistance ou

l'établissement dans une nouvelle région, dans les endroits caractérisés d'un climat autrement convenable, démontrant ainsi l'impact des températures extrêmes au déclin des espèces. J'ai testé des méthodes couramment utilisées pour prédire la distribution des espèces dans le cadre des changements climatiques futurs, et j'ai découvert que les espèces en déclin sont celles dont les modèles sont moins susceptibles d'être transférables à travers le temps (Chapitre 4). Ce travail a approfondi les connaissances sur les variations interspécifiques spatiales et temporelles de la distribution des espèces alors que les humains continuent de remodeler les écosystèmes et les processus climatiques de la Terre. Il pourra aider à améliorer la planification de la conservation des espèces qui déclinent face aux activités anthropiques.

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Indigenous affirmation

"Ni manàdjiyànànig Màmìwininì Anishinàbeg, ogog kà nàgadawàbandadjig iyo akì eko weshkad. Ako nongom egawìkàd kì mìgiwewàdj.
Ni manàdjiyànànig kakina Anishinàbeg ondaje kaye ogog kakina eniyagizidjig enigokamigàg Kanadàng eji ondàpinangig endàwàdjin Odàwàng.
Ninisidawinawànànig kenawendamòdjig kije kikenindamàwin; weshkinìgidjig kaye kejeyàdizidjig.
Nigijeweninmànànig ogog kà nìgànì sòngideyedjig; weshkad, nongom; kaye àyànikàdj."

"We pay respect to the Algonquin people, who are the traditional guardians of this land. We acknowledge their longstanding relationship with this territory, which remains unceded. We pay respect to all Indigenous people in this region, from all nations across Canada, who call Ottawa home. We acknowledge the traditional knowledge keepers, both young and old. And we honour their courageous leaders: past, present, and future."

The University of Ottawa's Indigenous Affirmation was written by the Office of Indigenous Affairs, in partnership with the Indigenous Education Council, Indigenous student groups, and members of the local Indigenous community, and can be found at https://www.uottawa.ca/about-us/indigenous/indigenous-affirmation to specially acknowledge and recognize the traditional territory of the Algonquin Nation on which the University of Ottawa sits, including the laboratory necessary to complete this work. I used odonate observation records collected across North America and Europe, since 1901, and these data originate from unceded territory of hundreds of indigenous communities. I recognize my own colonial history and strive to educate myself on these large and deep-rooted issues.

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Chapter 1: General introduction

Anthropogenic activities have become a driving force in defining Earth's climate, ecosystems, and biological communities, marking the start of the Anthropocene epoch (Crutzen 2006, Syvitski et al. 2020). Land use change and intensification, and other human activities (e.g. energy consumption of residential and commercial buildings, transportation, manufacturing, and industry, etc.) aggravate the ongoing climate crisis (Ripple et al. 2021) and degrade species' habitats; about 75% of the Earth's land surface is significantly altered, while wetland area has declined by 85% (IPBES 2019). Abundant documentation reports rising yearly mean temperatures, declines in ice volume while sea levels rise, changes in precipitation patterns, and increased probabilities of extreme temperature events (IPCC 2021). Climate and land use change are the main drivers of the ongoing biodiversity crisis (Dirzo et al. 2014, Haddad et al. 2015, Newbold et al. 2015, Ceballos et al. 2017), with current extinction rates 10 to 100 times higher than historic rates (IPBES 2019). These extinctions may degrade ecosystem stability and reduce ecosystem services for millions of years to come unless drastic conservation measures are undertaken (Neubauer et al. 2021).

Some insects are declining globally, but the magnitude and specific causes of decline remain uncertain (Goulson 2019). Results of several studies warn against the "insect apocalypse", but this is a debated topic within the scientific community (e.g. Montgomery et al. 2020, Saunders et al. 2020). A 2017 study reports that insect biomass in German protected areas declined by over 70% in 27 years (Hallmann et al. 2017). Similarly, a decline of 75 to 98% of Puerto Rican insects over 35 years was reported (Lister and Garcia 2018). A review of 73 studies on insect decline shows that alarming insect losses are likely not geographically isolated (Sánchez-Bayo and Wyckhuys 2019). However, abundance changes in insects are highly varied

among taxa (van Klink et al. 2020). There remain large taxonomic and geographic gaps in evidence to support the "insect apocalypse" as a global phenomenon (Montgomery et al. 2020, Saunders et al. 2020).

According to the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), approximately 1 million species, of which 75% are insects, are threatened with extinction (IPBES 2019). Among invertebrates assessed by the International Union for Conservation of Nature (IUCN), about 40 % of species are identified as threatened (Dirzo et al. 2014), but the vast majority of species remain unassessed and an unknown number remain to be discovered (Stork 2018, Montgomery et al. 2020). Quantifying rates of decline among invertebrates is highly complex and is among key uncertainties needing attention (IPBES 2019). In order of importance, land use change, applications of pesticides and other environmental pollutants, invasive species and pathogens, and climate change, are the main drivers of insect decline (Sánchez-Bayo and Wyckhuys 2019). However, trends of local invertebrate extinctions driven by climate change are rarely documented due to the difficulty of observing and identifying the effect, particularly when other threats are present, but climate-related extinctions are expected to grow far more frequent in the future (Urban 2015, Newbold 2018, Sirois-Delisle and Kerr 2018). It is critical to improve predictions of species' responses to global change and increase knowledge of mechanisms driving these declines, to better understand species-specific requirements and inform effective conservation actions.

Species' realised niche – i.e. the set of tolerated environmental conditions including all required abiotic (e.g. physical processes) and biotic factors (e.g. interactions with other species) – governs species' fitness according to the environmental conditions to which they are exposed (Hutchinson 1957). Climate change can create conditions within habitats that render them

unsuitable, and other pressures, such as pesticide applications, can exacerbate such challenges. According to niche theory, species' niche limits determine their local persistence, and therefore their geographical range limits (Chen et al., 2011; Sexton et al., 2009; Sunday et al., 2014; 2012). Studies have shown that niche limits often constrain range limits, so that fitness and suitability decline beyond range limits, but this isn't always the case (Hargreaves et al. 2014, Lee-Yaw et al. 2016). Species tracking suitable climates across geographic space may effectively reduce their exposure to conditions that are not tolerated (Parmesan et al. 1999, Parmesan and Yohe 2003), although phenology shifts can also help species remain within the boundaries of their ecological niche (Amano et al. 2014, Hassall 2015, Socolar et al. 2017). Mismatches between species' realised niche limits and inhabited areas may also arise due to variation in species' dispersal ability, aspects of life history, recolonization history, stochastic events (Holt et al. 2005, Sexton et al. 2009, Hargreaves and Eckert 2014, Hargreaves et al. 2014), and other population factors such as abundance and habitat availability (Mair et al. 2014).

Species' physiological traits, combined with external drivers of change, dictate whether species tolerate new conditions through adaptations or phenotypic plasticity, establish in new suitable areas leading to range shifts, or face local extinction (Chen et al. 2011, Kharouba et al. 2014). Latitudinal and elevational gradient shifts linked with climate change were first documented in species limited by low temperatures, like arctic or alpine plants, and highly mobile species such as birds and flying insects (Hughes 2000). Recent studies describing range shifts still primarily focus on plant, bird, and butterfly species due to the availability of historical data needed to conduct such studies (Parmesan and Yohe 2003, Root et al. 2003). Range boundaries may shift northward, and the timing of early-season life events may shift across time as spring temperatures warm, assisting species in remaining within their ecological niche limits

(Parmesan and Yohe 2003, Menzel 2006, Chen et al. 2011). These shifts may reduce risks of accumulated climate debt and consequent chances of local extinction (Saino et al. 2011, Devictor et al. 2012, Kerr et al. 2015, Urban 2015, Franks et al. 2018, Lustenhouwer et al. 2018). Groups without such capacities can be exposed to temperatures beyond their historical tolerances, which increases extinction risks in affected areas. Some species may shift in directions that are opposite to expectations in response to combinations of environmental changes, increasing exposures to unsuitable conditions (Chen et al. 2011, Rapacciuolo et al. 2014, Kerr et al. 2015). In theory, some ecological traits are likely to increase species' capacities to disperse and establish in new areas, but the effect of traits on range shift predictions shows considerable variation (Angert et al. 2011, Powney et al. 2015, MacLean and Beissinger 2017). In many cases, even species with high dispersal capacity can face significant lags in tracking climate change (Bedford et al. 2012, Devictor et al. 2012). Global change-induced range changes are expected to continue in future years in both Europe and North America (Newbold 2018, Sirois-Delisle and Kerr 2018), but understanding why some species persist while others decline remains unclear.

Improved predictions about distribution changes that species may face under future climate change are critical for informing effective conservation practices in a changing world (Pressey et al. 2007). By integrating species observations with information about the environmental conditions at the time of observation, species distribution models (SDMs) provide insight into species' potential performance in new areas, based on the projected geographical changes in the position of species' climatic niche limits subsequent to climate change (Lee-Yaw et al. 2016). SDMs can be constructed using a variety of statistical or machine-learning approaches, but any successful model should capture the environmental conditions that permit positive or stable population growth rates, which are among the conditions necessary for species

to persist or disperse to occupy new areas (Hutchinson 1957). SDMs link species occurrences and predicted absences to spatially or temporally distinct areas, based on the set of environmental conditions that characterise precise localities where they are found (Elith and Leathwick 2009). Georeferenced observations, pseudo-absences (i.e. random points where the species was not found) and detailed environmental data can be used in a variety of methods, depending on software accessibility, data availability type, and research goals (Elith and Leathwick 2009, Ahmed et al. 2015). Distribution projections under future climate change are one of the most common goals in studies using SDMs (Santini et al. 2021) but tests about whether they work through time are rare and yield contradictory results (Santini et al. 2021, Lee-Yaw et al. 2022).

Odonates (dragonflies and damselflies) are excellent model organisms to study species' shifts in distribution and phenology under global change, and the underlying mechanisms contributing to these shifts. These species can respond rapidly to climate and land use changes, both temporally (i.e. through phenological shifts) and spatially (i.e. through range shifts), and exhibit considerable interspecific variation in these responses (Gonseth and Monnerat 2003, Hickling et al. 2005, Hassall et al. 2007, Grewe et al. 2013, Ball-Damerow et al. 2015, Powney et al. 2015, Rapacciuolo et al. 2017, McCauley et al. 2018, Sirois-Delisle and Kerr 2055). Many odonates are in widespread decline due to habitat loss, so it is critical to acquire information about global responses to global change (IUCN Red list 2021). Odonates require freshwater ecosystems, one of the most threatened ecosystem types worldwide (Dudgeon et al. 2006, Reid et al. 2019). The taxon has also been identified as a suggested "barometer" of climate change due to its ability to respond to climatic changes temporally and spatially more quickly than other taxa in Britain (Hassall 2015).

Georeferenced databases of odonate observation records increased significantly over the past two decades, including digitized historical records and the collection and documentation of new specimens (Kalkman et al. 2018). These datasets have more recently made research analysing odonate distribution possible, although large-scale distributional studies have mainly focused on European species (Hof et al. 2006, 2012, Grewe et al. 2013). In contrast, studies of odonate distributions are very rare in North America and are executed at small scale (Ball-Damerow et al. 2015, Rapacciuolo et al. 2017). Using odonates as a study system allows the investigation of new research questions, as massive datasets of presence records exist due to high public interest and ease of identification (Kalkman et al. 2018).

The main objective of this thesis is to investigate interspecific distributional changes that occur in response to environmental change, potential mechanisms that relate to species' responses, and to evaluate commonly used, but rarely tested tools to assist in predictions of such changes, representing major challenges in conservation biology. In Chapter 2, I explore how major drivers of global change, such as climate change, land use change, and land use intensification impact odonate persistence after a period of rapid climate change across the USA. In Chapter 3, I investigate the relationship between range and emergence phenology shifts across Europe and North America. I test whether ecological traits or characteristics of species' ranges (e.g. temperature variability or the geographic position of species' range) predict interspecific spatial and temporal responses. In Chapter 4, I test the temporal transferability of methods commonly used to predict species' distributions under future climate change. I also determine whether anthropogenetic pressures are likely to cause models to fail over time, leading to higher error rates.

I assembled a dataset of over 2 million odonate observation records collected across Europe and North America to explore a variety of study questions at continental scales. I used a macroecological framework, which relies on global changes as a pseudo-experiment, that is robust to limitations around sampling, which can facilitate predictions of impacts of climate change on species (Kerr et al. 2007). I also compiled spatially and temporally explicit, high-resolution climate, land use, and pesticide application data to measure different forms of environmental change between historical and more recent time periods. I conducted three studies to analyse drivers of odonate decline, global shifts in the timing of emergence and position of range boundaries, and factors inhibiting species from dispersal or establishment in climatically suitable areas. The methods used here not only led to exciting discoveries but they can be applied to other taxa and geographical extents as well. More broadly, the discoveries described throughout this thesis provide evidence of critical factors that improve predictions of species' responses to global change.

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Chapter 2: Climate change aggravates non-target effects of pesticides on dragonflies at macroecological scales

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Abstract

Critical gaps in understanding how species respond to environmental change limit our capacity to address conservation risks in a timely way. Here, I examine the direct and interactive effects of key global change drivers, including climate change, land use change, and pesticide use, on persistence of 104 odonate species between two time periods (1980-2002 and 2008-2018) within 100 X 100 km quadrats across the United States using phylogenetic mixed models. Non-target effects of pesticides interacted with higher maximum temperatures to contribute to odonate declines. Closely related species responded similarly to global change drivers, indicating a potential role of inherited traits in species' persistence or decline. Species shifting their range to higher latitudes were more robust to negative impacts of global change drivers generally. Inherited traits related to dispersal abilities and establishment in new places may govern both species' acclimation to global change and their abilities to expand their range limits, respectively. This work is among the first to assess effects of climate change, land use change,

and land use intensification together on Odonata, a significant step that improves understanding of multi-species effects of global change on invertebrates, and further identifies conditions contributing to global insect loss.

Introduction

Human activities significantly modify, and even dominate, Earth system processes, marking the onset of the Anthropocene era (Crutzen 2006). Ongoing expansions of cities, intensification of agricultural activities, and associated industrial activities release massive quantities of greenhouse gases, pesticides, and other pollutants, accelerating climate change and habitat degradation (IPCC 2014). Such pressures were linked with local extinctions, expected to drastically increase in the future (Newbold et al. 2015, Sirois-Delisle and Kerr 2018), and with global insect declines (Dirzo et al. 2014, Hallmann et al. 2017). Causes of insect declines are much debated, but certainly include increased impacts of extreme weather events associated with climate change (like heat waves and drought), pesticide use, and intensive land use change (Iserbyt and Rasmont 2012, Goulson et al. 2015, Goulson 2019, Soroye et al. 2020). Among insects, research has focused primarily on butterfly and bee species because historical comparisons rely heavily on accessibility of older records. The availability of georeferenced observations for odonates (dragonflies and damselflies) has grown rapidly in recent years (Kalkman et al. 2018), permitting the exploration of novel questions regarding species responses to environmental change.

Land use change near agricultural or urban areas is linked with changes in odonate species richness, diversity, and community composition (Ball-Damerow et al. 2014, Powney et al. 2015, Goertzen and Suhling 2019). In urbanized areas, aquatic and terrestrial vegetation

diversity is a major determinant for odonate diversity and species assemblage structure (Goertzen and Suhling 2013). Land use change over time can cause homogenization of odonate species assemblage due to the success of highly mobile generalists and the decline of habitat specialists (Ball-Damerow et al. 2014). Despite effects of biotic homogenization, urban landscapes better maintain species diversity than agricultural landscapes (Goertzen and Suhling 2019). Their particular sensitivity to water quality and to surrounding terrestrial environments led odonates to be established as bioindicators of ecosystem health (Van Praet et al. 2012, Gerlach et al. 2013).

Odonates have terrestrial and aquatic life stages, including a multi-year nymph stage for some species, during which they have limited dispersal abilities, and may be in close contact with multiple environmental pollutants that contribute to local extinctions (Beketov et al. 2013, Nakanishi et al. 2018, Kita et al. 2020). Because pesticides can easily contaminate water bodies and soils outside target areas through leaching and spray drift, effects on non-target invertebrates are likely (Damalas and Eleftherohorinos 2011). Agricultural pollutants bioaccumulate in odonates' aquatic larvae (Van Praet et al. 2012) and may impact odonates' feeding rates, mobility, emergence probability and immune function (St Clair and Fuller 2018, Barmentlo et al. 2019, Hashimoto et al. 2019). The application of multiple pesticides also causes additive or synergistic effects on invertebrate diversity (Tsvetkov et al. 2017) with effects lasting for multiple weeks and across many trophic levels (Hasenbein et al. 2016). Pesticide toxicity data on odonates are contradictory and scarce, and may have been underestimated in recent, experimental work (Barmentlo et al. 2019). County-level, non-target effects of pesticide use, an indicator of land use intensification, were recently tested for bees at the continental scale (Douglas et al. 2020) but such effects have not previously been studied in aquatic invertebrates at this scale and resolution. While pesticide use and land use change can degrade habitats, climate

change acts independently to cause species' range shifts (Thomas 2010) and evaluation of all three global change drivers is needed.

Rapid range declines and expansions are reported in odonates at the scale of European countries (Knijf et al. 2001, Gonseth and Monnerat 2003, Hickling et al. 2005, Powney et al. 2015). Odonate species may expand toward northern latitudes overall (Grewe et al. 2013, Ball-Damerow et al. 2015) but habitat specialists tend to decline as generalists benefit from higher temperatures (Ball-Damerow et al. 2015, Rapacciuolo et al. 2017). However, the availability of historical observations for odonates has limited understanding of spatiotemporal changes in species' geographical ranges. While range expansions in odonate distributions have been linked to climate change in past studies (Hickling et al. 2005, Grewe et al. 2013), and some of those impacts are positive (e.g. Parmesan et al. 1999), assessments of geographical range shifts emphasize detection of shifts in species' range boundaries to a greater extent than testing for persistence more broadly within species' geographical ranges.

Dragonflies might respond more favorably to warming conditions than other semi-aquatic or aquatic organisms because of their broad thermal tolerances (Rosset and Oertli 2011). However, odonate species' resilience to environmental threats is highly variable, reflecting potential effects of species' dispersal abilities, habitat specialization, current and anticipated geographical ranges, and species' estimated habitat availability under future conditions (Rosset and Oertli 2011). For instance, tropical species at lower elevations are more tolerant to climate warming but are also vulnerable due to their limited geographic range size (Rocha-Ortega et al. 2020). Warming may be especially detrimental to odonate species adapted to cooler temperatures and to species that occupy areas where precipitation is decreasing (Hassall and Thompson 2008, Ball-Damerow et al. 2014). Experiments show that temperature rises similar to those expected in

the next century may lead to shorter development time, higher rates of mortality (McCauley et al. 2015, 2018), and reduced body size, a phenomenon more common in aquatic than terrestrial species, although debated (Forster et al. 2012, McCauley et al. 2018).

Understanding species' responses to recent global changes is an indispensable ingredient in predicting their future responses and informing potential conservation interventions. Here, I test individual and interactive effects of climate change, land use change, and land use intensification on odonate persistence in the United States. I am particularly interested in testing whether combined effects of climate change and pesticide application on odonate persistence are observable at macroecological scales. I evaluate these responses relative to species' shared evolutionary histories to assess the potential role of traits in shaping this taxon's responses to multiple stressors. I also assess whether species that have shifted their range limits towards higher latitudes also tended to be more likely to persist elsewhere, despite aspects of global change detected in those areas.

Methods

I used generalized linear mixed models to assess the effects of land use change, land use intensification and climate change on species persistence within 100 X 100 km quadrats across the United States of America (USA). The package MCMCglmm (Markov chain Monte Carlo generalized linear mixed model), available in R Statistical Software version 3.5.0., accounts for data non-independence potentially caused by phylogeny (Hadfield 2010).

Study area and species occurrence records

I assembled ~815,000 observation records for North American odonate species collected from 1980 to 2018 (see Appendix S1: Section S1 for details of data assembly and a species list). I restricted the study extent to the United States (area 9,857,306 km^2), which included ~ 212 000 unique location-year observations after data cleaning. The majority of the data were collected from GBIF (http://gbif.org/) and Canadensys (http://www.canadensys.net/), which are online dataset aggregators, but I also used data from Odonata Central (Abbott 2020) and other institutions (Appendix S1: Section S2). Data that are not systematically collected, such as GBIF data, may be biased spatially and temporally. However, such data are still useful to report long-term species occurrences as biases are less likely to affect global trends at greater spatial and temporal scales (Zattara and Aizen 2021). To further limit potential biases, data should be diligently curated, and results interpreted with caution (Samy et al. 2013, García-Roselló et al. 2015, Bartomeus et al. 2018).

Observation data were assigned to their respective 100 X 100 km quadrats and extracted by a historical time period (1980 – 2002) and a recent time period (2008 – 2018). Persistence was measured as a binary variable (0 – 1). The first time period was supplemented with additional years to account for lower sampling intensity in historical records compared to recent years, allowing greater certainty in species detection. I selected species sampled in at least 100 quadrats in both time periods resulting in observation records for 104 species across the USA (Figure 2.1). Here, I investigated more commonly sampled species, but future work including rare species is critical. I further refined quadrat selection to those that contained a minimum of 10, 15, 20 or 25 species observed to remove poorly sampled quadrats while limiting probabilities of including false absences, decreasing probabilities of including bias toward declines. Using

these different minimum values did not affect any of the results qualitatively. I reported results using a minimum of 15 species per quadrat. Subsequently, I used the Chao index for species richness estimation, a statistic to predict species richness with sampling intensity and sample completeness (Chao and Chiu 2016) from the R *vegan* package (Oksanen et al. 2019). I allowed a maximum of 10, 15, 20 or 25 species between the number of species observed and those estimated by the Chao index, excluding under-sampled quadrats. The results were not qualitatively different when using these different values. I reported results obtained when using a maximum of 15 species between estimates provided by the Chao index and the number of observed species per quadrat. Limiting analyses to the best sampled species and locations significantly decreases risks of including inconsistent and incomplete presence-only data (Kharouba et al. 2018).

Sampling intensity change was calculated to further restrict quadrat selection and included as a covariate in my models. Sampling intensity change corresponds to the difference in the number of species observed between both time periods. I selected quadrats with a difference of -8 to +8 unique species observations in the second time period compared to the first, leaving 295 quadrats to the analysis. Different values to restrict quadrats by the number of species observations were also tested, and all results described in this work remained qualitatively the same. Incrementally, I tested -5 to +5 species, to -20 to +20 species. Sensitivity analyses revealed that allowing larger sampling differences between time periods introduced sampling intensity effects. My goal was to maximize the number of unique species observations included in the analysis while limiting effects of sampling intensity change in the models.

I conducted a preliminary data assessment to estimate range declines among best sampled quadrats and species. As an index of range loss, I used the proportion of currently occupied

quadrats to those occupied in the baseline time period. Since potential range expansions are outside the scope of this work, local species' losses could be offset by gains elsewhere. This study does not assess species' global conservation risks.

Climate change, land use change and land use intensification data

The selected variables to represent key global change drivers in the model include changes in temperature and precipitation, cropland use, and pesticide application. I used high resolution gridded datasets from the Climatic Research Unit (CRU) as climate change data (available at http://www.cru.uea.ac.uk/data). I downloaded monthly average daily maximum temperature and monthly precipitation across the USA. For both climate variables, I extracted the average values per quadrat, across both time periods, and calculated the difference between the current and historical time periods to obtain a single value of change per quadrat.

I used HYDE 3.1 land use data (available at http://www.pbl.nl/hyde). The HYDE dataset incorporates satellite data and statistics of world population, cropland and pasture in 5 arc-minute resolution maps. I selected agricultural land use as croplands exert larger effects on odonate persistence than livestock grazing or human population density (Goertzen and Suhling 2019). I extracted the average cropland area per time period and per quadrat to obtain land use change values. Comparative trends in species presence change should be interpreted carefully because croplands were already established in the first time period and did not increase overall in the second time period across the total study extent.

I used pesticide application (in kg) data as a metric of land use intensification. Data were available between years 1992 and 2018 on the USGS website (available at https://pubs.usgs.gov/ds/752/). These data provide county level estimates of agricultural

pesticides of the conterminous United States for 459 compounds and are based on the US Department of Agriculture data for harvested-crop acreage as well as proprietary Crop Reporting District pesticide use (Thelin, G.P., and Stone 2013). I measured total pesticide use as per quadrat totals in each year and averaged those totals across all years in each of the two time periods to obtain a measure of pesticide application change. It should be noted that pesticide data starting in 2015 onwards exclude pesticides that are applied via seed treatment, which may underestimate application amounts and risks to species (Douglas et al. 2020).

Odonate phylogenetic data

Species that share more evolutionary history are likely to show similar responses to global change due to inherited biological traits (Stevens et al. 2010). To account for species relatedness, and to gather information on the importance of species relatedness into their responses to global change, I used the phylogenetic tree presented by the Odonate Phenotypic Database (Waller et al. 2019). This database was created with a combination of DNA-sequences and morphologically-based taxonomy (Waller and Svensson 2017), and is the most comprehensive and recent available resource for odonate phylogeny.

Phylogenetic mixed-effects models

The predictor variables considered for the main analysis include change in pesticide application (kg), precipitation (ml), monthly average daily maximum temperature (degrees Celsius), cropland use (km^2), and sampling intensity. I verified whether any trends attributed to aspects of environmental change might instead have arisen because of differences in sampling intensity through time. I tested hypotheses related to interactions between pesticide application

and both climate change variables. All predictor variables were Z-scored using the *scale* function in R to compare the differences in magnitude of the estimates calculated by the models. I explored potential non-independence of predictor variables by plotting all pairwise plots among them and calculating Pearson correlations among them (see Supporting Information: Figure 2.S1). These variables were independent.

I identified variables that have a non-zero effect using the credible intervals calculated by the mixed-effects models. I also reported DIC values (Deviance Information Criterion, which serves a similar function for Bayesian models as Akaike's Information Criterion does in other model types) and pseudo R^2 (Nakagawa et al. 2017), to improve ease of interpretation. Since many other variables that could not be included here are likely to affect odonate persistence and decline at this scale, I expected low R^2 values. Model parameters were based on 200,000 iterations. I evaluated trace and density figures of all the models that were tested to assess model convergence. I tested for effects of phylogeny on model variance by comparing DIC and pseudo R^2 values of both phylogenetic and non-phylogenetic models. I calculated Moran's I, testing for distance-based autocorrelation on the calculated quantile residuals, and concluded that global spatial autocorrelation was not present.

It is possible that species with greater tolerances to the environmental changes evaluated here are also more likely to expand their geographical ranges poleward with changing climatic conditions. I tested an additional hypothesis by constructing a phylogenetic mixed-effects model using the *MCMCglmm* R package, to assess whether species with higher probabilities of persistence expanded along their northern range limit. Persistence was set as a binary response variable per quadrat, with overall Z-scored species-specific latitudinal change as the predictor, using the term species as a random effect. Range limit shifts were calculated using the difference

between the mean of the 5, 10, and 15 furthest observation points from the equator in the historical and current time periods. I reported results using the 5 most northern points to calculate species' range limit shifts as results were qualitatively similar.

Results

Assessment of odonate persistence and decline

I first calculated an index for range loss, without considering potential range expansions, as a preliminary assessment of the data. Out of 104 odonate species analyzed, I found a mean quadrat loss of 29% of previously occupied quadrats (see Supporting Information: Figure 2.S2). Species declines were found across the entire study extent suggesting the relevance of testing for effects of broad-scale phenomena (Figure 2.2). It is important to note that species sampled in at least 100 quadrats in both time periods were kept according to my criteria for quadrat and species selection, so the declines found here are likely underestimated. This approach is conservative and could underestimate real losses by excluding relatively rare species.

Global change variables

The variables chosen to measure aspects of global change varied between the most recent and historical time periods across the USA. Pesticide applications (the difference between the most recent and historical time period) increased by an average of 37.64 kg per 100 X 100 km quadrat. Extreme cases were also found, where some regions experienced massive increases of c. 28 722 kg per quadrat. The extent of cropland decreased by an average of 0.70 km^2 per quadrat throughout the US, with values ranging from -9.80 to 3.65 km^2 per quadrat, though crop yields rose substantially over the study period (Bigelow and Borchers 2017). For this reason, I did not

expect to detect strong effects of land use conversions in the model. Monthly average daily maximum temperature increased by a mean of 0.32 ^{0}C per quadrat, ranging between -0.67 ^{0}C to 1.33 ^{0}C per quadrat. Precipitation increased by a mean of 0.28 mm per quadrat in the most recent time period and varied between -30.80 mm and 42.27 mm per quadrat.

Phylogenetic mixed-effects model results

I compared six phylogenetic mixed-effects models, outlined in Table 2.1. I reported the posterior means (Table 2.2) and credible intervals associated with the predictor variables of the tested models (see Supporting Information: Table 2.S1 for the full report of credible intervals). Models 2, 3, and 4 tested potential interactions between pesticide application and climate variables. The credible intervals showed that the interaction term pesticides:precipitation was not significant in Models 3 and 4. Models 2 and 4 identified pesticides:temperature as the most informative interaction. Further, the estimated posterior mean was markedly higher for the pesticides:temperature interaction in Model 2. The marginal value of the calculated pseudo R^2, which excludes the variance explained by the random effect, was highest for Model 2 than for any other model, and the DIC value was the lowest for Model 2. Model 2 supports the hypothesis that pesticide application and temperature change interact in their impact on odonate persistence. Trace and density estimates were reported for every tested model, which demonstrated model convergence and that there was no autocorrelation among predictor variables (see Supporting Information: Figures 2.S3-2.S8).

Figure 2.3 shows the relative importance of each Z-scored global change variable on explaining odonate presence change between the two time periods for Model 2. The interaction between pesticide application and temperature explained the majority of the model variance.

Species declined more strongly under both increasing temperatures and pesticide exposure. Precipitation change was also significant in the model and was positively associated with persistence. I mapped persistence predictions based on this model using raster data of each global change variable for data visualization purposes (Figure 2.4).

The phylogenetic Model 2 indicates better model fit than the non-phylogenetic Model 5. Odonate species' responses to these aspects of global change are more similar among species with greater shared evolutionary history (Table 2.2). Even though removing the phylogenetic term led to poorer model fit, the main effects of global change variables remained similar where characteristics of global change still exerted strong effects on odonate persistence.

Relationship between species' persistence and range limit shifts

I used Model 6 to determine if species' abilities to expand their range have a significant impact on species' persistence in historically-occupied areas. Species shifting their range towards higher northern latitudes in the USA were more likely to persist elsewhere in their ranges (Model 6, Table 2.2). Overall, odonates shifted their northern range limits by 158 km since 1980 in the USA. Most species in this study are also found in areas of Canada and Alaska, so caution is necessary in interpreting this result. The main goal of measuring range shifts was to create a metric to capture each species' dispersal toward historically unoccupied habitat at higher latitudes, not to assess a comprehensive measure of species' range shifts throughout the continent. Further research is necessary to report true range shifts of odonates at continental extents in North America.

Discussion

Odonate species declines related clearly to the interaction between rising temperatures and growing pesticide applications across the USA. At broad scales, odonate diversity is mainly governed by climate (Suhling et al. 2015), so climate change makes diversity change more likely (Kerr et al. 2007). Moreover, species nearer the edge of their physiological capacities may have reduced capacity to tolerate additional environmental changes, such as pesticides. Projected temperatures over the next century (+2.5 Celsius and +5 Celsius) will likely cause dragonfly larvae to emerge earlier and show higher rates of mortality (McCauley et al. 2015, 2018). It remains uncertain how acclimation to temperatures outside species' realized thermal limits will affect odonate species occurrences at broad extents. This is an area for future research. Increasing temperatures combined with exposure to pollutants can alter the metabolic transformation of pesticide residues, especially among aquatic species. Tolerant organisms may face higher toxicity to a pollutant as its metabolites become more bioactive under warming (Lydy et al. 1999, Buckman et al. 2007). Acute lethality can increase severely in species exposed to both warming temperatures and pesticides of the organophosphate class (Monserrat and Bianchini 1995) but these effects are likely to generalize to many contaminants under global warming.

Precipitation may also increase pesticide-related risks on humans and wildlife by increasing the volatilization of pollutants (Noyes et al. 2009). Alternatively, increased precipitation may be positively related to odonate abundance and diversity, especially where surface temperatures warmed (Hassall and Thompson 2008, Ball-Damerow et al. 2014). I detected a significant positive effect of precipitation on species persistence, although this effect was weaker than the pesticide-temperature interaction term. Precipitation in the USA increased

by 4% over the past century, but with large regional variation, and is projected to rise overall as climate change progresses (Easterling et al. 2017) possibly creating new habitats to odonates while other areas continue to face aggravated drought.

I detected small, negative effects of land use change on odonate persistence. Land use changes can threaten some dragonfly species (Clausnitzer et al. 2009, Goertzen and Suhling 2019). There are several potential reasons why my results showed smaller direct effects of land use change on these species. First, I distinguish between pesticide use and land use conversions. For species in this study, directly measured effects of pesticide applications, and their interaction with climate change, account for much of the overall effect on odonate decline that might otherwise be attributed to land use change. Second, odonate species in this study require aquatic habitats, so land use changes in adjacent, terrestrial environments are more likely to affect odonates indirectly, while nontarget impacts of pesticide applications may still pose significant risks. Finally, past wetland conversions across much of the USA almost certainly caused significant changes in odonate communities in many areas, though rates of conversion have likely declined (Lomnicky et al. 2019). Measurements of baseline species' distributions in the US very likely reflect historical wetland conversions prior to the beginning of this study.

Across the US, there has been a shift from applications of organophosphorus and N-methyl carbamate-based pesticides to more toxic and persistent neonicotinoids and pyrethroids over the last two decades (DiBartolomeis et al. 2019). Certain crop types including corn and soybean, are particularly associated with environmental accumulation of pesticide residues (DiBartolomeis et al. 2019). Pesticides remain in the environment from a few hours up to several years, and can be transported long distances from areas of application through the hydrological cycle, reaching surface water necessary to odonate habitat (de Souza et al. 2020). Alternatively,

the time periods chosen here may hinder detection and attribution of land use change effects since the total area of cropland in the USA decreased in recent years compared to baseline data (Bigelow and Borchers 2017). I faced limits in the ability to compare land use change effects to pesticide exposure, due to the lack of available pesticide data in previous years. This work emphasizes the importance of collecting and making available such data (with permission from the data owners), as they are crucial to understand the broader patterns of biodiversity responses.

Species with greater shared evolutionary history tend to respond in similar ways to the key global change drivers. With respect to climate change, odonates' evolved under tropical conditions (García-Robledo et al. 2016), so niche conservatism in species' tolerances to those conditions would explain species' similar responses to climate change (Kerr et al. 2015). Odonate species' biogeographical origin regulates both vulnerability to extinction, and species distributions (Rocha-Ortega et al. 2020). There are several inherited traits that may relate to species' ability to disperse and establish in newly suitable habitats, tolerate climatic disturbances, and for species to escape threats related to land use intensification. Zygoptera (damselfly) species of the genera *Enallagma* and *Lestes* consistently declined, while Anisoptera (dragonfly) species that belong to the *Leucorrhinia*, *Libellula*, and *Sympetrum* genera all displayed increased persistence between the two time periods. These Zygoptera taxa disperse less rapidly than anisopterans (dragonflies), and their spatial distributions are often constrained by specific habitat ecological and behavioral requirements (Corbet 1999). There are limits on the extent to which such generalized traits predict probabilities of persistence, as one of the damselfly genera (*Ischnura*) appeared to be relatively robust, while one of the dragonfly genera (*Aeshna*) declined more rapidly. Though complex, the relationships between body size, thermal limits, and breeding habitat – namely, lotic vs. lentic – with population abundance provide indications of extinction

risks (Rocha-Ortega et al. 2020). In general, breeding in lotic habitats, larger body size (for damselflies), smaller range size, and habitat specialism are negatively associated with odonate occurrences (Powney et al. 2015, Rocha-Ortega et al. 2020).

Species that shifted their ranges north were more likely to persist in areas they historically occupied. The capacity to disperse to, and establish populations in, new environments are key to range expansion, but these characteristics are also likely to help species escape potential threats of habitat degradation, find areas with better microclimates, or otherwise shelter from climate change. While range limits often reflect niche limits, environmental change can sometimes cause realized niche limits to shift in geographic space, creating gaps between niche and range limits (Bedford et al. 2012, Devictor et al. 2012, Lee-Yaw et al. 2016). When species ranges either expand or contract with exposure to unsuitable climates, dispersal abilities must be sufficient for organisms to reach new suitable habitats within their niche (Hargreaves et al. 2014). Odonates' strong dispersal abilities along with their broad geographical ranges may also lower their extinction risk in comparison to other invertebrates (Clausnitzer et al. 2009).

This work demonstrates the importance of global change on habitat degradation of odonates at a macroecological scale, a necessary step toward distinguishing between species that persist or even thrive as a result of global changes and others that may decline or face extinction. Climate change interacts with recent, rapid rises in pesticide applications to increase dragonfly and damselfly extinction risks, a clear demonstration that multi-stressor frameworks are vital to identifying risks related to global change. Potential non-target effects of pesticides merit broader consideration in terms of how – and how much – pesticides are applied to agricultural areas, particularly if those are near aquatic environments. Species shifting their range limits toward northern latitudes persisted more reliably elsewhere in their geographical ranges, suggesting that

traits like dispersal capacity that accelerate range shifts also facilitate persistence, trends that are reflected in the shared evolutionary histories of these species.

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Tables and figures

Table 2.1: Six phylogenetic models that were tested and compared to assess the effects of four global change variables and interactions between them, as well as species northern range limit shifts, on odonate persistence across the United States of America. All models except Model 5 account for phylogeny. These models were run using the *MCMCglmm* R package.

Variable	Model
Species*	1, 2, 3, 4, 5, 6
Pesticides	1, 2, 3, 4, 5
Temperature	1, 2, 3, 4, 5
Precipitation	1, 2, 3, 4, 5
Land use	1, 2, 3, 4, 5
Sampling intensity	1, 2, 3, 4, 5
Pesticides:Temperature	2, 4, 5
Pesticides:Precipitation	3, 4
Range expansion	6

Note: * = random effect

Table 2.2: Results of all MCMCglmm models considered to assess the effects of four global change variables, as well as species northern range limit shifts, on odonate persistence across the United States of America. All models except Model 5 take phylogeny into account. Values in the table represent the estimated posterior mean calculated by the *MCMCglmm* R package. An asterisk symbol indicates non-zero credible intervals, which confirms the significance of the variable in question. The dash symbol shows the variables that were not included in the associated model.

	Model 1	**Model 2**	**Model 3**	**Model 4**	**Model 5**	**Model 6**
Model variables						
(intercept)	0.782	0.677	0.771	0.640	0.770*	0.795
Pesticides	-0.211*	-0.280*	-0.290*	-0.26*	-0.280*	-
Temperature	-0.032	0.101	-0.035	0.104	0.064	-
Precipitation	0.079*	0.063*	0.055	0.068*	0.051	-
Land use	0.037	-0.066	0.018	-0.067	-0.062	-
Sampling intensity	0.091*	0.003	0.108*	-0.011	0.009	-
Pesticides:Temperature	-	-0.349*	-	-0.407*	-0.396*	-
Pesticides:Precipitation	-	-	-0.026	0.011	-	-
Range expansion	-	-	-	-	-	0.001*
Model evaluation metrics						
R^2	0.090	0.15	0.098	0.148	0.124	0.007
DIC	1431.47	1397.49	1429.73	1399.07	1406.30	4261.30

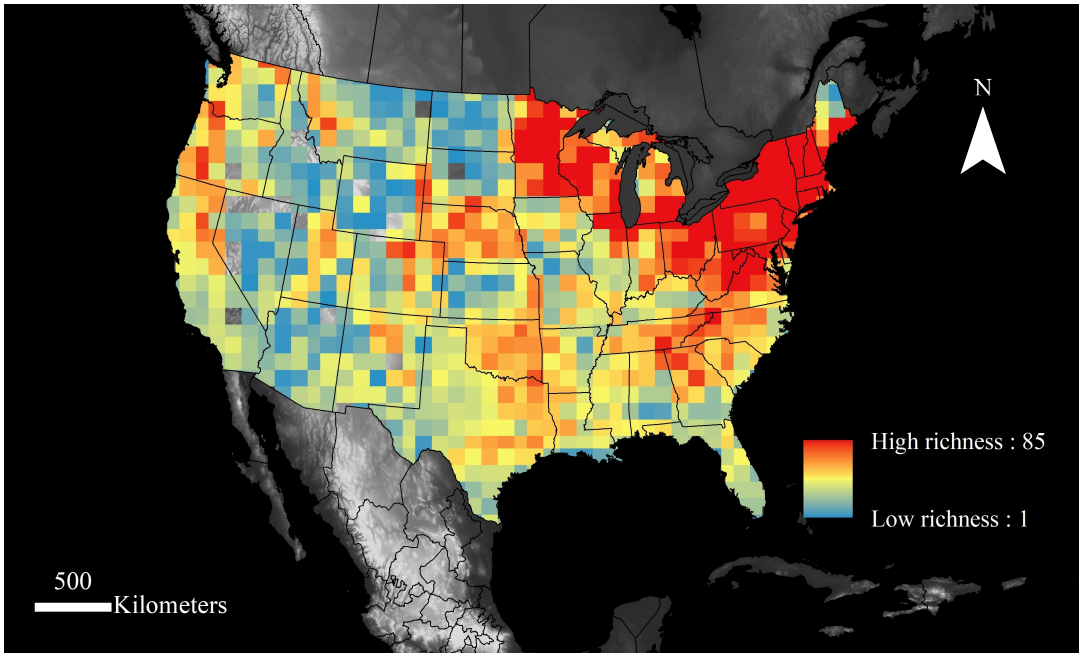


Figure 2.1: Total distribution and richness of 104 odonate species sampled in the United States of America between 1980 and 2018. Species included here are found in at least 100 quadrats of 100 X 100 km. Warm and cool colors show high and low richness respectively. This map was projected with the Albers Equal Area projection and produced with ArcGIS software version 10.7.1.

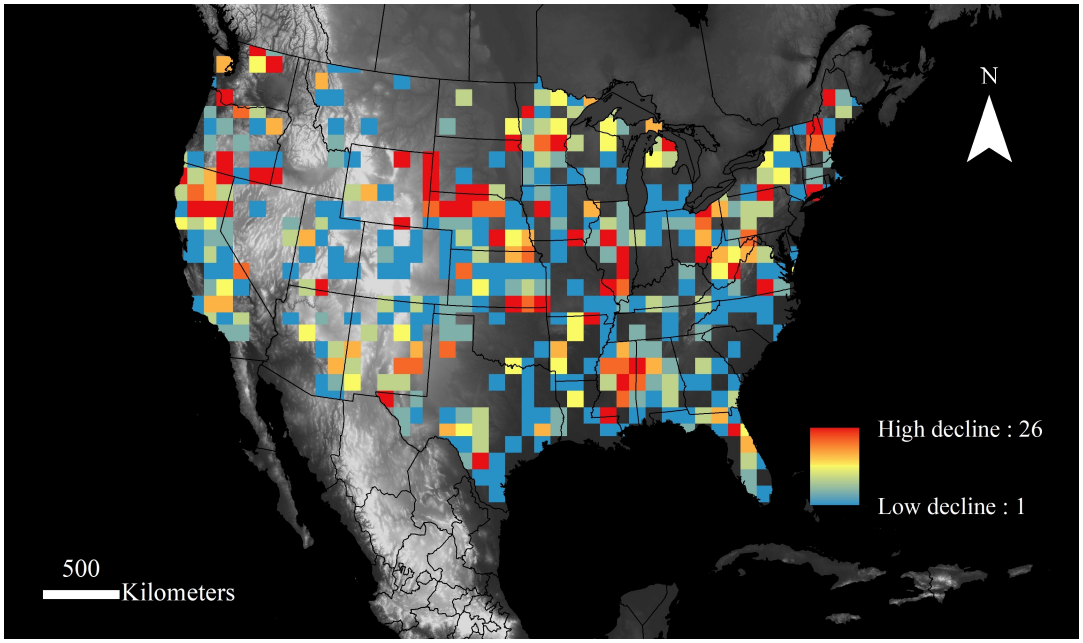


Figure 2.2: Decline of 104 odonate species richness per quadrat sampled in the USA between the first (1980 – 2002) and the second time period (2008 – 2018), within 100 X 100 km quadrats. Warm and cool colors show high and low numbers of species lost. To measure declines within species historical ranges, I used strict criteria of quadrat and species selection (detailed description in the methods section) to compensate for imperfect detection and sampling effort. This map was projected with the Albers Equal Area projection and produced with ArcGIS software version 10.7.1.

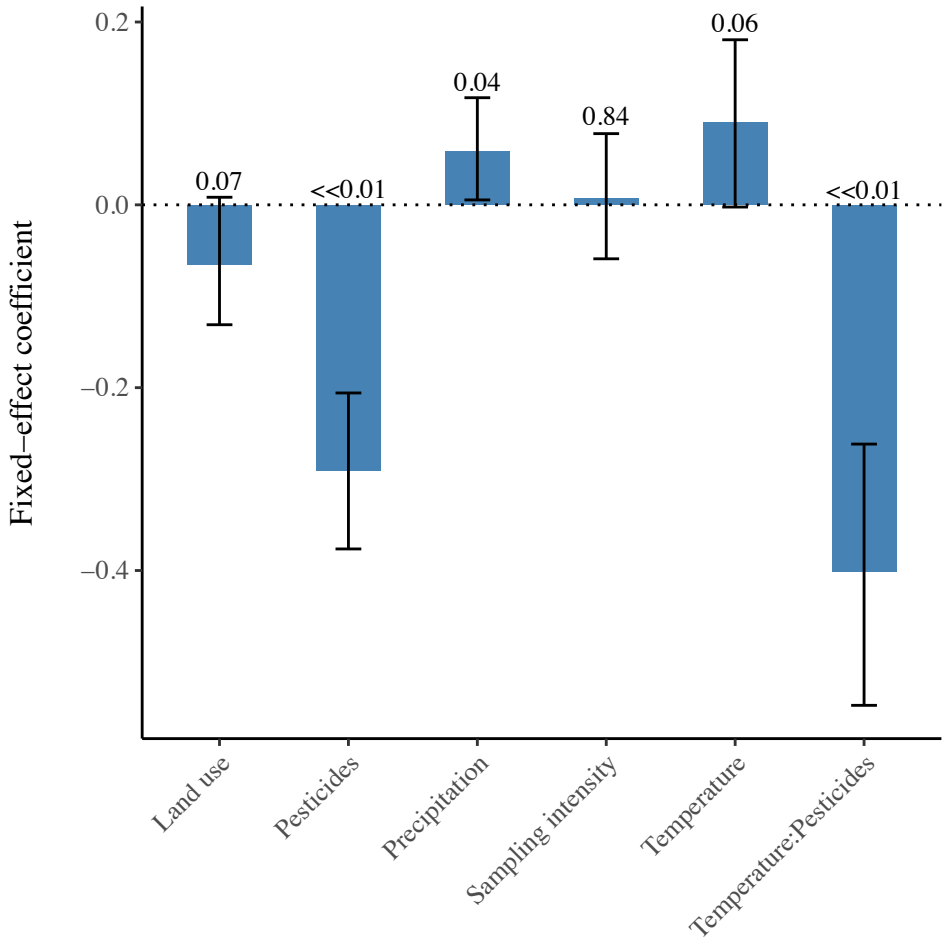


Figure 2.3: Effect of each Z-scored variable on odonate presence change between historical and current observation records, as determined by MCMCglmm model coefficients (Model 2) and their associated posterior distributions. Probabilities (p-values) for each variable in this model are indicated above the bars for ease of model interpretation.

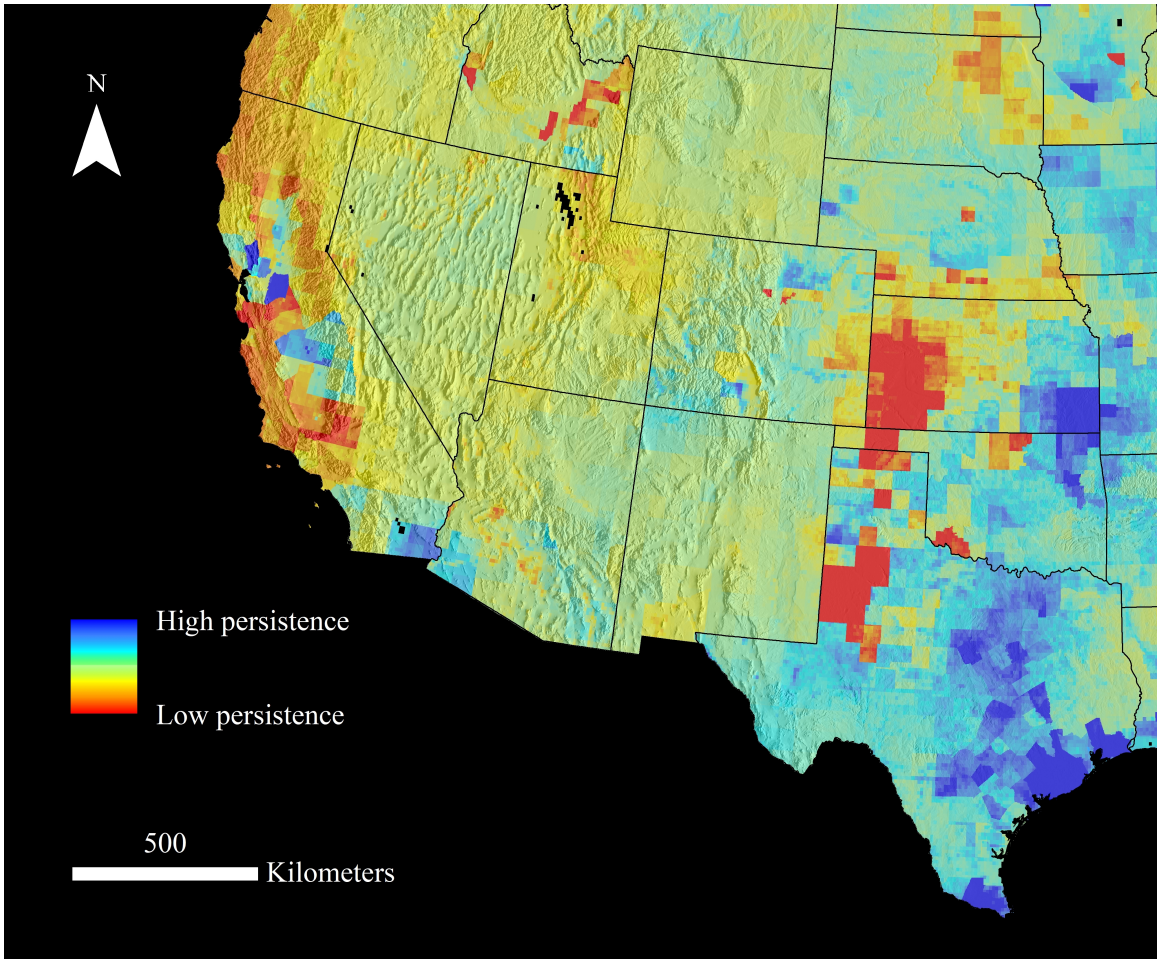


Figure 2.4: Data visualization of the impact of global change on odonate presence change between historical and current observation records, as determined by MCMCglmm model coefficients (Model 2). Coefficient values and statistical significance are shown in Figure 3. Warm and cool colors show areas where species are predicted to have declined or persisted respectively, between the first (1980 – 2002) and the second time period (2008 – 2018), based on climate, land use, and pesticide application change. This map was projected with the Albers Equal Area projection and produced with ArcGIS software version 10.7.1. High resolution elevation data used for the shaded relief layer originates from the WorldClim 2.1 database (downloaded at https://www.worldclim.org/data/worldclim21.html).

Supporting Information for Chapter 2

Section S1: Supplementary Design and Methodology

Odonate data

The full raw dataset includes over 2 million observations, including approximately 815 000 North American Odonata occurrence records. I first removed inadequate records from the primary dataset. Inadequate records were identified as those with incomplete information for species identification, year, or locality, inaccurate georeferenced points, and duplicate records. The United States of America (USA) was densely sampled compared to observation records of Northern Mexico and Northern Canada. I restricted the study extent because the pesticides data was only available in the USA, and because my assessment of range limit shifts benefits from including the most densely sampled locations for more accurate results. The following list enumerates 104 odonate species sampled across the USA between 1980 and 2018 which follow my criteria for quality observation records for inclusion in the analysis.

Aeshna canadensis
Aeshna constricta
Aeshna eremita
Aeshna interrupta
Aeshna juncea
Aeshna palmata
Aeshna sitchensis
Aeshna tuberculifera
Aeshna umbrosa
Amphiagrion abbreviatum
Amphiagrion saucium
Anax junius
Argia apicalis
Argia fumipennis
Argia moesta
Argia sedula
Argia tibialis
Argia vivida
Basiaeschna janata
Boyeria vinosa
Calopteryx aequabilis
Calopteryx maculata
Celithemis elisa
Celithemis eponina
Chromagrion conditum
Coenagrion resolutum
Cordulegaster maculata
Cordulia shurtleffii
Didymops transversa
Dorocordulia libera
Dromogomphus spinosus
Enallagma annexum
Enallagma antennatum
Enallagma aspersum
Enallagma basidens
Enallagma boreale
Enallagma carunculatum
Enallagma civile
Enallagma ebrium
Enallagma exsulans
Enallagma geminatum
Enallagma hageni
Enallagma signatum
Enallagma vesperum
Epitheca canis
Epitheca cynosura
Epitheca princeps
Epitheca spinigera
Erythemis simplicicollis
Hagenius brevistylus
Hetaerina americana
Ischnura cervula
Ischnura hastata
Ischnura perparva
Ischnura posita
Ischnura verticalis
Ladona julia

Lestes congener
Lestes disjunctus
Lestes dryas
Lestes forcipatus
Lestes inaequalis
Lestes rectangularis
Lestes unguiculatus
Lestes vigilax
Leucorrhinia frigida
Leucorrhinia glacialis
Leucorrhinia hudsonica
Leucorrhinia intacta
Leucorrhinia proxima
Libellula forensis
Libellula incesta
Libellula luctuosa
Libellula pulchella
Libellula quadrimaculata
Libellula saturata
Macromia illinoiensis
Nehalennia irene
Ophiogomphus severus
Pachydiplax longipennis
Pantala flavescens
Pantala hymenaea
Perithemis tenera
Phanogomphus exilis
Phanogomphus lividus
Phanogomphus spicatus
Plathemis lydia
Rhionaeschna californica
Rhionaeschna multicolor
Somatochlora franklini
Somatochlora minor
Somatochlora semicircularis
Somatochlora walshii
Stylogomphus albistylus
Sympetrum corruptum
Sympetrum costiferum
Sympetrum danae
Sympetrum internum
Sympetrum obtrusum
Sympetrum pallipes
Sympetrum rubicundulum
Sympetrum semicinctum
Sympetrum vicinum
Tramea lacerata

Model information and statements

I report the full base model statement 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 associated with a binary response variable, and a categorical random variable. The family "threshold" was selected because of the binary nature of the data.

```
Aphylo ← vcv(phylogeny, model = "Brownian", corr = T)
Ainv ← inverseA(phylogeny, nodes = "TIPS", scale = F)$Ainv

prior ← list(R=list(V=1,fix=1),
        G=list(G1=list(V=1,nu=0.02)))

MCMCglmm(Persistence ~ Pesticides + Temperature + Precipitation + Land use + Sampling intensity, random = ~ Species, ginverse = list(species = Ainv), family = "threshold", prior = prior, DIC = T, nitt = 200000, thin = 50, burnin = 20000, data)
```

Further, I tested whether species that expand their range more strongly are also expected to persist or decline between a historical and a recent time period.

```
MCMCglmm(Persistence ~ Range expansion, random = ~ Species, ginverse = list(species = Ainv), family = "threshold", prior = prior, DIC = T, nitt = 100000, thin = 50, burnin = 10000, data)
```

Section S2: Supplementary Acknowledgements

I sincerely thank data contributors who have made this project possible. The majority of observation records were downloaded from two online aggregators of databases, GBIF (GBIF.org) and Canadensys (canadensys.net). I supplemented the dataset with data originating from other institutions including OdonataCentral (Abbott 2020), the Ontario Odonata Atlas Database (Ontario Ministry of Natural Resources and Forestry), a repository of seven entomological collections of Québec (Favret et al. 2020), and entomological collections of the Royal Ontario Museum, the Royal BC Museum, and the California Academy of Sciences. The following list enumerates all institutions within the full raw dataset, ordered by the number of records contributed.

Institution Name	Number of records contributed
Odonata Central	251269
iNaturalist Research-grade Observations	137000
Ontario Odonata Atlas Database	98309
Ouellet-Robert entomological collection (QMOR)	81132
NMNH Extant Specimen Records	51000
Université de Montréal Biodiversity Centre	31980
Royal BC Museum	30770
BugGuide - Identification, Images, & Information For Insects, Spiders & Their Kin For the United States & Canada	17000
Royal Ontario Museum	14510
University of British Columbia - Spencer Entomological Collection (UBCZ)	14257
Illinois Natural History Survey Insect Collection	11000
C.A. Triplehorn Insect Collection (OSUC), Ohio State University	8000
Snow Entomological Museum Collection	8000
Odonata de Veracruz	6000
Collection entomologique de l'Université Laval (ULQC)	5149
Cleveland Museum of Natural History.	4000
Odonates des Antilles françaises	4000
Entomology Division, Yale Peabody Museum	3000
Insecta of Costa Rica (INBio)	3000
International Barcode of Life project (iBOL)	3000

Odonata de la huasteca potosina (insecta)	3000
Texas A&M University Insect Collection	3000
California Academy of Sciences	2615
Insectarium de Montréal (IMQC)	2004
CAS Entomology (ENT)	2000
Diversidad de ocho grupos de insecta (Odonata, Lycidae, Phengodidae, Lampyridae, Cantharidae, Cerambycidae, Syrphidae y Vespidae) en tres regiones con bosque tropical caducifolio en México	2000
UAM Insect Collection (Arctos)	2000
Lyman Entomological Museum (LEMQ)	1921
University of Guelph Insect Collection (DEBU)	1738
Espace pour la vie (CIQ)	1641
Centre for Biodiversity Genomics - Canadian Specimens	1000
Recent Invertebrates Specimens	1000
Stuart M. Fullerton Collection of Arthropods (UCFC), University of Central Florida	1000
University of Alberta Freshwater Invertebrate Collection (UAFIC)	989
Reconocimiento de la biodiversidad de la Reserva de la Biósfera Calakmul: Odonata, psocóptera y díptera acuáticos (Insecta)	858
Field Museum of Natural History (Zoology) Insect, Arachnid and Myriapod Collection	613
naturgucker	607
Diversidad de grupos selectos de vertebrados (Reptilia, Amphibia) e insectos (Lepidoptera: Papilionoidea y Hesperioidea; Odonata; Diptera: Bombyliidae) en el Valle de Cuatrociénegas y Sierra de la Madera, Coahuila, México	533
Geographically tagged INSDC sequences	487
Entomology Collection at the Natural History Museum of Utah	464
Bishop's University Insect Collection (BUIC)	456
CNIN/Tipos Odonata	225
University of Alberta E. H. Strickland Entomological Museum (UASM)	218
Insectarium René-Martineau (IRM)	214
UAM Insect Observations (Arctos)	176
Diversidad y distribución geográfica de las especies de culícidos de importancia médica en la región centro-occidental de México	164
A synopsis of the Neotropical genus Protoneura (Odonata: Coenagrionidae)	140
New species of the damselfly genus Argia from Mexico, Central America and Ecuador with an emphasis on Costa Rica (Insecta: Odonata: Coenagrionidae)	139
Colorado Plateau Museum of Arthropod Biodiversity	132
Macaulay Library Audio and Video Collection	132
Paleobiology Database	124
Questagame weekly feed	118

Fauna acuática de importancia ecológica (crustáceos, insectos y peces) de la cuenca del río Moctezuma Querétaro-Hidalgo	99
CHAS Entomology Collection (Arctos)	91
UPRM Invertebrate Collection	91
Computarización de la Colección Nacional de insectos Dr. Alfredo Barrera Marín del Museo de Historia Natural de la Ciudad de México	67
Invertebrate Paleontology Division, Yale Peabody Museum	49
Inventaire entomologique standardisé des ZNIEFF de Martinique, protocole utilisé en 2014 et 2015	48
Ontario BioBlitz Species Records	48
Inventory and BioBlitz Records from rare Charitable Research Reserve	45
Biodiversity Institute of Ontario	44
Données photographiques validées de la galerie du forum "Le Monde des Insectes"	42
CU Invertebrate Paleontology	40
Base de datos de la Colección zoológica del Instituto de Investigación de zonas desérticas de la Universidad Autónoma de San Luis Potosí (BDCZIID-UASLP)	35
Inventaire entomologique standardisé des ZNIEFF de Martinique, protocole utilisé de 2011 à 2013	35
Colección Macroinvertebrados Acuáticos Universidad Católica de Oriente	33
Ville de Trois-Rivières	32
Macroinvertebrados y perifiton pertenecientes a cuatro regiones de Colombia	29
Atlantic Reference Centre (ARC) Museum of Canadian Atlantic Organisms - Invertebrates and Fishes Data	29
KNWR Entomology Collection	21
Étude entomologique des forêts publiques de Martinique, pour l'ONF	20
USGS Patuxent Wildlife Research Center Seabirds Compendium	19
Caracterización de fauna y flora para el establecimiento de límites funcionales de humedales en tres ventanas piloto: Ciénaga de la Virgen, Ciénaga Zapatosa y Complejo de humedales Paz de Ariporo - Hato Corozal	13
Natural History Museum Rotterdam (NL) - Insecta collection	11
Rapid Assessment Program (RAP) Biodiversity Survey Database	11
Paleobiology Database	10
Colección Limnológica del Chocó	8
Museum of Southwestern Biology, Division of Arthropods	8
Borror Lab of Bioacoustics (BLB), Ohio State University	7
Colección Entomológica de Piedras Blancas	7
Entomological Collections (NHRS), Swedish Museum of Natural History (NRM)	6
Harold W. Manter Laboratory of Parasitology Collection	6
VMNH Invertebrate Paleontology	6
BoBO - Botanic Garden and Botanical Museum Berlin-Dahlem Observations	5
Cordulegaster virginiae sp. nov. from Mexico, including a comparison with C. diadema Selys, 1868, and a redescription of its larva (Odonata: Cordulegastridae)	5

Arizona State University Hasbrouck Insect Collection	3
Australian National Insect Collection	3
Colección de Referencia de Macroinvertebrados Bentónicos del Museo de Ciencias de la Universidad El Bosque	3
Entomology at ZMUC, Natural History Musem of Denmark	3
Essig Museum of Entomology	3
The genus Heteragrion (Odonata: Zygoptera) in Northwestern Colombia, with the description of Heteragrion tatama sp. nov.	3
UCMC_Entomology	3
Données de type contact de Guadeloupe	2
Estonian Museum of Natural History	2
Museum of Comparative Zoology, Harvard University	2
Erpetogomphus oxybelis sp. nov. from Veracruz, Mexico (Odonata: Gomphidae)	1
Natusfera Citizen Science Observation Dataset	1
Observations naturalistes et collection entomologique de Julien TOUROULT	1
Odonata del Museo de Entomología de la Universidad del Valle	1
Phyllogomphoides enriquei (Odonata: Gomphidae) a new species from Mexico	1
USGS PWRC - Native Bee Inventory and Monitoring Lab (BIML)	1
Vegetación vascular terrestre, entomofauna y macrofauna de la Isla Cayo Serrana durante la Expedición Seaflower 2016 - Proyecto Colombia BIO	1

Section S3: Supplementary Figures 2.S1 – 2.S8

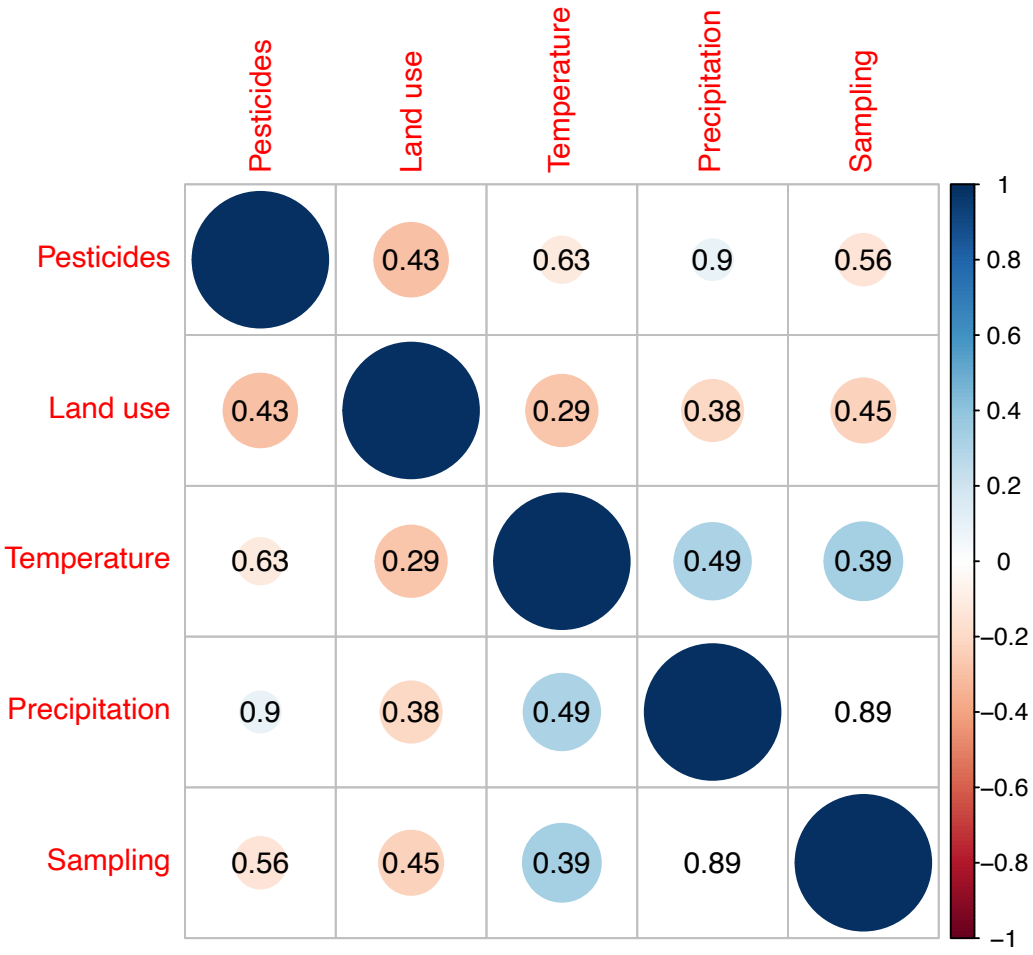


Figure 2.S1: Pearson correlation coefficients between all predictor variables likely to impact changes in odonate persistence. The criteria of p-value < 0.05 was used to determine whether potential correlations between variables were significant. P-values of the correlation test are shown for each pairwise test. P-values were calculated with the *cor* base function in R statistical software.

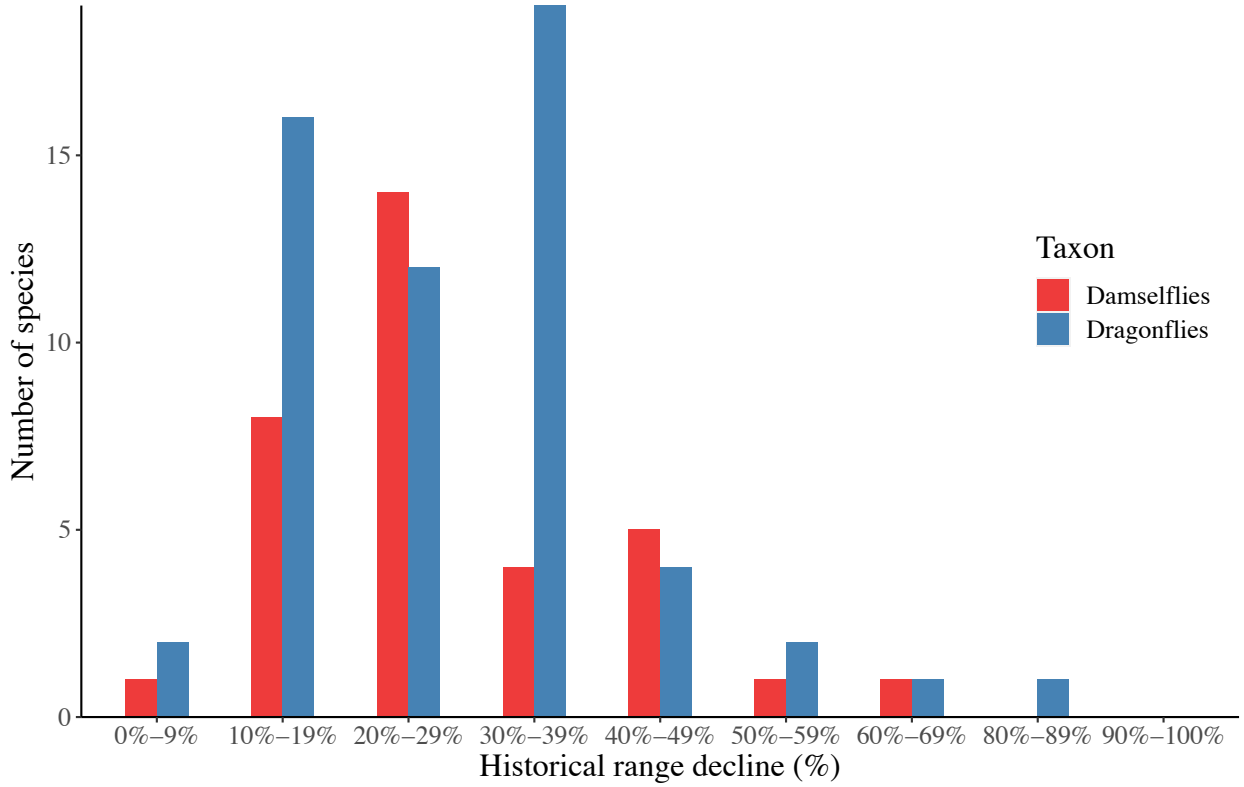
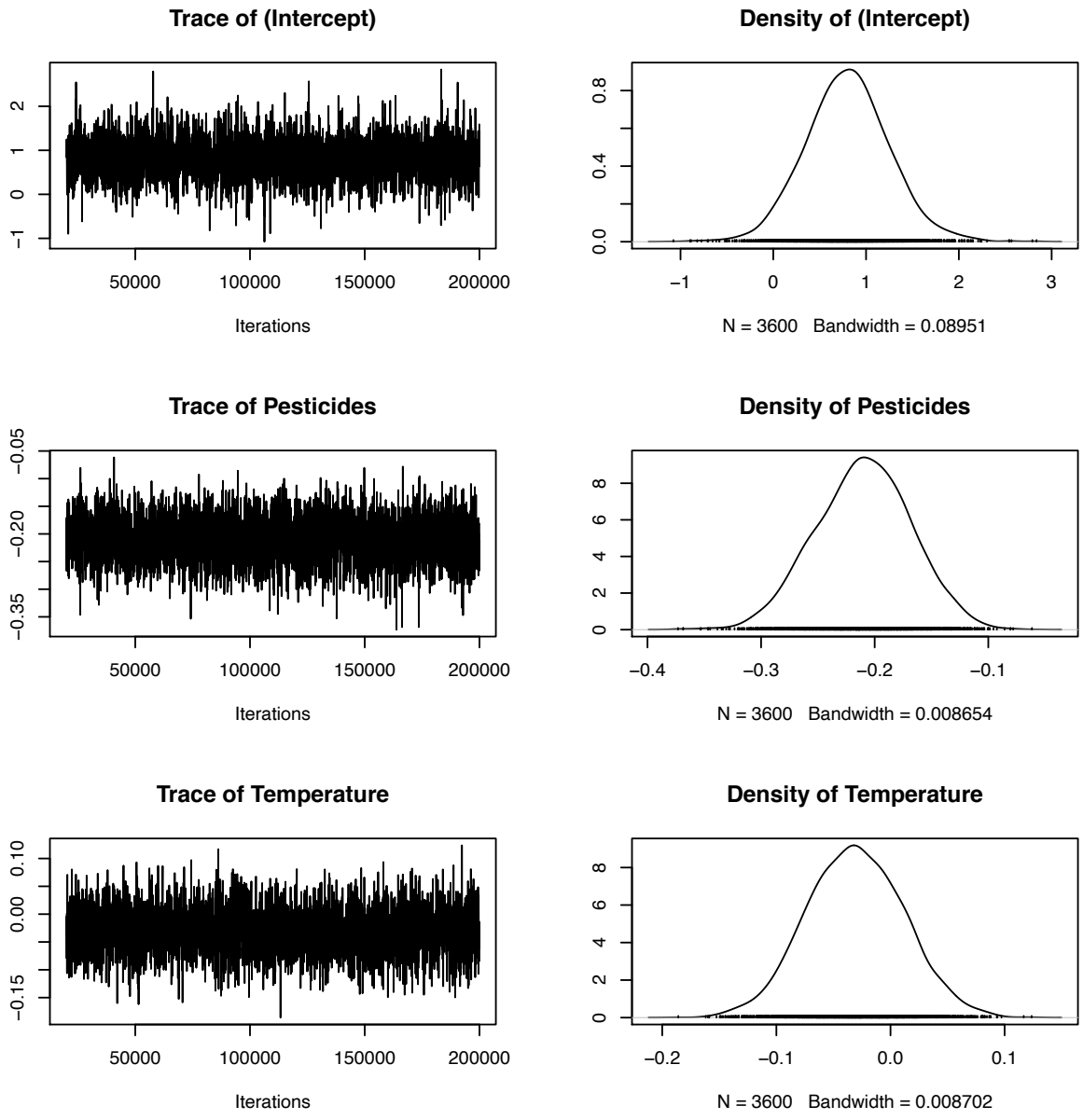


Figure 2.S2: Summary histogram ordered by category of decline in 104 species in the United States of America, showing the percentage of quadrats lost in recent years (2008-2018) compared to historical presences (1980-2002).

Figure 2.S3, A


Trace of (Intercept)
Density of (Intercept)
Iterations
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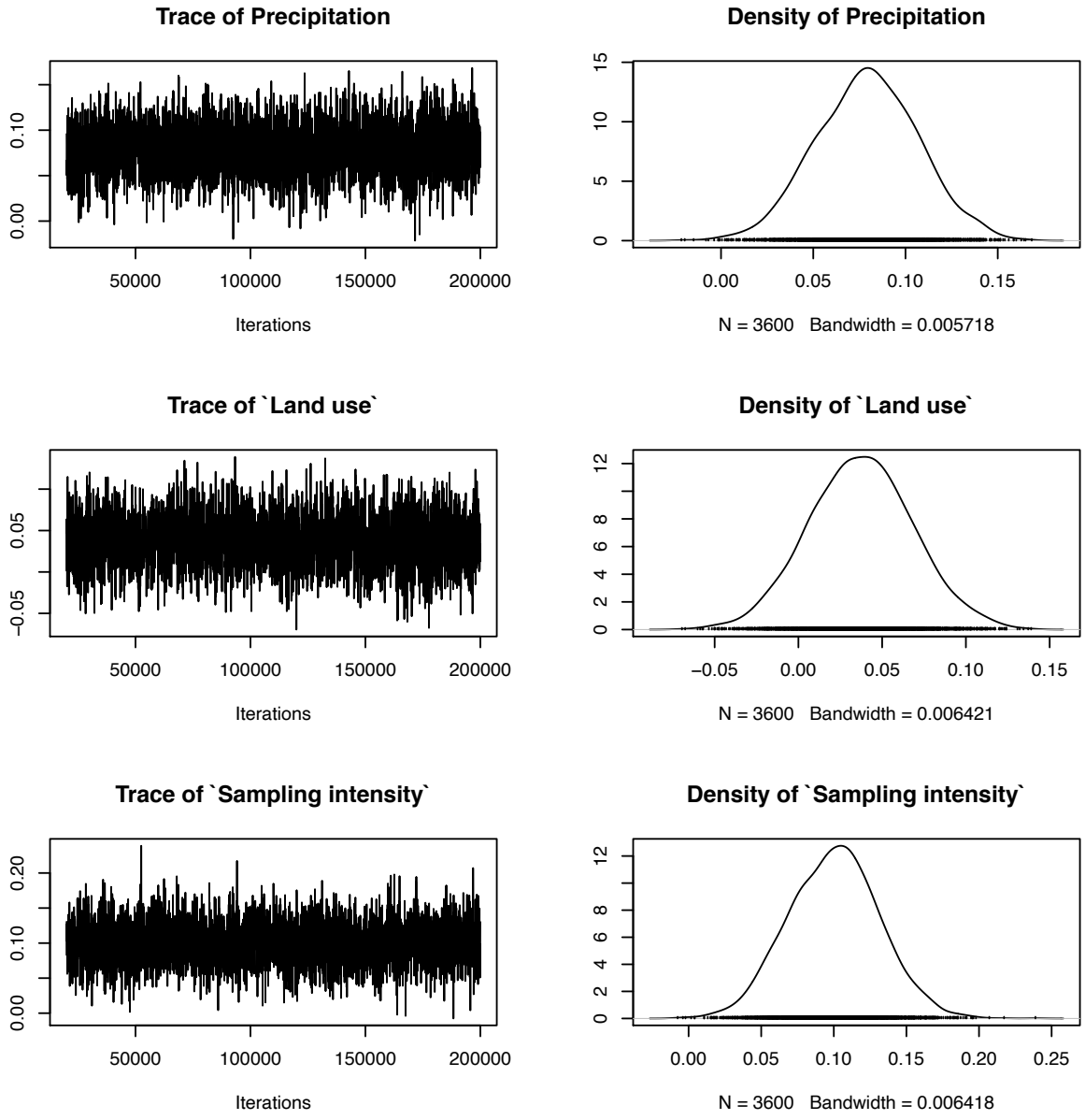
Trace of Pesticides
Density of Pesticides
Iterations
N = 3600 Bandwidth = 0.008654
Trace of Temperature
Density of Temperature
Iterations
N = 3600 Bandwidth = 0.008702

Figure 2.S3, B


Trace of Precipitation
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200000
Iterations
Density of Precipitation
0
5
10
15
0.00
0.05
0.10
0.15
N = 3600 Bandwidth = 0.005718
Trace of `Land use`
−0.05
0.05
50000
100000
150000
200000
Iterations
Density of `Land use`
0
2
4
6
8
12
−0.05
0.00
0.05
0.10
0.15
N = 3600 Bandwidth = 0.006421
Trace of `Sampling intensity`
0.00
0.10
0.20
50000
100000
150000
200000
Iterations
Density of `Sampling intensity`
0
2
4
6
8
12
0.00
0.05
0.10
0.15
0.20
0.25
N = 3600 Bandwidth = 0.006418

Figure 2.S3, C

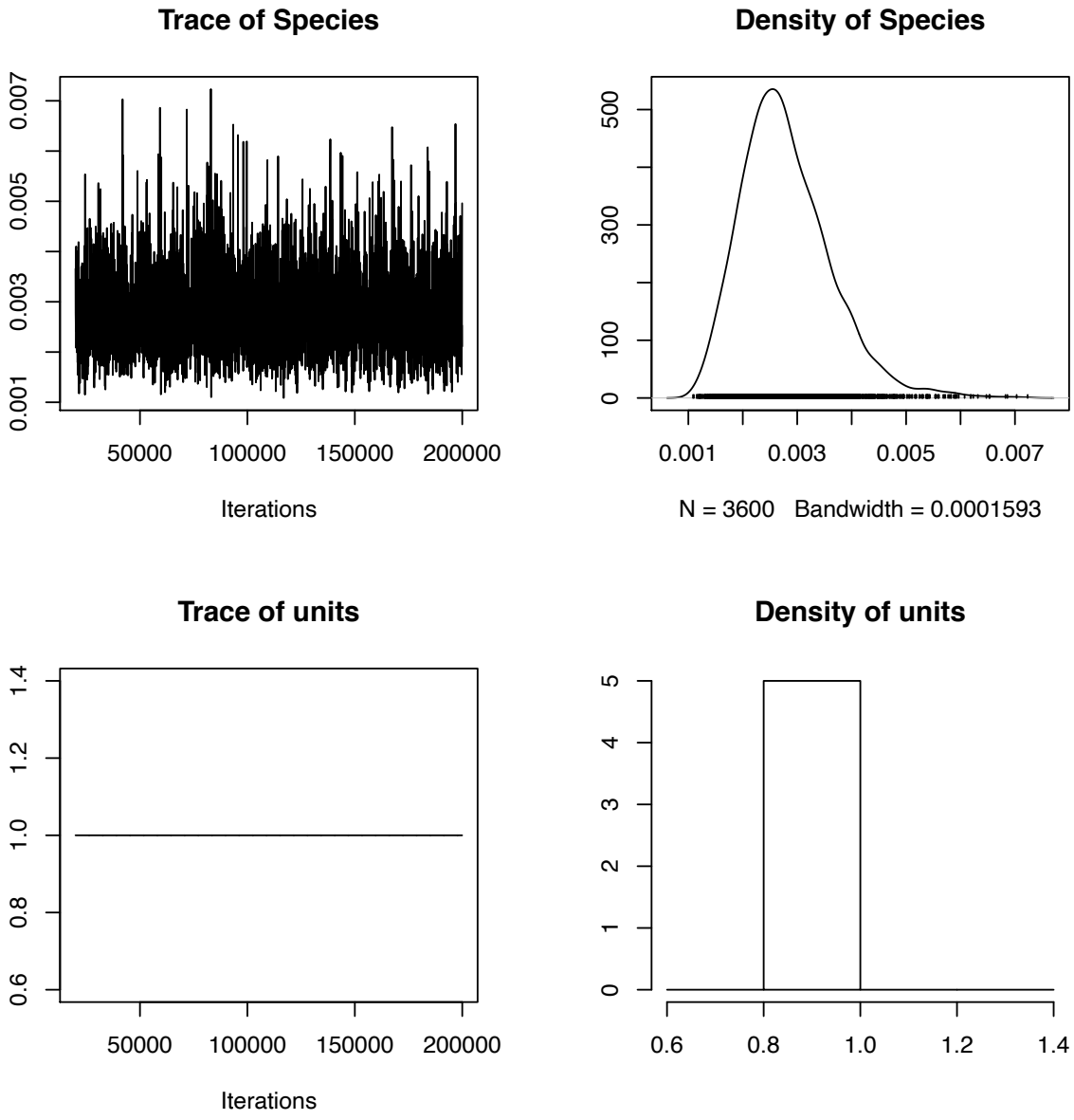

Figure 2.S3: Panels A, B and C show the trace and density estimates of Model 1, a phylogenetic mixed effects model using global change variables to explain odonate persistence in the United States of America, with species as a random effect. 200 000 iterations were run to produce these results. These plots verify model convergence and absence of autocorrelation among the explanatory variables.

Figure 2.S4, A

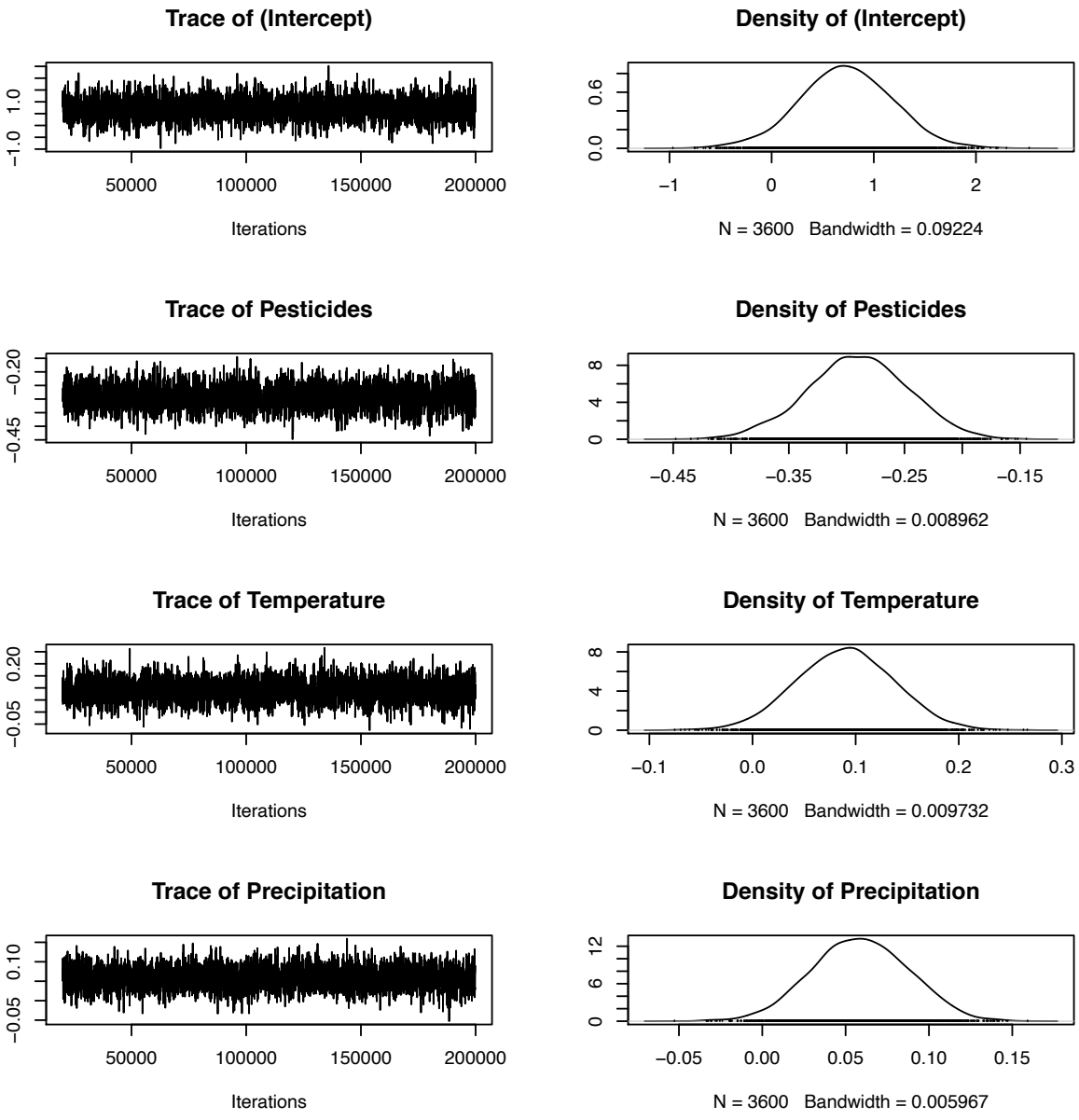
Trace of (Intercept)
Density of (Intercept)
Iterations
N = 3600 Bandwidth = 0.09224
Trace of Pesticides
Density of Pesticides
Iterations
N = 3600 Bandwidth = 0.008962
Trace of Temperature
Density of Temperature
Iterations
N = 3600 Bandwidth = 0.009732
Trace of Precipitation
Density of Precipitation
Iterations
N = 3600 Bandwidth = 0.005967

Figure 2.S4, B

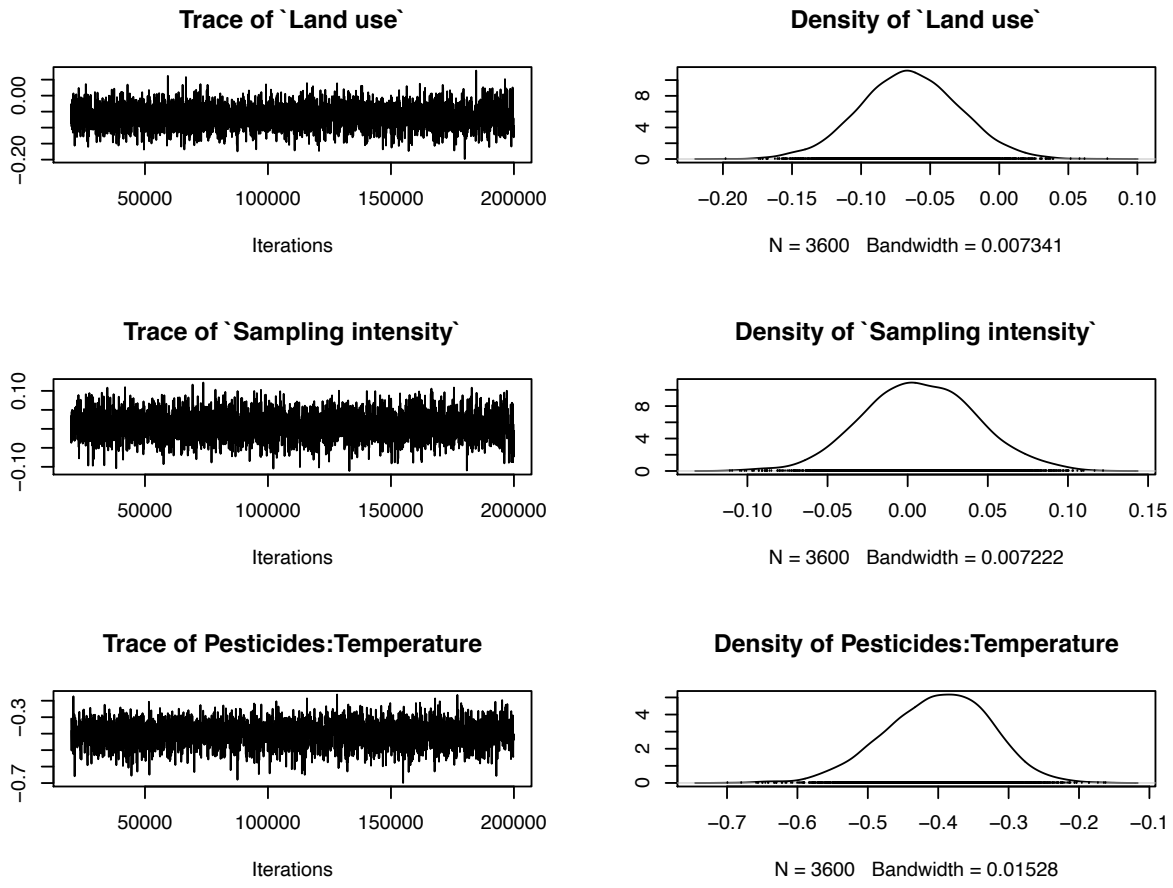
Trace of `Land use`
Density of `Land use`
Iterations
N = 3600 Bandwidth = 0.007341
Trace of `Sampling intensity`
Density of `Sampling intensity`
Iterations
N = 3600 Bandwidth = 0.007222
Trace of Pesticides:Temperature
Density of Pesticides:Temperature
Iterations
N = 3600 Bandwidth = 0.01528

Figure 2.S4, C

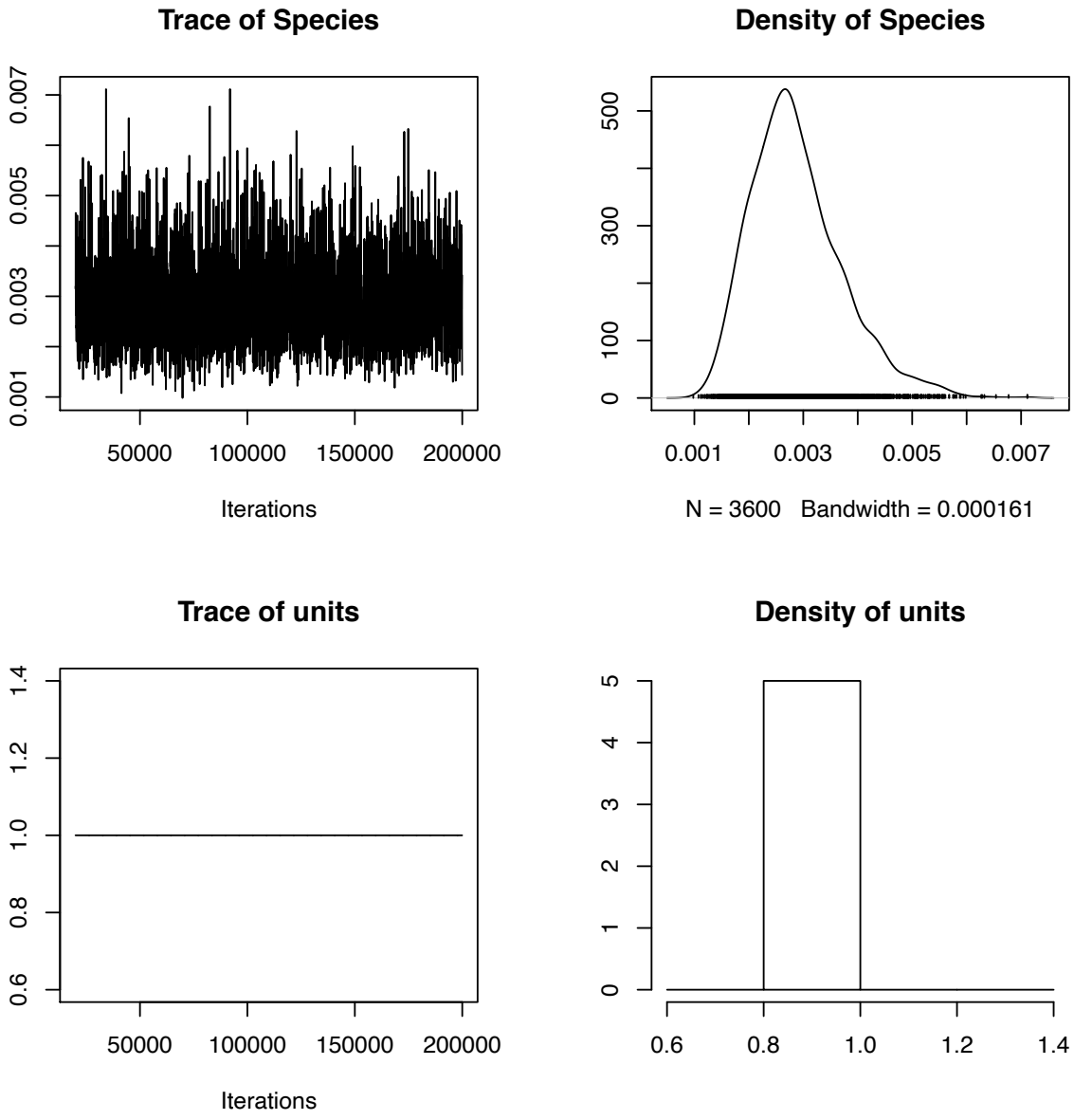

Figure 2.S4: Panels A, B and C show the trace and density estimates of Model 2, a phylogenetic mixed effects model using global change variables to explain odonate persistence in the United States of America, with species as a random effect. 200 000 iterations were run to produce these results. These plots verify model convergence and absence of autocorrelation among the explanatory variables.

Figure 2.S5, A

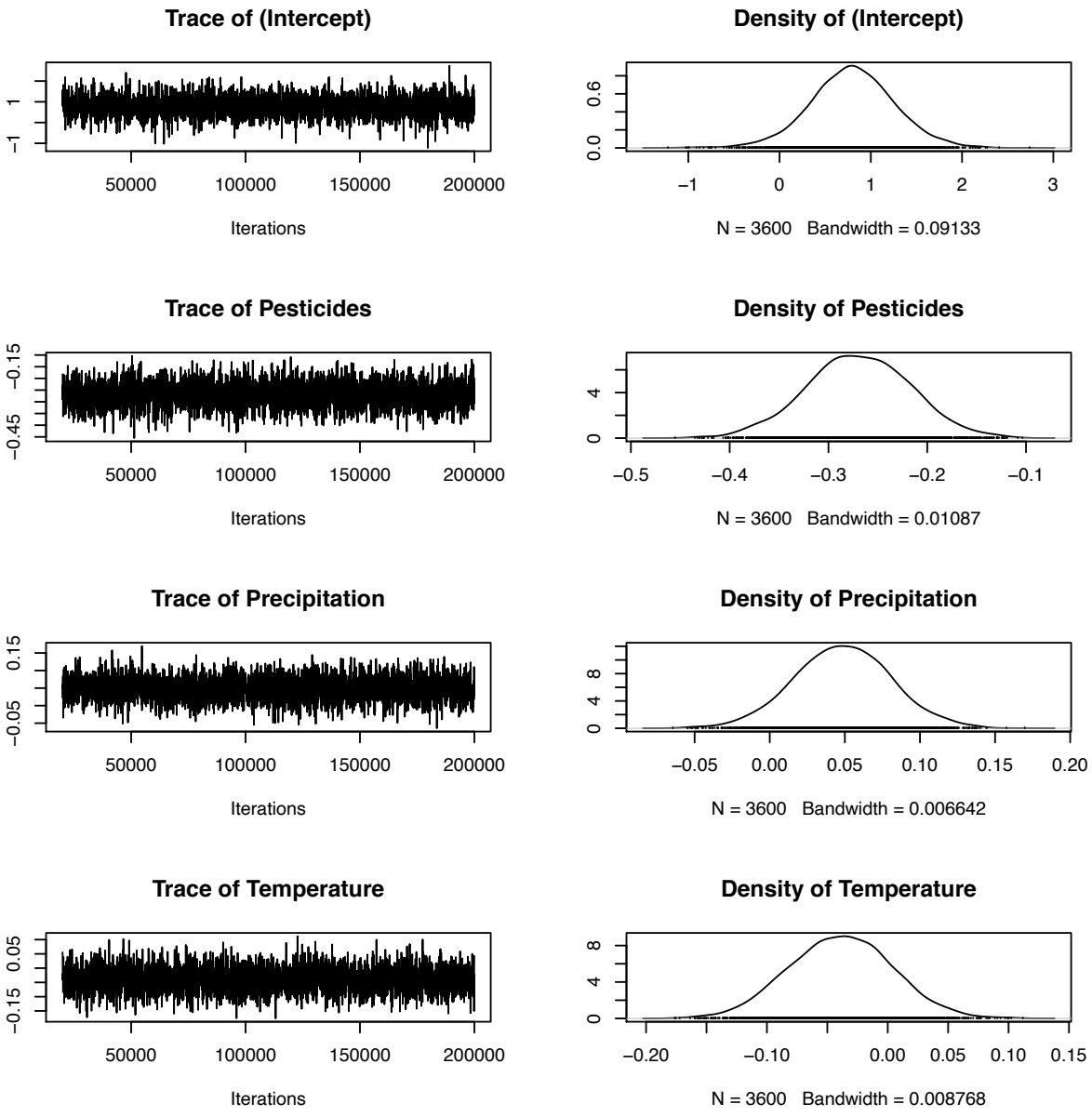
Trace of (Intercept)
Density of (Intercept)
Iterations
N = 3600 Bandwidth = 0.09133
Trace of Pesticides
Density of Pesticides
Iterations
N = 3600 Bandwidth = 0.01087
Trace of Precipitation
Density of Precipitation
Iterations
N = 3600 Bandwidth = 0.006642
Trace of Temperature
Density of Temperature
Iterations
N = 3600 Bandwidth = 0.008768

Figure 2.S5, B

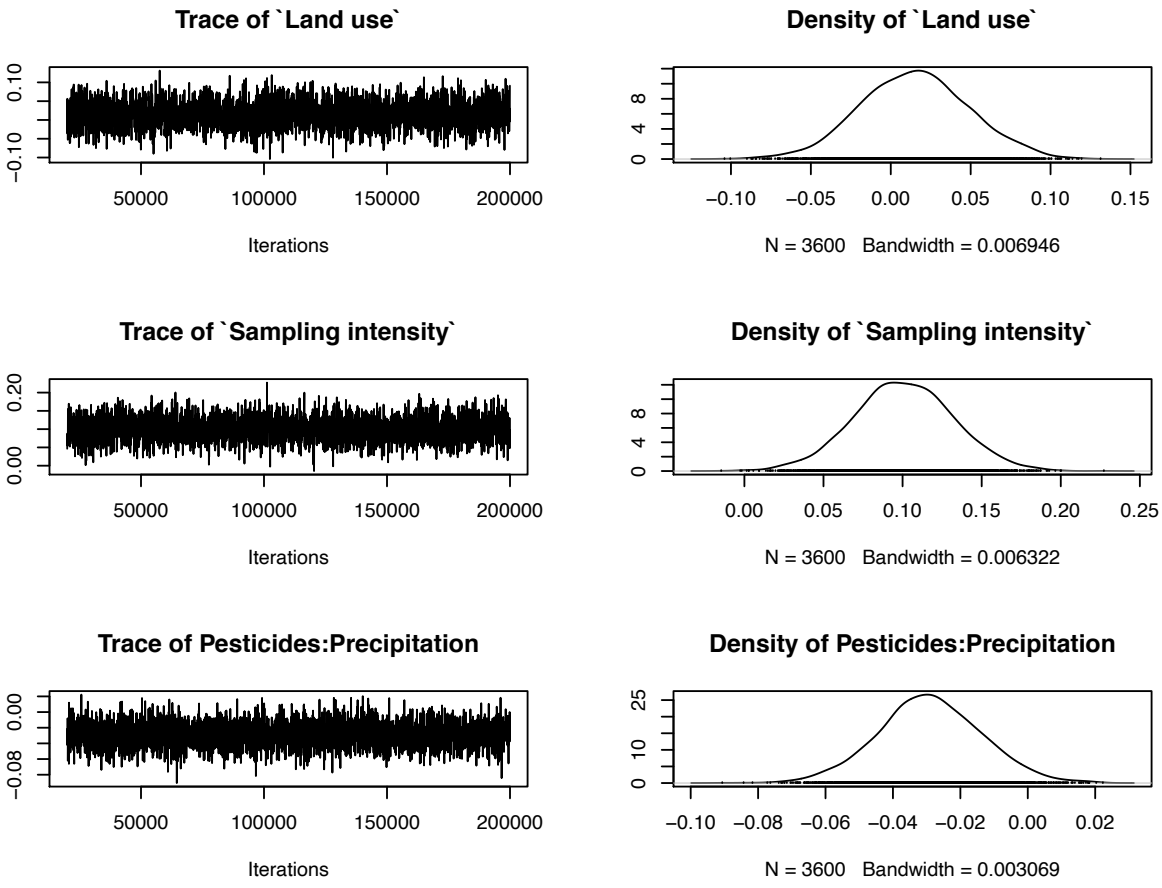
Trace of `Land use`
Density of `Land use`
Iterations
N = 3600 Bandwidth = 0.006946
Trace of `Sampling intensity`
Density of `Sampling intensity`
Iterations
N = 3600 Bandwidth = 0.006322
Trace of Pesticides:Precipitation
Density of Pesticides:Precipitation
Iterations
N = 3600 Bandwidth = 0.003069

Figure 2.S5, C

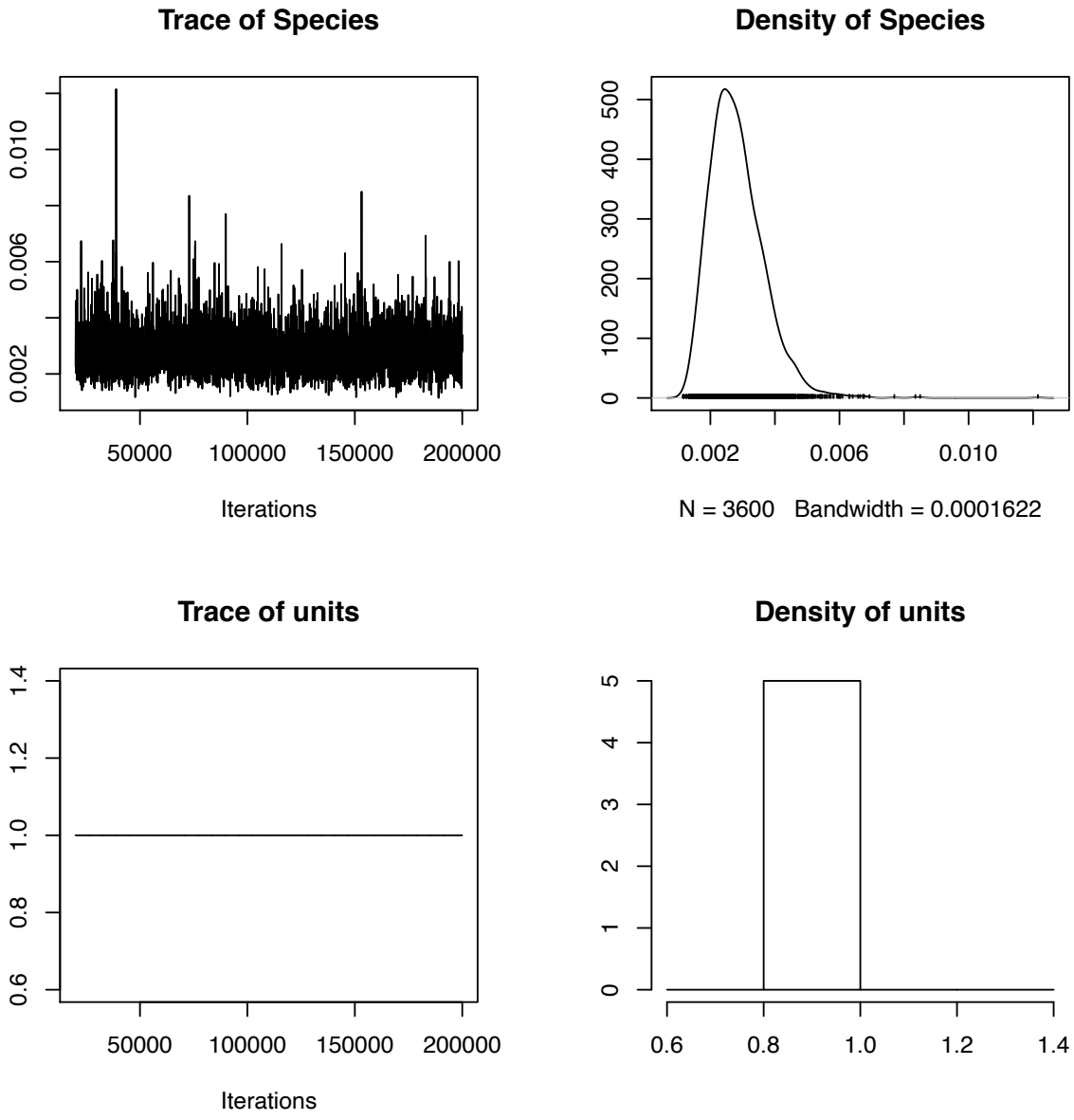

Figure 2.S5: Panels A, B and C show the trace and density estimates of Model 3, a phylogenetic mixed effects model using global change variables to explain odonate persistence in the United States of America, with species as a random effect. 200 000 iterations were run to produce these results. These plots verify model convergence and absence of autocorrelation among the explanatory variables.

Figure 2.S6, A

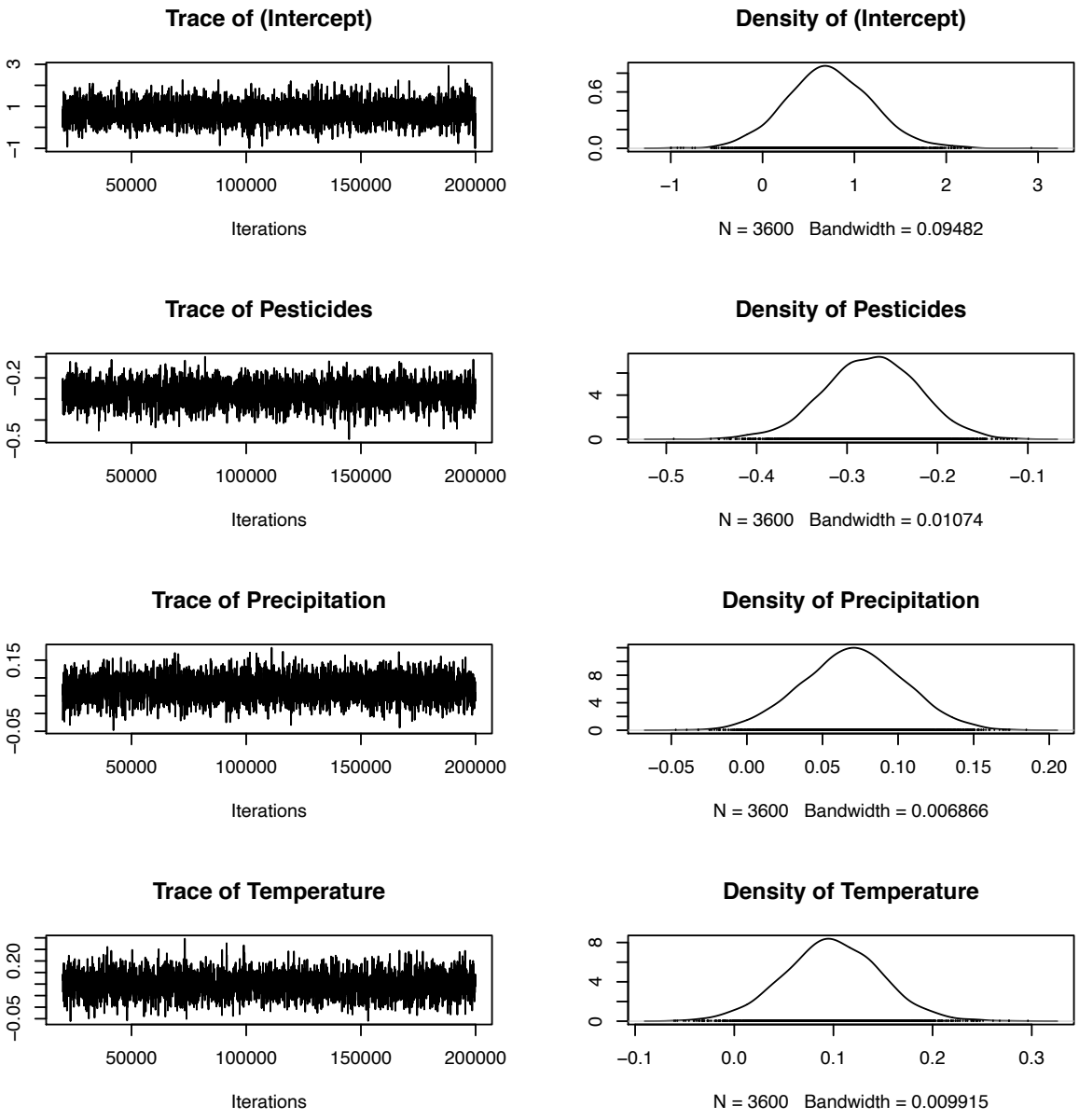
Trace of (Intercept)
Density of (Intercept)
Iterations
N = 3600 Bandwidth = 0.09482
Trace of Pesticides
Density of Pesticides
Iterations
N = 3600 Bandwidth = 0.01074
Trace of Precipitation
Density of Precipitation
Iterations
N = 3600 Bandwidth = 0.006866
Trace of Temperature
Density of Temperature
Iterations
N = 3600 Bandwidth = 0.009915

Figure 2.S6, B

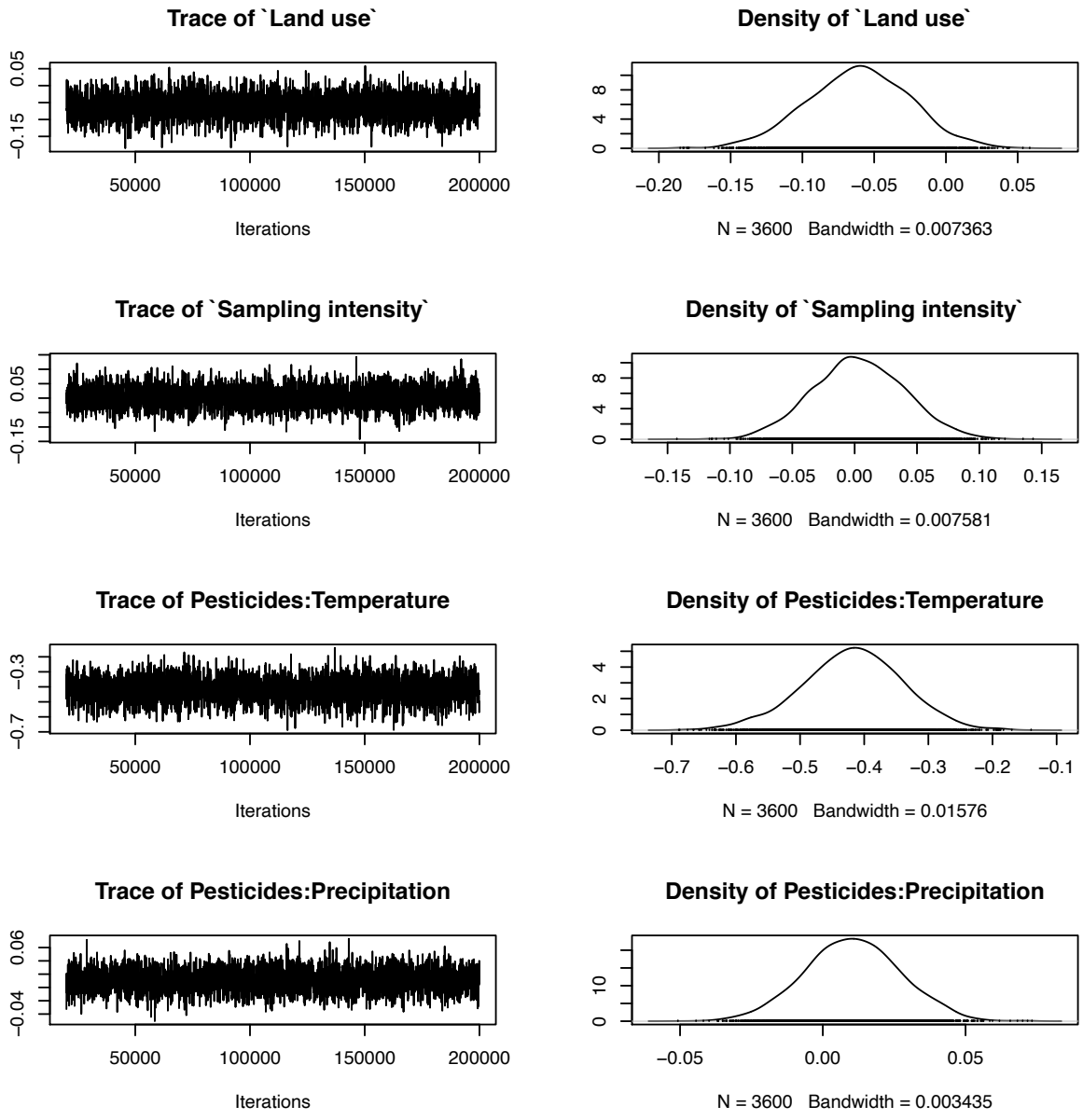
Trace of `Land use`
Density of `Land use`
Iterations
N = 3600 Bandwidth = 0.007363
Trace of `Sampling intensity`
Density of `Sampling intensity`
Iterations
N = 3600 Bandwidth = 0.007581
Trace of Pesticides:Temperature
Density of Pesticides:Temperature
Iterations
N = 3600 Bandwidth = 0.01576
Trace of Pesticides:Precipitation
Density of Pesticides:Precipitation
Iterations
N = 3600 Bandwidth = 0.003435

Figure 2.S6, C

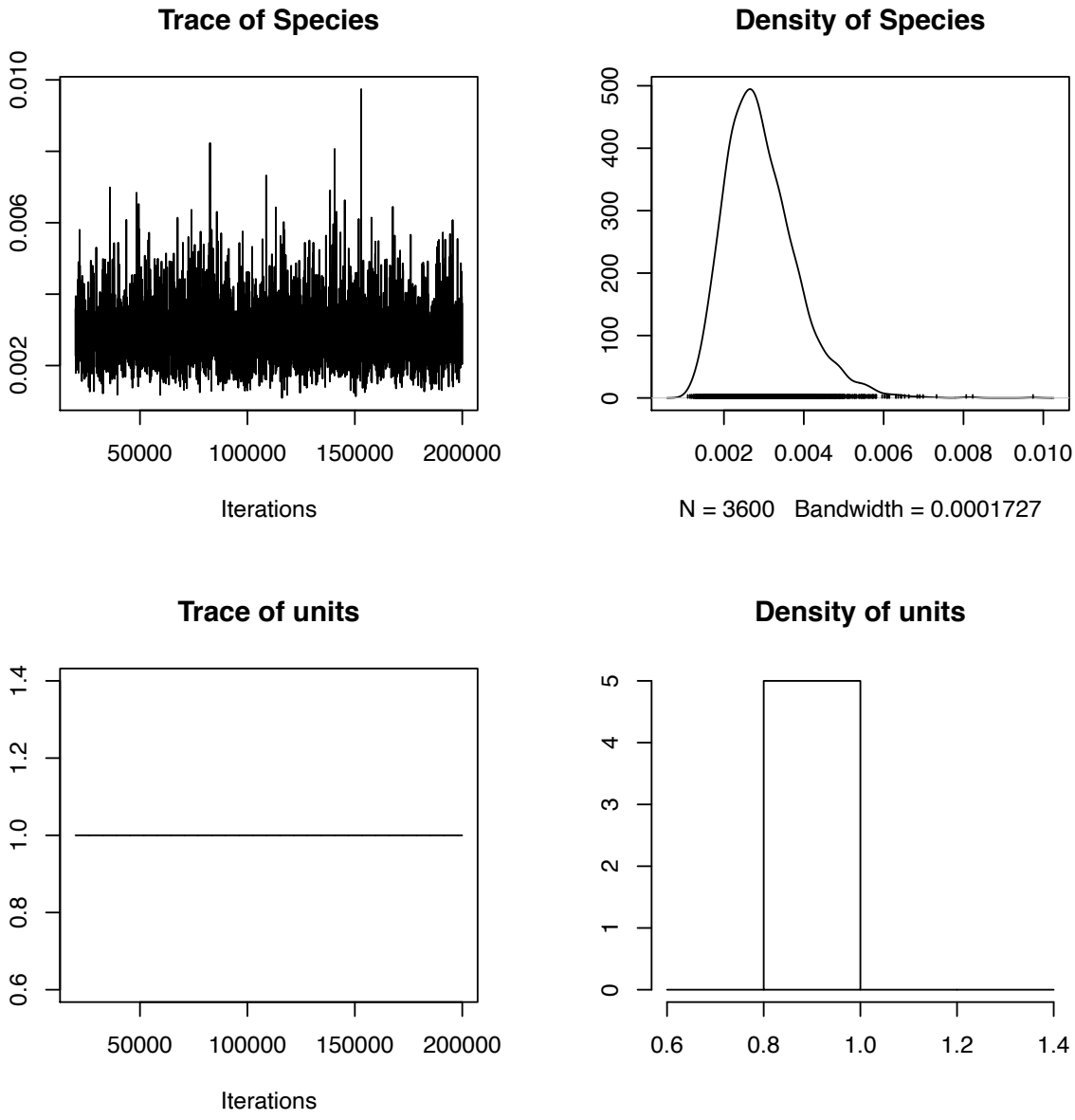

Figure 2.S6: Panels A, B and C show the trace and density estimates of Model 4, a phylogenetic mixed effects model using global change variables to explain odonate persistence in the United States of America, with species as a random effect. 200 000 iterations were run to produce these results. These plots verify model convergence and absence of autocorrelation among the explanatory variables.

Figure 2.S7, A

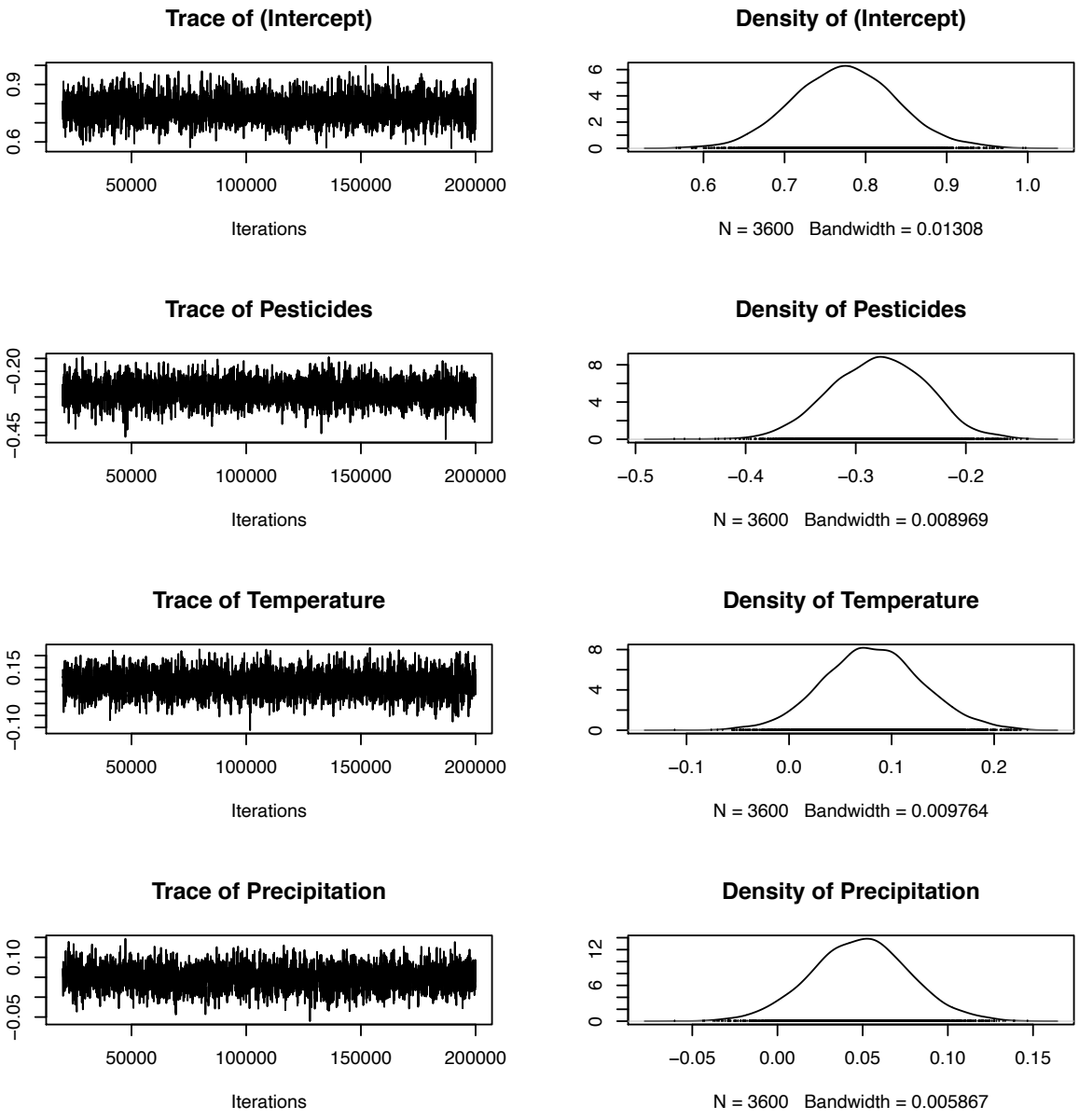
Trace of (Intercept)
Density of (Intercept)
Iterations
N = 3600 Bandwidth = 0.01308
Trace of Pesticides
Density of Pesticides
Iterations
N = 3600 Bandwidth = 0.008969
Trace of Temperature
Density of Temperature
Iterations
N = 3600 Bandwidth = 0.009764
Trace of Precipitation
Density of Precipitation
Iterations
N = 3600 Bandwidth = 0.005867

Figure 2.S7, B

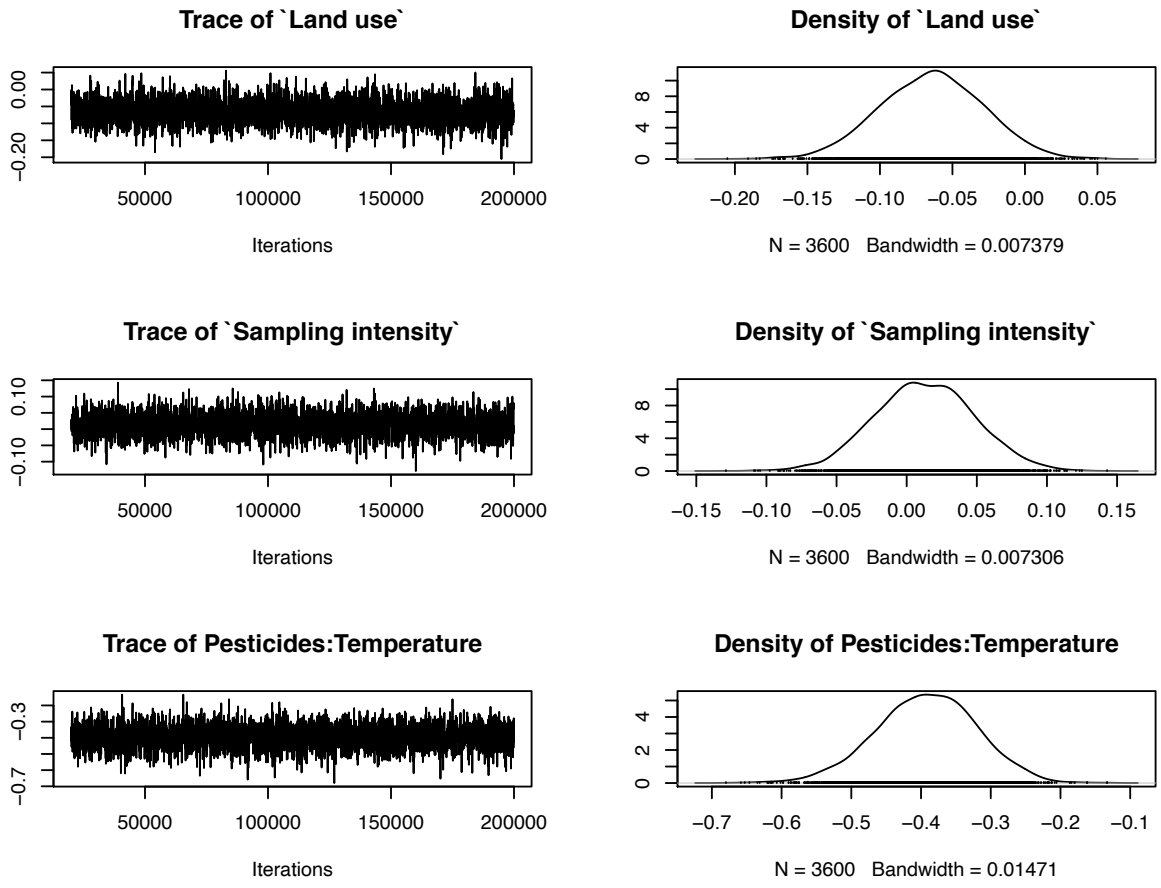
Trace of `Land use`
Density of `Land use`
Iterations
N = 3600 Bandwidth = 0.007379
Trace of `Sampling intensity`
Density of `Sampling intensity`
Iterations
N = 3600 Bandwidth = 0.007306
Trace of Pesticides:Temperature
Density of Pesticides:Temperature
Iterations
N = 3600 Bandwidth = 0.01471

Figure 2.S7, C

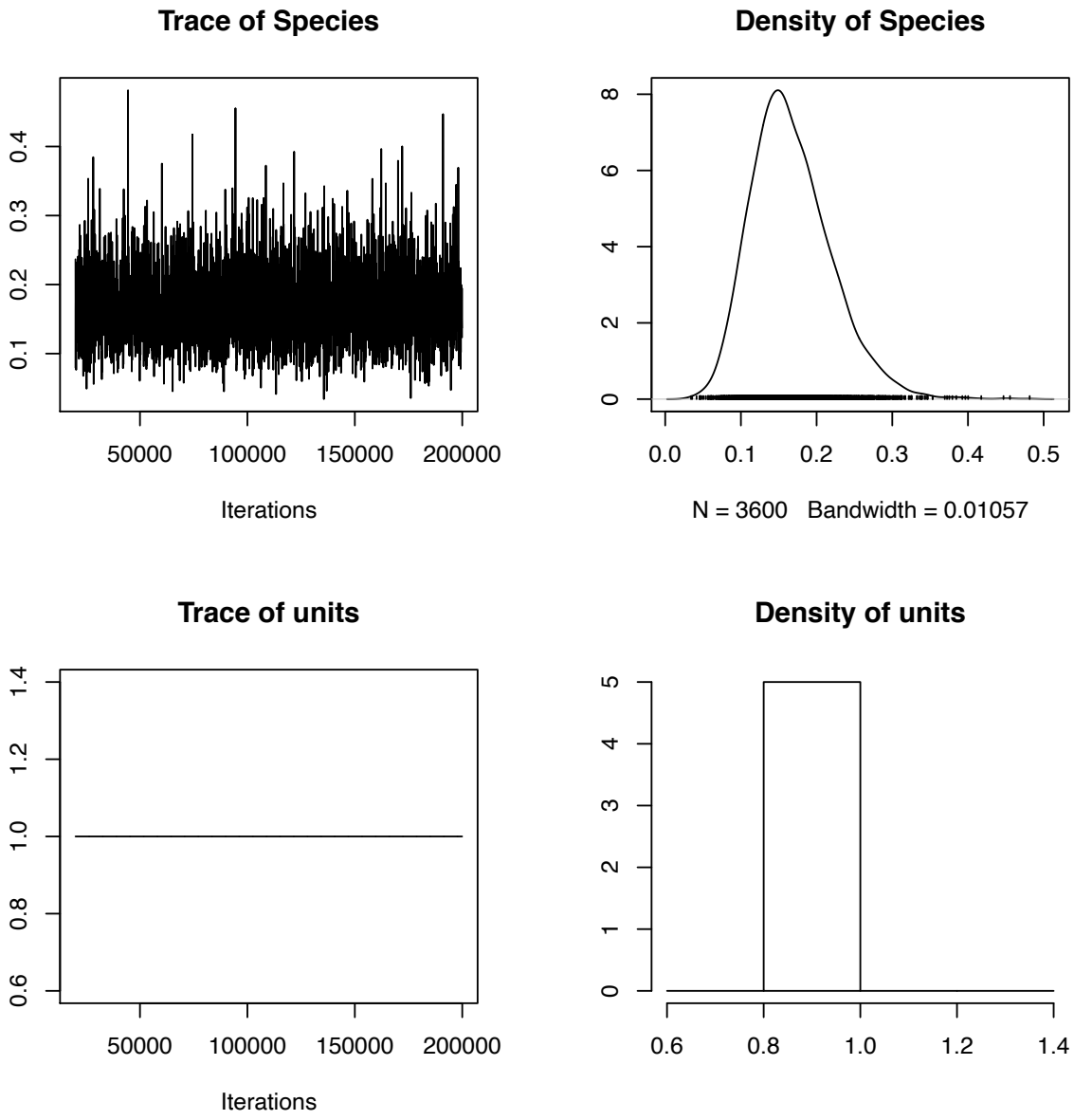

Figure 2.S7: Panels A, B and C show the trace and density estimates of Model 5, a non-phylogenetic mixed effects model using global change variables to explain odonate persistence in the United States of America, with species as a random effect. 200 000 iterations were run to produce these results. These plots verify model convergence and absence of autocorrelation among the explanatory variables.

Figure 2.S8, A

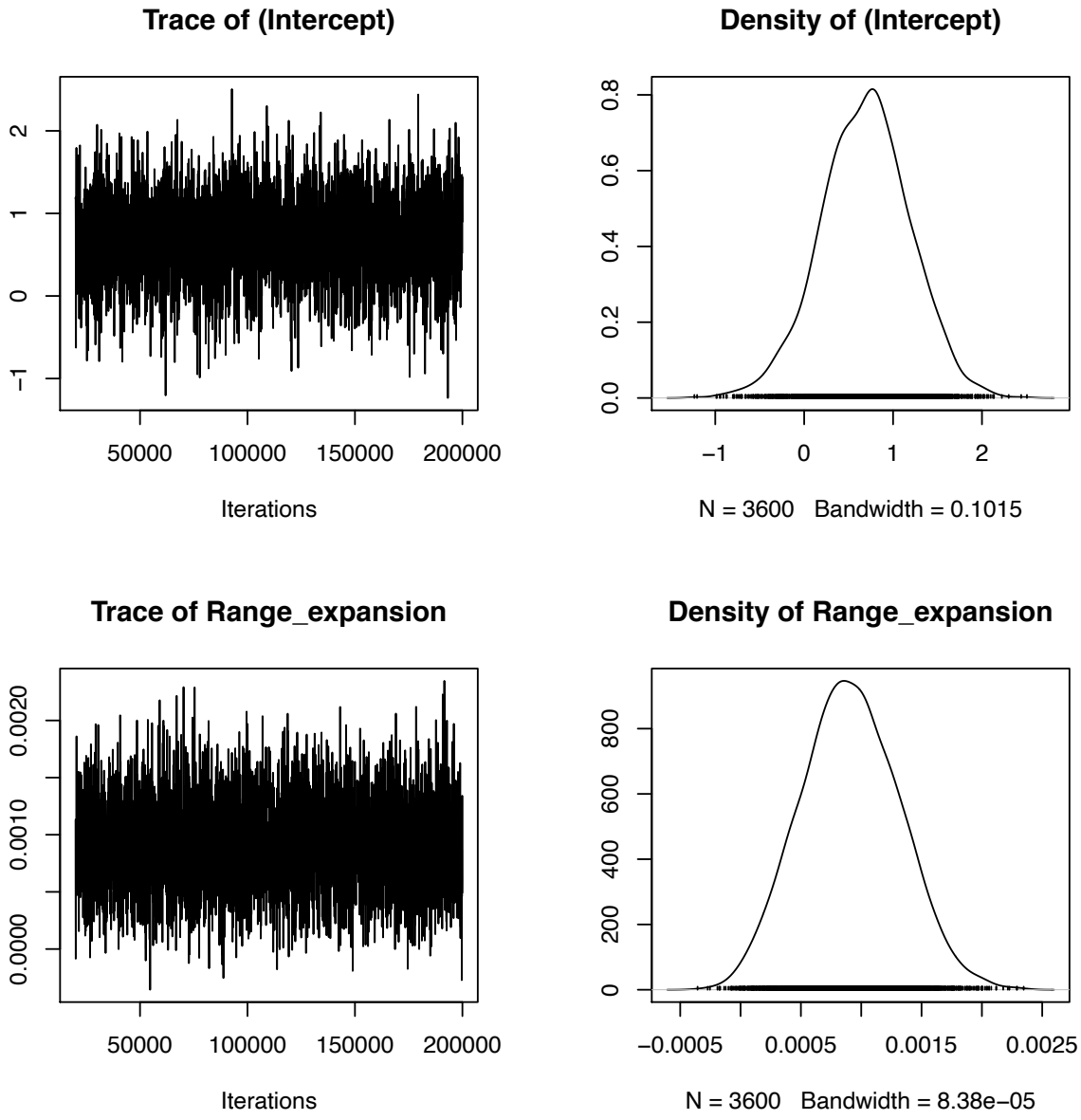
Trace of (Intercept)
Density of (Intercept)
Iterations
N = 3600 Bandwidth = 0.1015
Trace of Range_expansion
Density of Range_expansion
Iterations
N = 3600 Bandwidth = 8.38e−05

Figure 2.S8, B

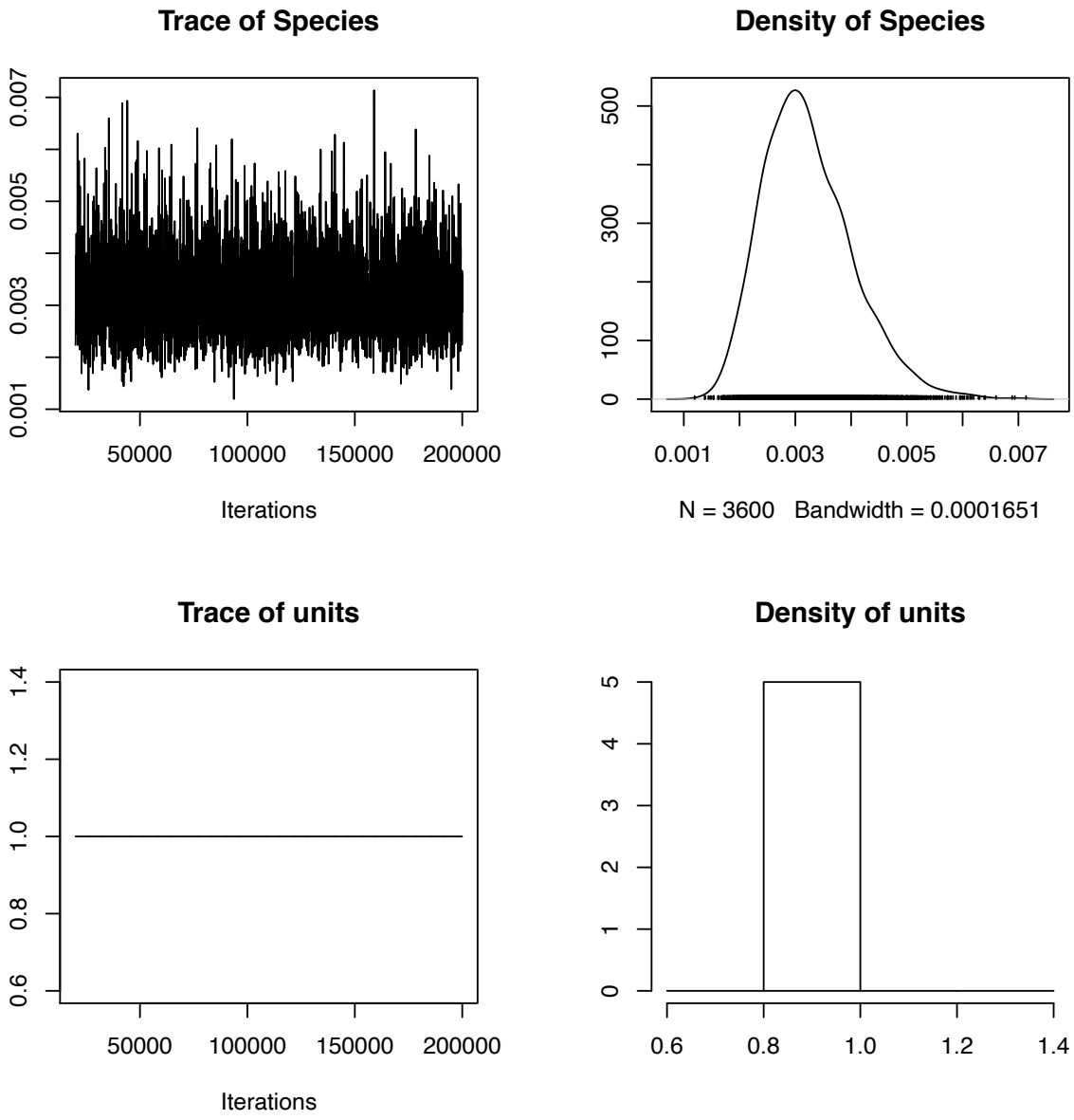

Figure 2.S8: Panels A and B show the trace and density estimates of Model 6, a phylogenetic mixed effects model using species' range expansions to explain odonate persistence in the United States of America, with species as a random effect. 200 000 iterations were run to produce these results. These plots verify model convergence and absence of autocorrelation among the explanatory variables.

Section S4: Supplementary Table 2.S1

Table 2.S1: Credible intervals of all MCMCglmm models considered to assess the effects of four global change variables, as well as species Northern range limit shifts, on odonate persistence across the United States of America. All models except Model 5 take phylogeny into account.

	95th lower credible interval	95th upper credible interval
Model 1		
(Intercept)	-0.1612	1.5876
Pesticides	-0.2935	-0.1356
Temperature	-0.1105	0.0508
Precipitation	0.0242	0.1337
Land use	-0.0274	0.0954
Sampling intensity	0.0410	0.1643
Model 2		
(Intercept)	-0.2042	1.6062
Pesticides	-0.3764	-0.2058
Temperature	-0.0024	0.1806
Precipitation	0.0054	0.1172
Land use	-0.1312	0.0083
Sampling intensity	-0.0590	0.0779
Pesticides:Temperature	-0.5475	-0.2617
Model 3		
(Intercept)	-0.0775	1.7808
Pesticides	-0.3738	-0.1666
Temperature	-0.1243	0.0422
Precipitation	-0.0185	0.1096
Land use	-0.0486	0.0830
Sampling intensity	0.0417	0.1661
Pesticides:Precipitation	-0.0594	0.0013
Model 4		
(Intercept)	-0.2004	1.6517
Pesticides	-0.3776	-0.1720
Temperature	-0.0019	0.1903
Precipitation	0.0056	0.1353
Land use	-0.1294	0.0123
Sampling intensity	-0.0688	0.0749
Pesticides:Temperature	-0.5787	-0.2687
Pesticides:Precipitation	-0.0200	0.0448
Model 5		
(Intercept)	0.6494	0.8962
Pesticides	-0.3660	-0.1985
Temperature	-0.0202	0.1708
Precipitation	-0.0060	0.1074
Land use	-0.1307	0.0080

Sampling intensity	-0.0552	0.0808
Pesticides:Temperature	-0.5428	-0.2615
Model 6		
(Intercept)	-0.3052	1.6396
Range expansion	0.0001	0.0016

Section S5: References

Abbott, J. C. 2020. OdonataCentral: An online resource for the distribution and identification of Odonata. http://www.odonatacentral.org.

Canadensys. *Atlantic Reference Center, Biodiversity Institute of Ontario, Espace pour la vie, Royal Ontario Museum, Université de Montréal Biodiversity Centre, University of Alberta Museums, University of British Columbia, University of Guelph, Ville de Trois-Rivière* http://data.canadensys.net/explorer.

Favret, C., J. M. De Serres, M. Larrivée, and J. P. Lessard. 2020. The Odonata of Quebec: Specimen data from seven collections. Biodiversity Data Journal 8.

GBIF.org. *GBIF Occurrence Download* https://doi.org/10.15468/dl.uqhp4p.

Ontario Odonata Atlas Database. Natural Heritage Information Centre, Ontario Ministry of Natural Resources and Forestry. Queried on Aug 30, 2018 by C.D. Jones. 2018. .

Chapter 3: Space and time; convergent phenological and geographical range responses to climate change across continents

This chapter is a slightly modified version of the manuscript that was submitted for publication in a peer-reviewed journal. It is currently under revision.

Abstract

Insect species are confronted by an array of environmental challenges that combine to elevate extinction risk among many taxa. Among potential global change threats, climate change presents distinct challenges, leading to geographical range shifts and changes in species' life histories. Understanding how these responses relate to each other, and whether ecological traits can be used to assess species' vulnerability to global change-related threats, remains unclear. I assessed range and phenological shifts of European and North American odonate species between two time periods (1980-2002 and 2008-2018) to measure the strength and direction of the association between both responses. Species expanded their range limits by an average of 53 km northward and emerged two days earlier since 1980. I uncovered a significant relationship between range and phenology shifts and found that these responses converge across continents, despite highly divergent land use and biogeographical histories in these regions. Species with the greatest poleward range shifts also showed the largest phenological shifts toward earlier annual activity periods. Where earlier seasonal timing was sustained, greater local population growth might be possible, in turn increasing the likelihood of long-distance dispersal. Nevertheless, increasing temperature variability hindered range shifts, providing further evidence of the negative impacts of extreme weather for insect conservation. Species' spatial or phenological shifts were not related to breeding habitat type, oviposition behaviour, body size or flight

duration, and species responded independently of their shared evolutionary history. Southern species shifted their range limits more strongly. Odonate species have generally benefitted from climate changes to date in Europe and North America, yet similarity in species' sensitivities to temperature change and variability suggest they share vulnerability to increasing temperature variability associated with anthropogenic warming.

Introduction

Unprecedented rates of climate change create pressures on insect communities that contribute to rapid population declines for many species (Goulson 2019, IPCC 2021). Species may survive such changes through adaptation or phenotypic plasticity, or by dispersing to new areas where conditions remain, or have become, suitable (Davis et al. 2005). Species' geographical range limits and seasonal timing depend strongly on climate and habitat conditions, so ranges and phenological timing of key life history activities shift in response to climate and land use changes (Parmesan and Yohe 2003, Davis et al. 2005, Hallfors et al. 2021). The average timing of early-season activities may advance as temperatures warm while range boundaries may shift northward, assisting species in remaining within the limits of their ecological niches (Figure 3.1; Chen et al., 2011; Menzel, 2006; Parmesan & Yohe, 2003). Both phenological plasticity and dispersal outside historical range limits permit populations to grow, despite changing environments, reducing risks of climate debt and extinction (Saino et al. 2011, Devictor et al. 2012, Kerr et al. 2015, Urban 2015, Franks et al. 2018, Lustenhouwer et al. 2018). Positive population trends can be stronger in species that show both responses, rather than only one response (Hallfors et al. 2021).

It is possible that a trade-off occurs 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 selection pressures 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 phenology shifts due to plasticity or adaptations may mitigate the need for range shifts as species better tolerate new

climatic conditions. Alternatively, greater phenological plasticity under warmer spring temperatures may increase reproductive success, and lead to greater population growth and range expansions (Macgregor et al. 2019). Positive or stable trends in species abundance and habitat availability are essential for range shifts to occur (Mair et al. 2014, Platts et al. 2019). Cross continental studies report converging patterns of climate change effects on species' range limit shifts (Kerr et al. 2015) and in variation in abundance trends (Stephens et al. 2016), but potential relationships between phenological and range shift responses has not yet been detected at continental scales.

Dragonflies and damselflies respond relatively rapidly to climate change, both spatially (Hickling et al. 2005, Grewe et al. 2013, Ball-Damerow et al. 2015, Powney et al. 2015, Rapacciuolo et al. 2017, Sirois-Delisle and Kerr 2055) and temporally (Hassall et al. 2007, Hassall 2015, McCauley et al. 2018). Global change research on insects emphasizes butterflies and some bee taxa because of the relative accessibility of historical observations of their distributions in temperate regions, but massive databases on odonate distributions can also be assembled to answer new questions about insect responses to global change (Kalkman et al. 2018). British odonates may serve as an indicator to climate change due to strong phenological and geographical responses relative to other taxa, but no statistically significant relationship to relate both responses has been discovered in odonates (Hassall 2015). Few studies have tested for convergent responses among these or other taxa in terms of seasonal timing and range responses across continents.

Traits occasionally contribute to species' geographical range and phenological responses to climate change (Kharouba et al. 2009, Chen et al. 2011, Schuetz et al. 2019, Zografou et al. 2021), but these relationships generalize poorly taxonomically and geographically (Angert et al.

2011, Buckley and Kingsolver 2012, Estrada et al. 2016, MacLean and Beissinger 2017). There is some evidence that species traits relate to odonates' interspecific variation in range shifts (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). Yet, tests of convergence in phenological and geographical range responses to climate have not been attempted for odonates or other taxa at this cross-continental extent (Buckley and Kingsolver 2012, Estrada et al. 2016, MacLean and Beissinger 2017), and ecological traits plausibly explain those responses.

I identified and measured physiological and life history traits, which are likely to relate with dispersal and growth rates among odonates. Species with larger populations are more likely to colonize new areas and distributions of their emergence timing should also include earlier time periods. Species with high population growth rates can retain more genetic variation as they colonize new areas, minimizing genetic bottlenecks and facilitating local adaptation to novel environmental conditions (Gomez-Mestre and Jovani 2013). A number of traits are known to contribute to such responses. I predict that habitat generalists should respond more rapidly to warming, both phenologically and geographically, as generalists outperform specialists as climate and land uses change (Hassall and Thompson 2008, Ball-Damerow et al. 2014, 2015, Powney et al. 2015, Rapacciuolo et al. 2017). Lentic species (i.e. species breeding in slow moving water like lakes or ponds) tend to track their climate niche more closely than lotic species (i.e. fast moving water-dwelling species) due to stronger dispersal capacities and lower habitat stability of lentic environments (Hof et al. 2006, Grewe et al. 2013). 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. Species requiring exophytic egg-laying habitat (i.e. eggs laid in water or on land, relatively larger in number), could be associated with greater northward range limit shifts, compared to species using endophytic egg-laying habitat (i.e. eggs laid inside plants, usually fewer in number; Angert et al., 2011), although evidence is limited. Longer flight periods are also linked with stronger dispersal abilities, increasing reproduction, population size, and rates of establishment in new areas (Grewe et al. 2013). Large-bodied species should be stronger competitors (Powney et al. 2015), although the relationship between morphological traits and range boundary shifts is variable in odonates (Rundle et al. 2007, Grewe et al. 2013).

Although not biological traits *per se*, geographic locations and environmental characteristics of species' range may explain species' responses to climate change, rather than functional and life history traits (MacLean and Beissinger 2017, Pacifici et al. 2020). For instance, exposure to extreme climate events (e.g. drought, heat waves, or storms) within species ranges may disturb species' dispersal abilities, and capacities to tolerate new conditions, rather than overall averages over long periods of time (Kerr 2020, Román-Palacios and Wiens 2020). Exposure to extreme thermal anomalies can rapidly change entire communities and create shifts towards new ecosystems, with potential to lead to local declines over time (Grant et al. 2017, Day et al. 2018, Harris et al. 2018, Román-Palacios and Wiens 2020). Further, the position of species' historic range limits predicts variation in range shifts better than traits, although effect sizes vary (MacLean and Beissinger 2017). European odonates with southern ranges responded positively to climate change, which was attributed to the relationship between 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).

This study has three main goals. First, I test whether odonate species with stronger, observed geographical range shifts also advance their emergence phenologies or, alternatively, if one response offsets the need for the other. Second, I determine whether biological traits, range geography, or temperature variability predict range shifts at species' northern range limits, and third, whether similar predictors to those explaining range expansions also predict shifts in species emergence phenology. Common underlying processes related to traits or shared evolutionary history that govern widely reported responses to climate change among species could create the possibility that a common framework could predict both phenological and geographical range shifts. Alternatively, species might respond to rapid climate changes in ways that reflect their geographical position, suggesting that where they are found is a better predictor of their conservation risk from global change than their intrinsic biological characteristics.

Methods

Biological records

I assembled ~2 million observations records for North American and European odonate species collected between 1980 and 2018. Observation data originated from a variety of sources, including online dataset aggregators GBIF (http://gbif.org/) and Canadensys (http://www.canadensys.net/), Odonata Central (Abbott 2020) and from other institutions (see Acknowledgments). This dataset was used in previous work (Sirois-Delisle and Kerr 2021). There are no systematic protocols in sampling opportunistic data, such as those from dataset aggregators used in this work, potentially creating spatial and temporal biases (Hassall and Thompson 2010, Isaac et al. 2014). However, biases associated with data that are not systematically collected are less likely to affect global trends at greater spatial and temporal

scales, and if data are obtained from many, independent sources (Pyke and Ehrlich 2010, Zattara and Aizen 2021).

I removed records with incomplete or missing species identification, year, or locality information. I selected unique observations for species, location, year, and Julian day of collection, and restricted the data to continental North America and Europe. I mapped species-specific observations using ArcGIS software version 10.7.1 and qualitatively verified species ranges. In the event that the same species was found in both Europe and North America, I selected records from the continent containing the largest number of observations (Supporting Information; Section S1).

I assigned species presences to 100 X 100 km quadrats to identify the best sampled species. I excluded species found in fewer than 50 quadrats to increase the likelihood of accurately predicting the position of species northern range boundaries, but future work should include rare species as well. I retained ~1,000,000 records, including 77 species (Figure 3.2). Observation records were separated into two time periods, to compare species' current phenologies and northern range limits (years 2008 to 2018 inclusively) to conditions in a historical time period (years 1980 to 2002 inclusively).

Spatial and temporal change metrics

Species' northern range boundaries were calculated using the mean distance (km) from the equator of the 5, 10, 15, or 20 most northern points of each species range in both the current (2008 – 2018) and historical (1980 – 2002) time periods (as in Kerr et al. 2015). I used the difference between range limit positions in the historical and current time periods to estimate species' northern range limit shifts. I reported results using the 10 most northern points to

calculate species' range limit shifts as results were otherwise highly similar. There were 77 species in the final dataset for range shift estimates.

Since spatiotemporal biases sometimes inflate range shift measurements (Kujala et al. 2013), I 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 using numbers of species-specific geographical points per time period that were identical to actual numbers of observations for those species, holding their maximum and minimum latitude and longitude values constant relative to observed values. I calculated range limit shifts using the difference in the mean of the 10 most northern points in both time periods according to each of these datasets. I used GLMs to test whether species-specific range limit shifts, according to each random dataset, predict range shifts measured from the observation data. I reported p-values and model coefficients (Supporting Information; Figure 3.S1-3.S2). These preliminary analyses show that observed northern range limit shifts are not consistent with expectations derived from changes in sampling intensity.

I estimated species-specific emergence phenology in 200 X 200 km quadrats, and in each time period. Opting for larger quadrats increases probabilities of detecting signals of emergence phenology, which may otherwise be lost due to gaps in data density. I retained quadrats that contained at least 25, 30 or 35 observations for a given species across each time period; this choice did not qualitatively affect the final results in this study, so I reported results when using a minimum of 25 observations per quadrat. Phenology shifts could only be inferred in quadrats with reasonable numbers of species observations in both time periods. To estimate phenology per area, I used the *weib.limit* function of the *WeibullR* R package (Pearse et al. 2017). This function

uses the Weibull distribution, to calculate the tail of distributions to estimate the Julian day of a species' first appearance in a region, 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 (Robbirt et al. 2011, Brooks et al. 2014) tend to overestimate the timing of biological events due to temporal bias towards later days in the species' active period (Pearse et al. 2017). I retained 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. 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. I calculated the difference in the day of emergence per quadrat between both time periods, and mean phenology change across all quadrats for each species. The number of quadrats per species used to calculate their mean phenological shift varied between 25 and 97. There are 68 species found across 64 unique quadrats that met these criteria, and these species were all included within the larger group of species (n = 77) for which I estimated range shifts.

Null models were used to assess whether my approach to estimate phenology shifts was robust, as potential issues may arise due to spatiotemporal biases in the underlying data (Kujala et al. 2013). I constructed 1000 randomized datasets of species' hypothetical days of occurrence, using the same number of quadrats, and number of points within quadrats, as in each time period of the observation records. I assigned the maximum and minimum Julian day of occurrence from the observation records to limit values in the randomized datasets. I applied the same method and criteria of inclusion to the randomized datasets as 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 I measured. I reported the p-values and coefficients of these models (Supporting Information; Figure 3.S3-3.S4). No discernable pattern emerged in these preliminary analyses, indicating that observed shifts in phenology are not consistent with expectations derived from differences in sampling intensity over time.

Climate data

Temperature variability during species' flight season may be relevant to success or failure to establish in new locations or shift their phenological emergence timing the following year. I downloaded a high-resolution gridded dataset for monthly average daily maximum temperature from the Climatic Research Unit (CRU) (available at http://www.cru.uea.ac.uk/data). I extracted average values per 100 X 100 km quadrat across the months of April to October for each year included in the study. I 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. I used the difference between current and historical measures as an estimate of temperature variability change. Including other climatic variables is outside the scope of this work but is a clear direction for future research investigating species responses to global change.

Ecological traits data

I used field guides (Cannings 2002, Jones et al. 2008, Paulson 2012) and existing trait databases (Powney et al. 2014, Waller et al. 2019) to assemble trait data for the 77 species in the database. I 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) are different from species' traits. These 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), I selected four traits likely to be biologically relevant to spatial and temporal responses to climate change. Traits included flight duration, breeding habitat type (lotic, lentic, or both), egg laying habitat (exophytic vs. endophytic) and body size. Species' flight period is 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 is assigned to species according to species uses of lotic, lentic, or both habitat types. Body size corresponds to the mean length of the abdomen of each species. Traits that I left out included overwintering stage and range size, as data were incomplete for many species. I also excluded migratory behaviour, as nearly all species included in the study were non-migratory.

I verified the absence of correlation amongst all predictors by calculating the Predictive Power Statistic (PPS) and Pearson correlations among traits (van der Laken 2021). PPS is a useful statistic for its ability to work with continuous and categorical variable pairs and capture linear and non-linear relationships. The traits and attributes that I selected were not correlated.

Statistical analyses

The first research question I investigated tests whether there is a relationship between species' range and phenological shifts across continents. I assessed the relationship between both responses with a by-species Generalized Linear Model (GLM) and with a Markov chain Monte Carlo generalized linear mixed model (MCMCglmm) (Hadfield 2010) accounting for phylogeny, in R statistical software version 3.5.0. I compared results using frequentist and Bayesian approaches to improve the overall robustness of the results. The phenology shift metric was assigned to the response variable, and range shift estimates to the predictor variable. I randomly assigned response and predictor variables since I am not presenting a causal pathway between responses. All continuous variables were Z-scored using the *scale* function in R to compare the differences in magnitude of the estimates calculated by the models. Including phylogeny in the MCMCglmm model may account for similarities between closely related species. I used the phylogenetic tree published by the Odonate Phenotypic Database (Waller et al. 2019), which was generated using a combination of DNA-sequences and species' taxonomy based on morphology (Waller and Svensson 2017). Since species that are closely related are likely to show similar traits, it is probable that a phylogenetic signal exists in spatial and temporal responses assessed here. I report AIC values (Akaike's Information Criterion), pseudo R^2 (Nakagawa et al. 2017), and DIC (Deviance Information Criterion) to ease interpretation of the effect size.

I also investigated whether biological traits, range geography, or temperature variability predict range shifts at species' northern range limits, and whether similar predictors to those explaining range expansions also predict shifts in species emergence phenology. To explore these questions, I constructed statistical models – GLM and a MCMCglmm accounting for phylogeny – to predict species northern range limit or emergence phenology shifts as the

response variable with species' traits, range geography, and temperature variability as predictor variables.

In addition to the inclusion of phylogeny in statistical models to account for potential data non-independence, I measured the phylogenetic signal in range and phenological shifts. I used the *phylosig* function of the *Phytools* package version 0.7-70 (Revell 2012) using two models of trait evolution; Pagel's lambda, and Brownian motion, and report the p-value, Pagel's lambda and Blomberg's K.

Results

Range and phenology shifts

Many species (69% of those included, showing mean range expansions of 169 km) expanded their northern range limits toward higher latitudes. Across all species, average range expansions were 53 km northward (Supporting Information; Figure 3.S5). Small range retractions may result from sampling variability or stochastic population fluctuations along the northern range edge. *Libellula luctuosa* showed the smallest range retraction (-18 km). Conversely, *Pantala flavescens* shifted very strongly northward, perhaps a reflection of its extraordinary long distance dispersal capacity (e.g. migrations across the Indian ocean; Anderson 2009). Most species (59% of assessed species) maintained or advanced their emergence phenology (mean of -2.00 days in emergence phenology shifts among all species; Supporting Information; Figure 3.S6). Analyses including phenology shifts (N = 68) included fewer species than for analyses of range shifts (N = 77) due to the data intensity required to capture phenology shifts within a study site. Many species (41% of them) showed both advancing emergence phenology and range expansions, while 16% of species showed neither range nor phenological

shifts relative to historical baselines. Species that may not have responded to climate change temporally or spatially include *Coenagrion mercuriale*, a European species listed as near threatened by the IUCN redlist (IUCN 2021) and that is projected to lose 68% of its range by 2035 (Jaeschke et al. 2013). The statistical distribution of the datasets can be found in the Supplementary Materials (Figure 3.S5; Figure 3.S6).

Species that shifted their northern range limits to higher latitudes also showed stronger advances in their emergence phenology (Figure 3.3), according to both GLM and Bayesian analyses ($p < 0.05$; Table 3.1; $R^2 = 14\%$ and 13%, for GLM and MCMCglmm models, respectively). This trend is convergent between continents and is consistent among both dragonflies and damselflies, though there is considerable interspecific variation in the extent to which species shifted their northern range limit or shifted their emergence phenology. Accounting for phylogeny did not improve model predictions and did not explain greater model variance (Table 3.1). Trace and density plots for the MCMCglmm model revealed no issues with autocorrelation or model convergence (Supporting Information; Figure 3.S7).

Trait based analyses of range and phenology shifts

Models that assessed mechanisms underlying range shifts showed that range geography and climate variability, rather than ecological traits, predict cross-continental range shifts. Species with southern distributions shifted their northern range limits towards higher latitudes to a greater extent, relative to northern and widespread species ($p < 0.05$; Table 3.2; $R^2 = 23\%$ and 20%, for GLM and MCMCglmm models, respectively). Range geography was consistently the strongest predictor of range shifts. Smaller changes in interannual temperature variability were also related to a higher likelihood of northern range limit shifts, compared to species facing

larger changes in temperature variability ($p < 0.05$). The trend between range shifts and significant predictors remained similar according to both model types, however, smaller amount of model variance was explained when accounting for phylogeny. Neither range geography nor climate variability predicted emergence phenology shifts. Even though both response types are related, the mechanisms underlying phenological shifts are likely different than those underlying range shifts according to the variables included here.

Species' ecological traits did not relate to the extent of observed phenological or geographical range shifts in tests using GLM and MCMCglmm models. These ecological traits were also unrelated to each other, according to the PPS and correlation coefficients. Trace and density plots for the MCMCglmm models did not indicate limitations related to autocorrelation or model convergence, regardless of whether models sought to predict geographical range or phenological shifts, respectively (Supporting Information; Figure 3.S8).

A phylogenetic signal may indicate that there are traits, other than those measured in this study, that determine species' spatial and temporal responses to changing climate. Yet, I detected no phylogenetic signal using Pagel's lambda or Brownian motion (Table 3.2) in either geographical range or phenological responses, despite pronounced recent warming. This is further confirmed by comparing the two model types in the case of phenological shifts as well as range shifts, where MCMCglmm models accounting for phylogeny did not show a different pattern amongst the predictors compared to the GLMs. Model performance was not improved when accounting for phylogeny in my mechanistic assessment of northern range shifts.

Discussion

Dragonfly and damselfly species show pronounced geographical range and phenological shifts, relative to climate change, that converge across both Europe and North America. Species expanding their ranges poleward also emerge earlier in the spring concurrently with rapid climate change (Figure 3.3) despite vast differences in biogeographic regions, divergent land use patterns and histories, and dissimilarity in species assemblages between continents. This result suggests that some species are "universal winners" with respect to climate change, demonstrating the flexibility to respond both temporally and spatially to the onset of rapid climate change, regardless of potentially negative effects of land use changes and intensification. Conversely, species that show neither geographic nor phenological shifts may be particularly vulnerable to climate change. Few studies have attempted to assess phenology and range shifts concurrently, particularly across very broad areas.

Earlier seasonal timing leads to higher local population growth and greater frequency of long distance dispersal (Leroux et al. 2013, Macgregor et al. 2019, Kerr 2020). In odonates, early emergence is related to larger larval sizes during overwintering periods, with greater proportions of larvae reaching "winter critical size" thresholds that cause early spring emergence of adult odonates (Norling 1984, Chuine 2010). At equilibrium with local climatic conditions, increased voltinism is then possible, but phenological plasticity can also be maladaptive (Zettlemoyer and Peterson 2021), where the additional generation is exposed to particularly extreme conditions that cause increased mortality. Greater local population sizes are a prerequisite to range expansions (Mair et al. 2014), while only small numbers of odonate adults undertake long range dispersal (Conrad et al. 1999). Among British butterflies, species must be plastic in both phenology and voltinism for phenology advances to facilitate northward range shift; phenology

inhibits range shifts in species that are not plastic (Macgregor et al. 2019). Probability of survival and reproductive success may increase if the extent of habitat availability is sufficient to permit successful colonization at longer term (Mair et al. 2014). Species that adapt or show increased phenological plasticity over time would continue to have a positive effect on abundance, and lead to greater probabilities of long distance dispersal events. The underlying mechanisms for correlated range and phenological responses that I observe here across continents may be a consequence of species' phenotypic plasticity. As warming proceeds in a given area, species can both emerge at an earlier date, but also experience greater opportunity for dispersal to new, historically-unoccupied areas. Species that combine both temporal advances and northern range shifts under climate change may have increased population viability (Hallfors et al. 2021).

Increasing frequency and severity of extreme weather nevertheless limited species' geographical range responses (Table 3.2). This trend was independent of traits that are mechanistically linked to species' climate change responses, such as dispersal abilities or habitat preference. Indeed, extreme temperatures contribute to local extinctions and reduced population sizes (Román-Palacios and Wiens 2020), making range expansions from such areas less likely (Mair et al. 2014). Odonate populations that respond to unusual spring temperatures may experience very high density-independent mortality if temperatures return to seasonal conditions. If earlier phenological timing facilitates more rapid, positive range responses to climate change, then later phenological timing could act in the opposite way. Species emerging later should have generally lower voltinism, reduced population growth, and reduced likelihood of dispersal to new areas that is necessary for geographical range expansion. Results suggest the link between phenology and range responses to climate change that I have discovered can cut both ways.

Extreme weather events have previously been linked to regional extinction risks among insect species and to insect population decline (Román-Palacios and Wiens 2020). By focusing on range responses and phenological shifts within the integrated framework I have proposed here, I have both extended previous work to include odonate species but also suggested mechanisms that govern species' responses to climate change independent of commonly measured traits. Yet, species' tolerances to increasingly variable temperatures help predict extinction risk during climate change (Kerr 2020). Experimental evidence has demonstrated that odonate larval mortality rises with short-term extreme weather, particularly if it involves hot temperatures (McCauley et al. 2015). Climate velocity and sensitivity, rather than ecological traits, better predict range shifts and abilities to track thermal preferences in several marine taxa (Pinsky et al. 2013, Schuetz et al. 2019). It is possible that traits simply do not help predict range and phenological shifts among odonate species across these broad areas. Conversely, traits may determine how, but not how much, individual odonate species respond to climate change and associated extreme weather events. Finally, it is possible that I simply could not measure the traits that most strongly affected those responses. Future research needs to focus on gathering measures of dispersal behaviour, rather than relying on proxies of dispersal such as traits, or measures of range expansions. Detailed mechanistic models that incorporate more multiple independent processes may help untangle these patterns, though challenges remain around parameterizing them (Urban et al. 2022).

Southern species were more likely to expand their ranges northward than northern or widespread species. The 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). Temperature extremes,

associated with climate warming, lead to community shifts which can be predicted from species' thermal niches (Day et al. 2018). Species with narrower climatic niche breadths, such as southern species, as opposed to widespread species or those adapted to temperate environments (Slatyer et al. 2013), tend to respond rapidly to climate change as they have a greater need to track preferred thermal conditions due to differences in climatic tolerances (Herrera et al. 2018). My results show that southern odonates consistently respond geographically, rather than temporally; integrating climate connectivity in long term odonate conservation plans needs to be prioritized. Facilitating climate-driven range shifts through conservation planning is a rapidly evolving area of research (Littlefield et al. 2019).

Previous work suggests that geographically contingent processes are "wildcards" that should hinder, not improve, predictions of climate change responses (Srivastava et al. 2021). Yet, 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). Shared geography can completely overwhelm putative effects of traits to determine the extent of fish species responses to climate change (Schuetz et al. 2019), an effect attributed to local adaptation. In other words, traits matter, but patterns related to traits can be wholly masked by unique environmental changes that vary geographically. This process is consistent with my observations for odonates, suggesting that tests of local adaptation in critical traits, like thermal tolerances among larval life stages, would be valuable. This process would 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, as I have found; Grewe et al., 2013; Gutiérrez & Wilson, 2021; Sunday et al., 2015; Zografou et al., 2021).

Given the lack of trait-related trends, it is unsurprising that species' spatial and temporal responses were independent of phylogenetic history. The phylogenetic approach did not improve model predictions in any model that I tested, and there was no phylogenetic signal in either response according to Pagel's lambda or using Brownian models of trait evolution (Table 3.2). Past local extinctions of odonate populations also showed no phylogenetic trend (Suhonen et al. 2022). While counterintuitive, there might be strong variation in species' thermal niches among closely related species. Closely related species that are geographically isolated adapt to different local climates while populations that coexist may experience divergent selection in their climate tolerances (Schuetz et al. 2019). Selection may reduce competition for resources in related taxa, further diversifying species' climate sensitivities at local levels of biological organization (Schuetz et al. 2019). If this is true, ecological traits may simply not have the potential to explain species' spatial or phenological shifts at continental scales.

Climate change contributes to the strong, convergent relationship between range and phenology shifts across continents. Critically, increasing temperature variation hinders geographical range responses broadly among these species in both Europe and North America. I have proposed a unifying framework to consider both responses at once and I propose a mechanism linking geographical range responses among odonate species with phenological timing and consequent *in situ* population growth. Species' conservation risks from global change depend on environmental pressures within their current range. Geography has previously been identified as a wildcard, but is a predictor of species' conservation trajectories to date, at least among odonate species considered here. The missing links between species' traits and responses to climate change makes predictions of species' vulnerabilities more challenging. I focus on the broadest, macroecological extents, which enabled me to include all or most of species'

geographical ranges within the study zone, and focusing on different levels of biological organization would likely yield different results.

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Tables and figures

Table 3.1: Assessment of the relationship between range shifts and emergence phenology change. Two model types were used to validate model results; GLM, and MCMCglmm accounting for phylogeny). 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). CI gives the 95% credible intervals of the MCMCglmm model.

	Phenology shift (N = 68)					
	GLM		**MCMCglmm**			
Predictors	**Est.**	**p**	**Post.m**	**p**	**Lower CI**	**Upper CI**
(intercept)	0.04	0.83	0.04	0.81	-0.33	0.41
Range shift	-0.43	<0.01*	-0.43	<0.01*	-0.77	-0.13
Continent	-0.12	0.68	-0.11	0.68	-0.62	0.48
Model evaluation						
AIC/DIC	191.27		191.30			
Null model	196.96		197.00			
Pseudo R^2	14.09%		12.80%			

Table 3.2: Predictive effect of ecological traits and other characteristics on geographical responses to climate change. Two model types were used to validate model results; GLM, and MCMCglmm accounting for phylogeny. Results shown report the best model according to AIC/DIC. N gives the number of species involved in its associated model, an asterisk indicates statistical significance of the variable in question (p-value < 0.05), and a dash symbol shows that the variable is excluded from the best model according to AIC/DIC. The pseudo R^2 type is Nagelkerke (Nagelkerke 1991). For the categorical variables breeding habitat type and range geography, I used lotic habitat type and Northern range as reference levels, respectively. Phenology shifts were unrelated to any of the predictor variables that I tested. CI gives the 95% credible intervals of the MCMCglmm model.

	Range shift (N = 77)					
	GLM		**MCMCglmm**			
Predictors	**Est.**	**p**	**Post.m**	**p**	**Lower CI**	**Upper CI**
(intercept)	-0.61	0.03*	-0.61	0.03*	-1.14	-0.05
Southern range	0.90	<0.01*	0.90	<0.01*	0.29	1.51
Widespread	0.32	0.34	0.31	0.36	-0.42	0.93
T ° variability	-0.34	<0.01*	-0.34	<0.01*	-0.55	-0.13
Both hab. Types	-	-	-	-	-	-
Lentic habitat	-	-	-	-	-	-
Flight duration	-	-	-	-	-	-
Oviposition	-	-	-	-	-	-
Body size	-	-	-	-	-	-
Model evaluation						
AIC/DIC	208.99		209.06			
Null model	221.51		221.49			
Pseudo R^2	22.72%		20.42%			
Phylogenetic signal						
Pagel's lambda (p)	0.07 (0.78)					
Blomberg's K (p)	0.01 (0.94)					

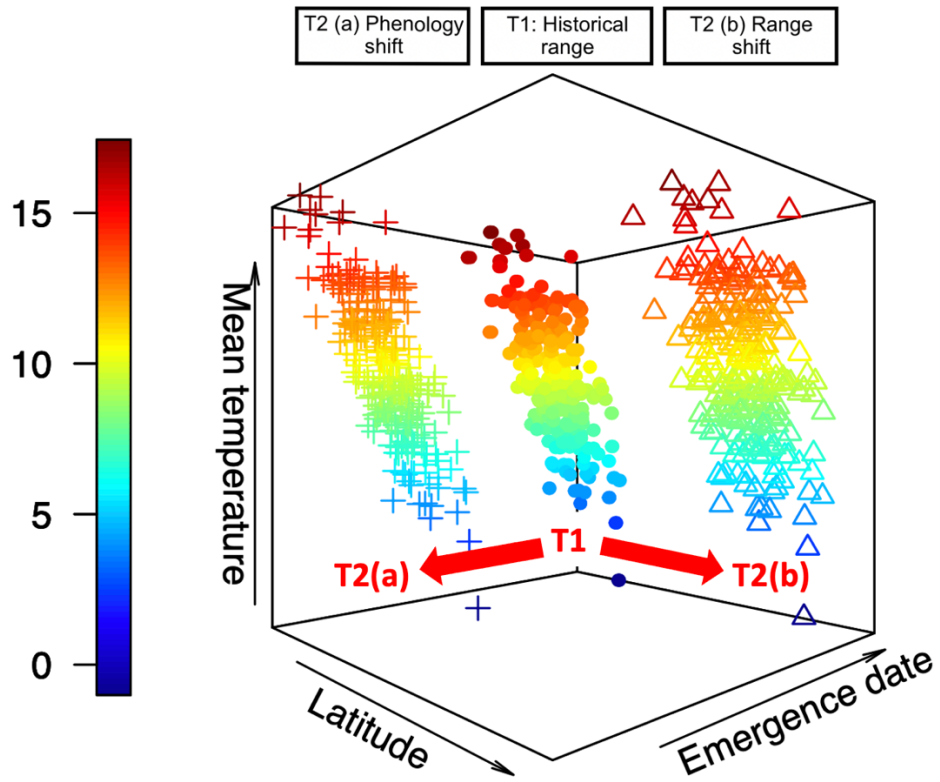

Figure 3.1: Representation of temporal and geographical limits characterising the ecological niche of one hypothetical odonate species. Points show 250 individuals according to their Julian day of emergence, latitudinal position, and temperatures to which each individual is exposed. Points represent historical observations, 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.

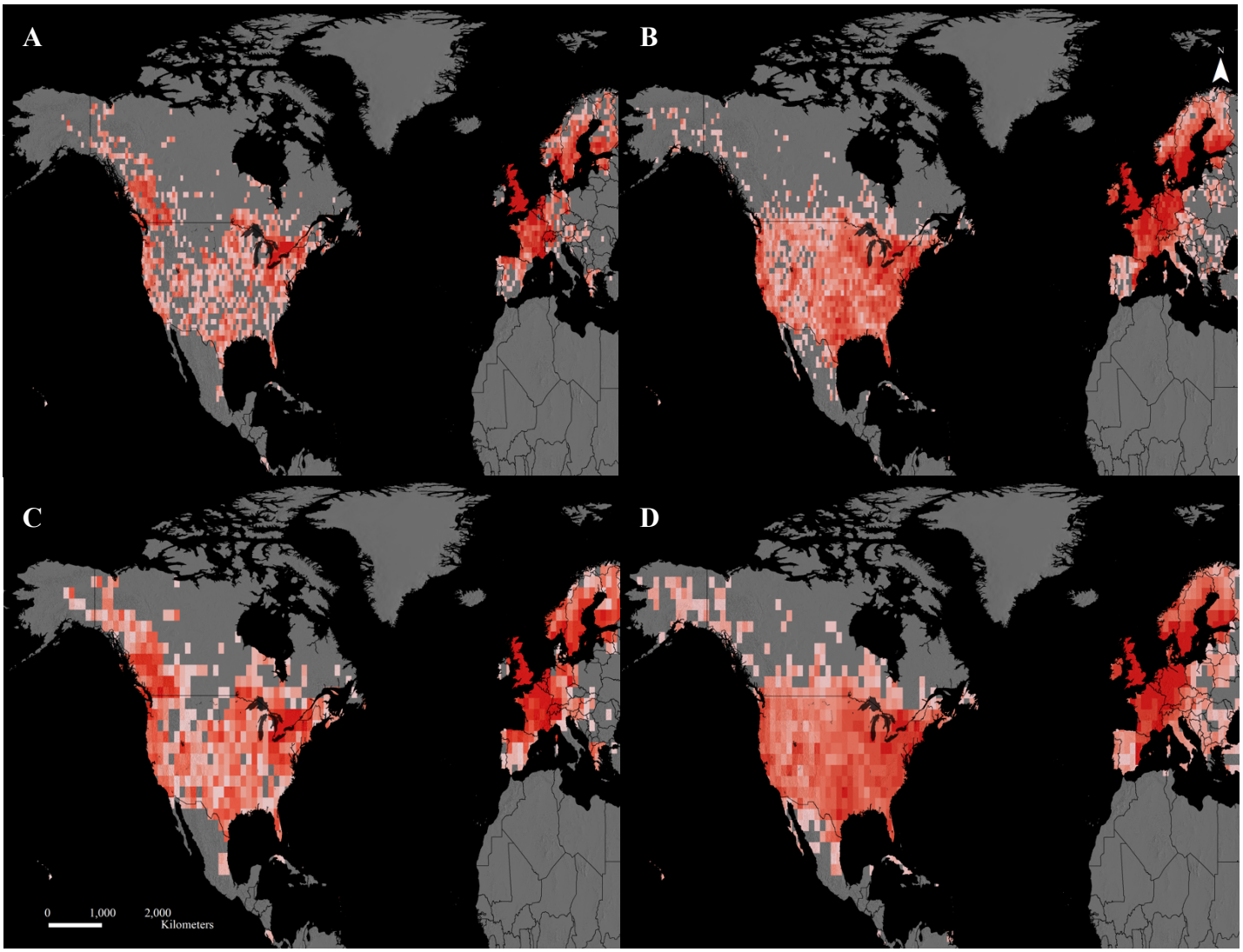

Figure 3.2: Distribution of 77 odonate species records sampled in North America and Europe between 1980 and 2018. Dark and light colors show high and low observation numbers, respectively, per 100 X 100 km quadrats (panes A and B), and per 200 X 200 km quadrats (panes C and D). In pane A, values range from 1 to 24,202; pane B, 1 to 11,928; pane C, 1 to 62,812, and; pane D, 1 to 27,726. I tested for the effect of differences in sampling intensity using two different null models, as explained in the Methods section, under *Spatial and temporal change metrics*. Data used to produce this map originated from many sources (see Methods). This map

was projected using the Equidistant Cylindrical World projection and produced with ArcGIS software version 10.7.1.

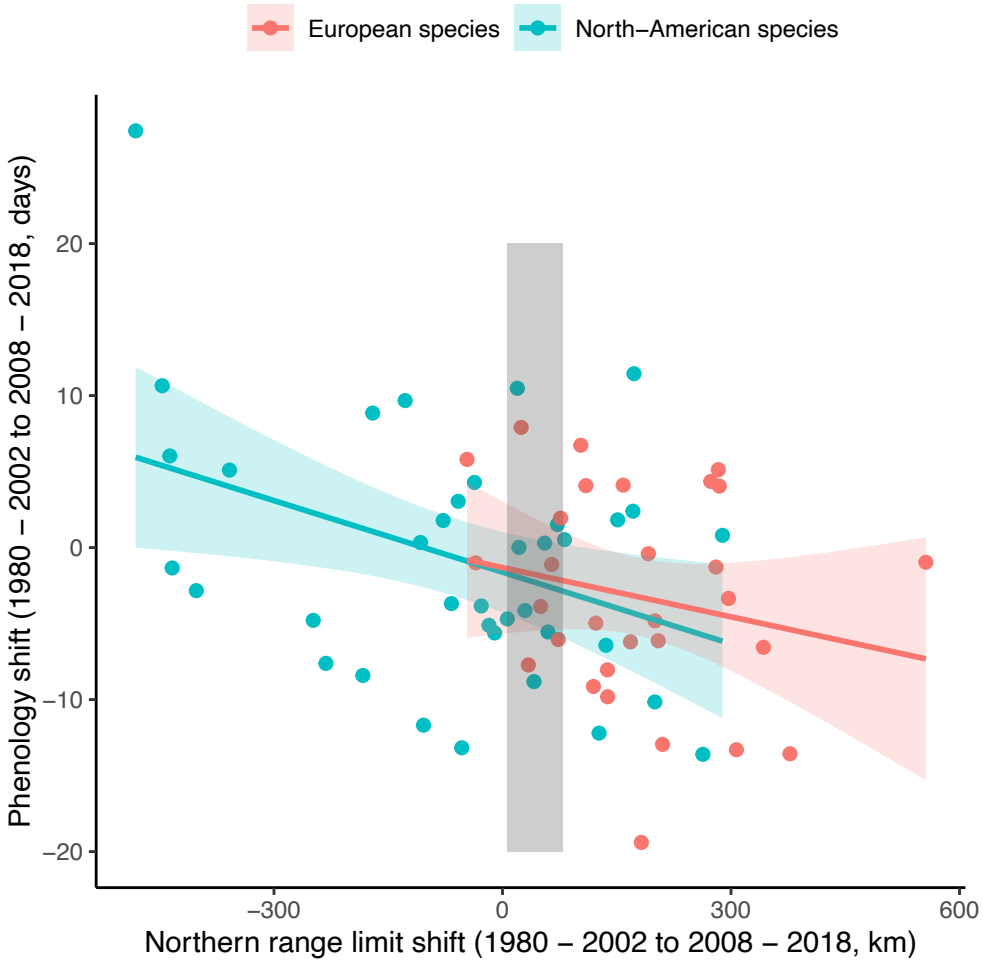

Figure 3.3: Relationship between two responses to climate change, range shifts and emergence phenology shifts, among North American and European odonate species (N = 68). The shaded area shows mean latitudinal range shifts of terrestrial taxa according to Lenoir et al. (2020), calculated as the yearly mean dispersal rate of 1.11 +/- 0.96 km per year over 38 years, which is presented for comparative purposes.

Supporting Information for Chapter 3

Section S1: Supplementary Design and Methodology

Odonate data

The full raw dataset includes ~2 million Odonata occurrence records. I first removed inadequate records from my primary dataset. Inadequate records were identified as those with incomplete information for species identification, year, or locality, inaccurate georeferenced points, and duplicate records. I retained ~1,000,000 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, I 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 I 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

I 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. My methods do not enable tests of those ideas, however. For example, *Aeshna umbrosa* has a surprisingly high phenology shift (>25 days) and a strong range retraction (<-300 km). For this species, I retained 8 quadrats to estimate mean phenology shifts. 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.

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 & Ehrlich, 2010; Zattara & Aizen, 2021). Here, I put in place several criteria including careful interpretation of results, as described in the Methods section of the main text. *Nehalennia irene* was removed from the dataset, as its range positions were highly unusual, and likely due to other factors than global change (>800 km). Further, among preliminary examinations of the data, I tested for the effect of sampling onto my phenology and range shift estimates. I found no effect of sampling on range or phenology responses that I calculated here. I 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, I built a Generalized Linear Model to assess whether the number of quadrats in which each species is sampled predicts species' range shifts that I computed. If spatial bias was present

here, I would expect the number of quadrats in which species are found to increase the position of species' northern range boundaries. The p-value of the predictor variable, sampling change per species, was not significant.

Model information and statements

I 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 for continuous response variables. The number of iterations, burnin, and thinning parameters were tested and confirmed with an 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 = "gaussian", 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)

Section S2: Supplementary Tables 3.S1 – 3.S3

Table 3.S1: 77 species sampled across North America and Europe between 1980 and 2018 follow my criteria for quality observation records for inclusion in the 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. I 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	64.60
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
Libellula quadrimaculata	Europe	7250.59	7593.18	342.59
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

Table 3.S2: 68 species sampled across North America and Europe between 1980 and 2018 follow my criteria for quality observation records for inclusion in the 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. The number of quadrats shown was 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 hastata	3	11.44
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
Libellula quadrimaculata	45	-6.56
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 3.S3: Ecological and geographical traits of 77 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 a species' range, which can be widespread (W), southern (S), northern (N), southern and widespread (SW), or northern and widespread (NW). Oviposition 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, I 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
Libellula quadrimaculata	Both	W	2.5	Exophytic	44
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

Section S3: Supplementary Figures 3.S1 – 3.S8

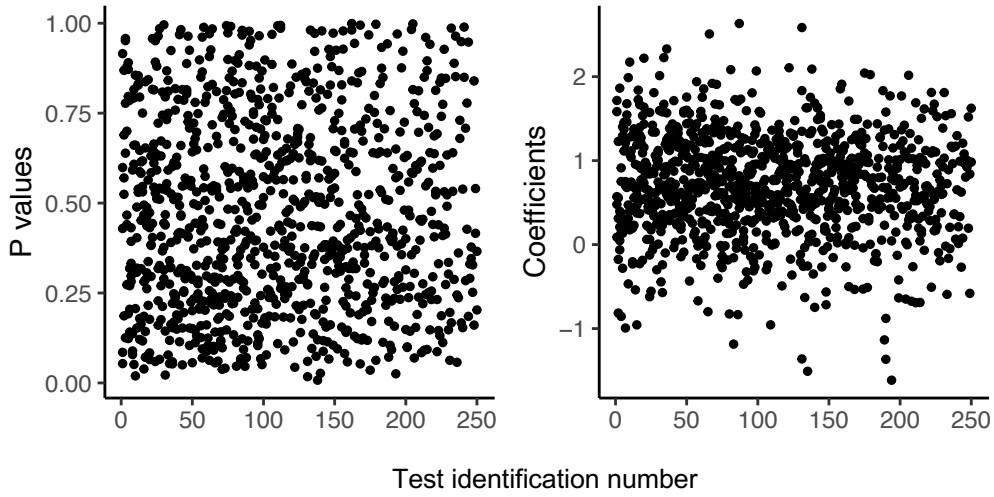

Figure 3.S1: P-values and coefficients of 1000 GLMs built to test whether range shifts as calculated from random datasets predict the range shifts measured in the study. Each point shows the results of a single GLM model, with measured range shifts as the dependant variable and range shifts calculated from a random dataset as the independent variable.

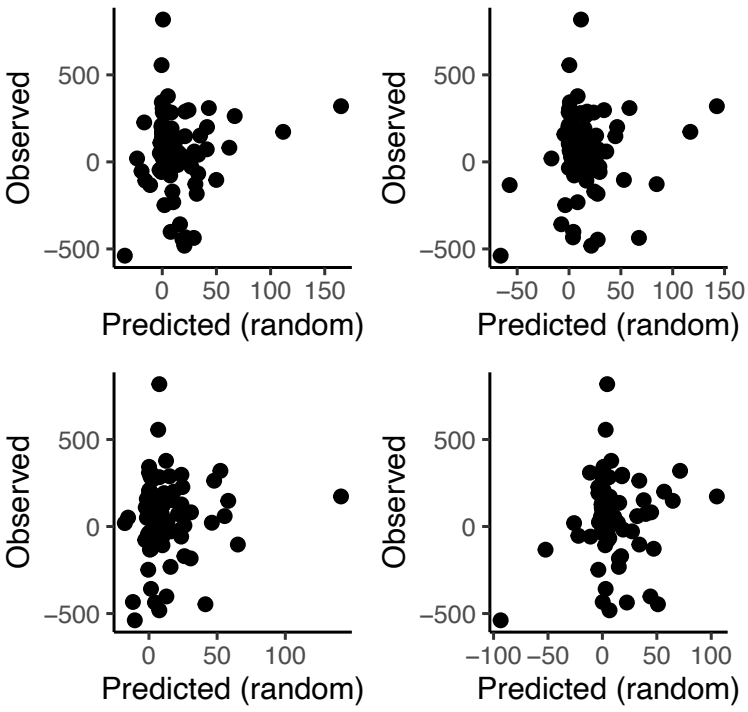

Figure 3.S2: Observed range shifts in km from the equator, against predicted values according to 4 random datasets, shown in 4 different panes. Points represent species. There is no consistent relationship between predicted and observed datapoints.

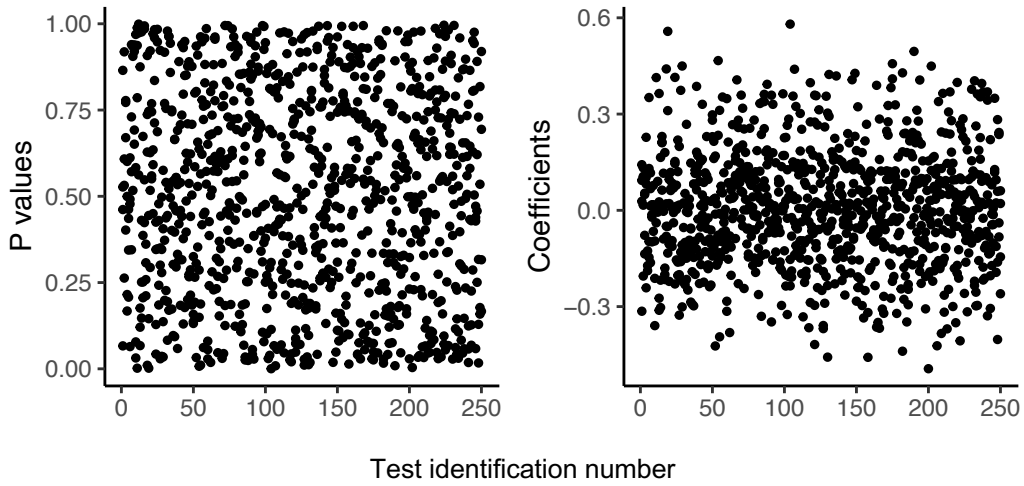

Figure 3.S3: P-values and coefficients of 1000 GLMs built to test whether phenology shifts as calculated from random datasets predict the phenology shifts measured in the study. Each point shows the results of a single GLM model, with measured phenology shifts as the dependant variable and phenology shifts calculated from a random dataset as the independent variable.

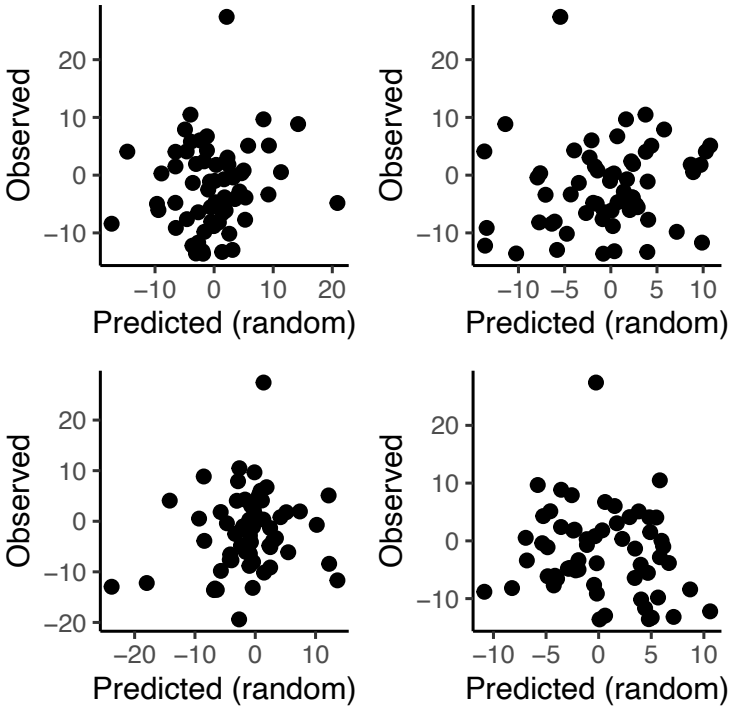

Figure 3.S4: Observed phenology shifts in Julian day, against predicted values according to 4 random datasets, shown in 4 different panes. Points represent species. There is no consistent relationship between predicted and observed datapoints.

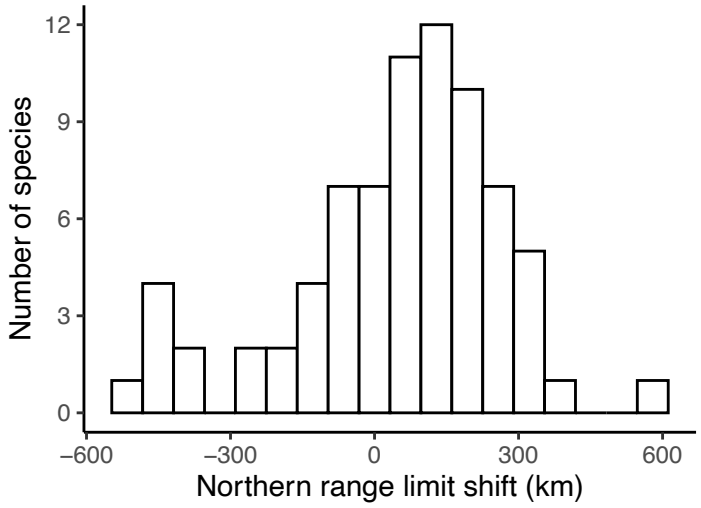

Figure 3.S5: Distribution of values computed for range shifts of 77 European and North American species between a current time period (2008 - 2018) and a historical time period (1980 - 2002). See Methods section of the main text for full details on data assembly, and steps undertaken to produce these preliminary results.

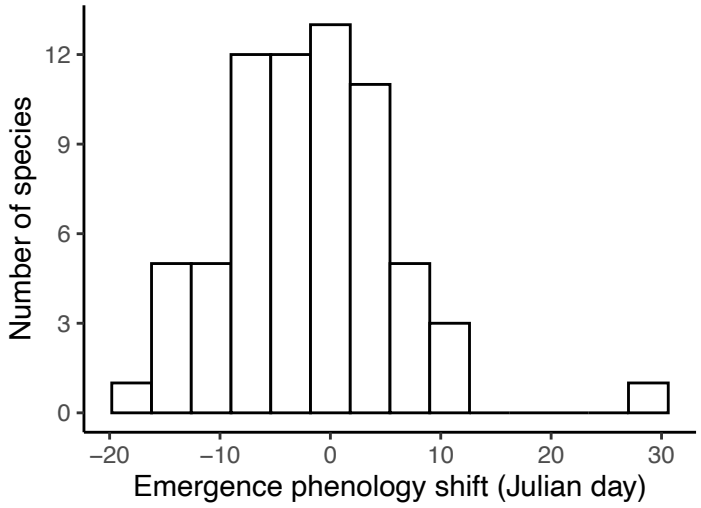

Figure 3.S6: Distribution of values computed for phenology shifts of 68 European and North American species between a current time period (2008 - 2018) and a historical time period (1980 - 2002). See Methods section of the main text for full details on data assembly, and steps undertaken to produce these preliminary results.

Figure 3.S7, A

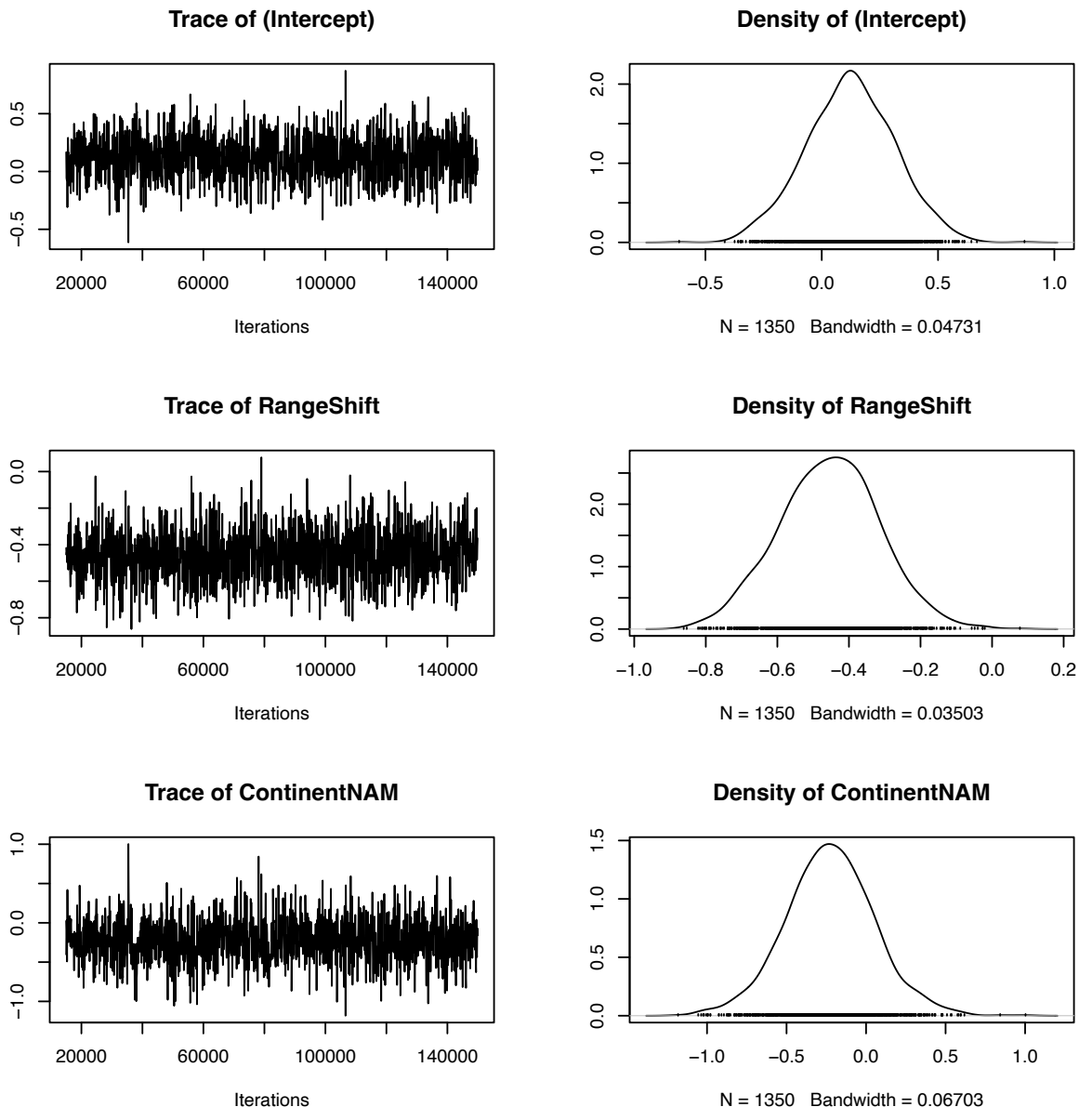
Trace of (Intercept)
Density of (Intercept)
Iterations
N = 1350 Bandwidth = 0.04731
Trace of RangeShift
Density of RangeShift
Iterations
N = 1350 Bandwidth = 0.03503
Trace of ContinentNAM
Density of ContinentNAM
Iterations
N = 1350 Bandwidth = 0.06703

Figure 3.S7, B

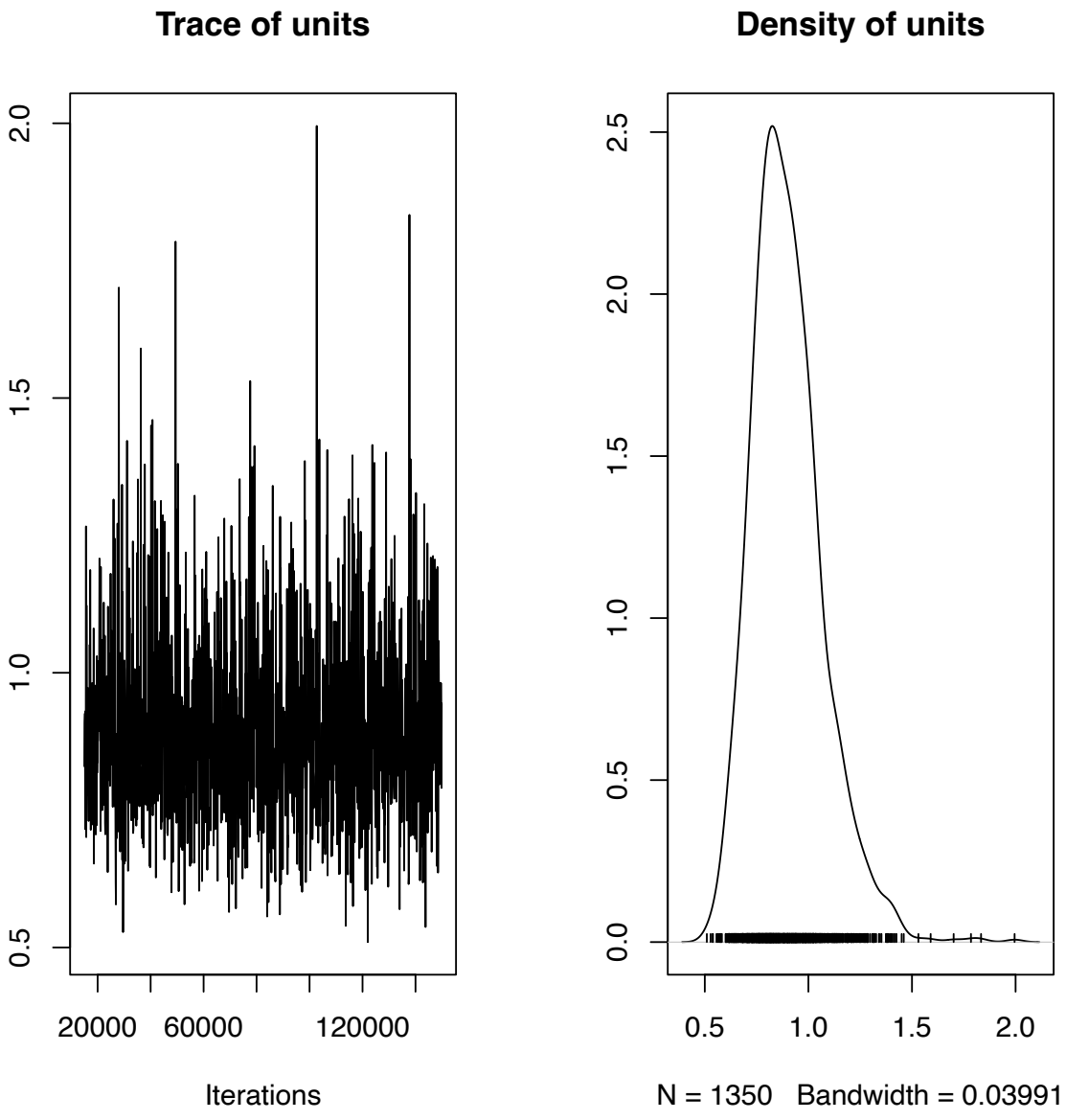

Figure 3.S7: Panels A and B show the trace and density estimates of a phylogenetic mixed effects model exploring the relationship between range and phenology shifts in North American and European odonates (N = 68). 150,000 iterations were run to produce these results. These plots verify model convergence and absence of autocorrelation within the explanatory variables.

Figure 3.S8, A

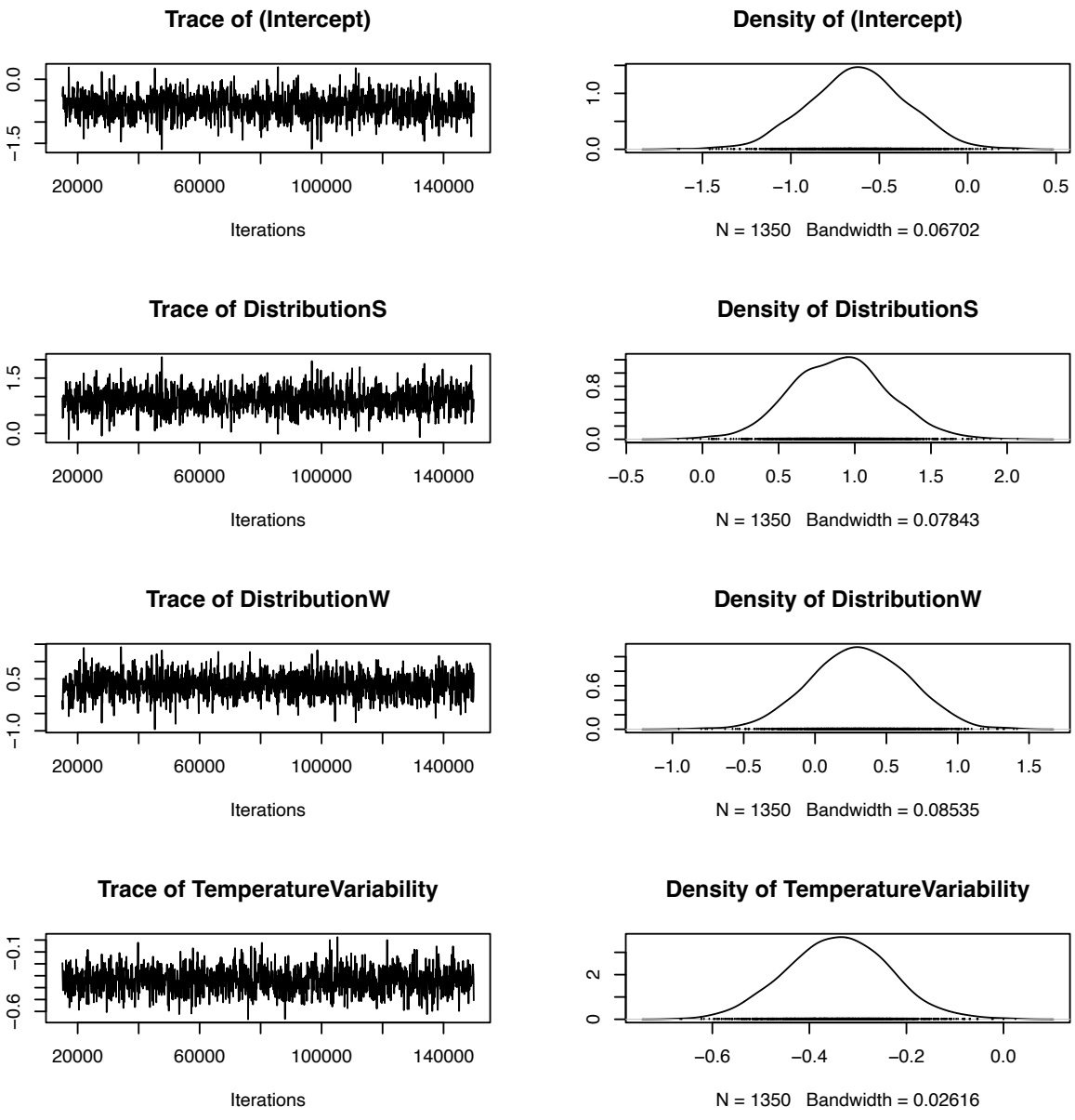
Trace of (Intercept)
Density of (Intercept)
Iterations
N = 1350 Bandwidth = 0.06702
Trace of DistributionS
Density of DistributionS
Iterations
N = 1350 Bandwidth = 0.07843
Trace of DistributionW
Density of DistributionW
Iterations
N = 1350 Bandwidth = 0.08535
Trace of TemperatureVariability
Density of TemperatureVariability
Iterations
N = 1350 Bandwidth = 0.02616

Figure 3.S8, B

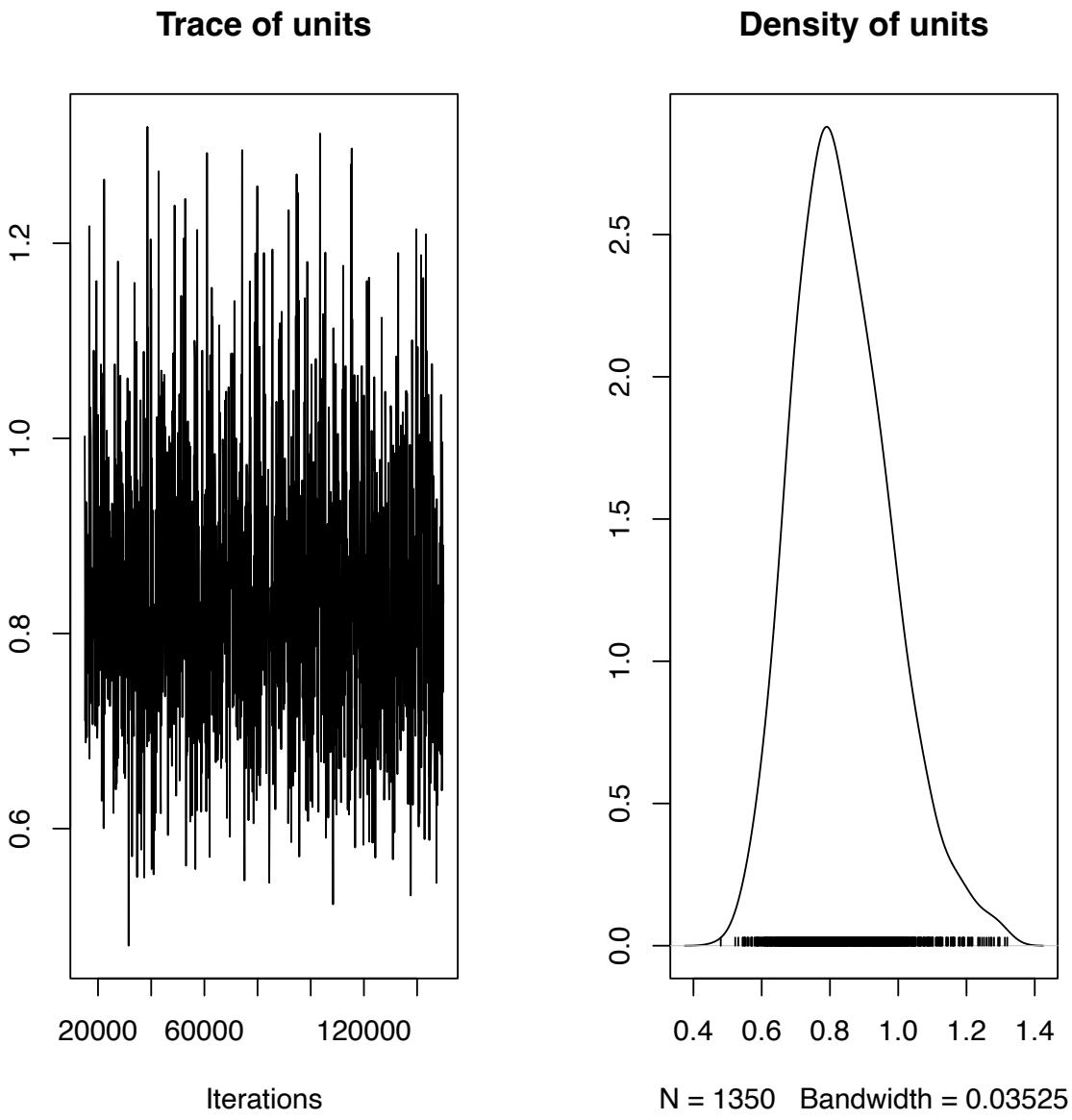

Figure 3.S8: Panels A and B show the trace and density estimates a phylogenetic mixed effects model testing whether ecological traits, and geographic and climatic attributes predict range shifts in North American and European odonates (N = 77). 150,000 iterations were run to produce these results. Results of the best model, according to DIC, are shown here. These plots verify model convergence and absence of autocorrelation within the explanatory variables.

Section S4: References

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Pyke, G. H., & Ehrlich, P. R. (2010). Biological collections and ecological/environmental research: A review, some observations and a look to the future. *Biological Reviews*, *85*(2), 247–266. https://doi.org/10.1111/j.1469-185X.2009.00098.x

Zattara, E. E., & Aizen, M. A. (2021). Worldwide occurrence records reflect a global decline in bee species richness. *BioRxiv*, *869784*. https://doi.org/https://doi.org/10.1016/j.oneear.2020.12.005

Chapter 4: Temperature variability and pesticides limit dragonflies and damselflies from tracking their niches through time

This chapter is a slightly modified version of the manuscript that was submitted for publication in a peer-reviewed journal. It is currently under revision.

Abstract

Under growing anthropogenic threats, improving our understanding of biodiversity responses to climate change is among several urgent needs to support timely conservation goals of freshwater ecosystems. However, there remain critical challenges in understanding how rapid climate change and anthropogenic activities threaten species' ability to persist or establish in new areas. Using historical observation records of 132 odonate species, I used Species Distribution Models (SDMs) to project distributions to a current time period, within the continental USA. I used temporally independent data to assess whether probabilities of presence as projected by the models predict species' observations. Including only skillfully modeled species, I assessed whether anthropogenic pressures hinder species from occupying ecologically suitable areas and tracking their ecological niche across space. I discovered that human pressures hindered species' persistence or establishment in areas that are otherwise climatically suitable. Pesticide applications interacted with climate variability, and this interaction was the strongest predictor of species' absences in regions suitable to many species, according to species-specific probabilities of presence. Species with poor temporal transferability were more likely to decline overall. Two broad issues emerge from these findings; first, predictions of extreme events are likely unreliable

in climate models so regions likely to be poorly modeled are difficult to identify, and second, distributions of declining species can be overestimated across regions facing such pressures. Crucial information may be missed in distribution projections when temporal transferability is unknown, and when regions face external pressures, leading to overoptimistic response predictions. This work provides further evidence of interactive impacts of climate change and land use intensification on invertebrate response to global change.

Introduction

The world is confronted by both global change and biodiversity crises (Dirzo et al. 2014, Ripple et al. 2021). Rapid climate change contributes to latitudinal and altitudinal range shifts, and shifts along other spatial gradients among terrestrial taxa (Chen et al. 2011, Lenoir et al. 2020). Species may track their ecological niche, or the set of biotic and abiotic factors required to maintain viable populations, across geographic space, given sufficient dispersal abilities and absence of natural or anthropogenic barriers (Svenning et al. 2008, Devictor et al. 2012, Hargreaves and Eckert 2014, Hargreaves et al. 2014). Dispersal and subsequent establishment in new areas, phenotypic plasticity, and adaptation may reduce climate debt – i.e. the lag between climate change and biotic responses – and prevent or slow regional extinctions (Devictor et al. 2012, Kerr et al. 2015, Urban 2015, Franks et al. 2018). In the absence of such responses, unsuitable conditions may cause local extinctions, and ultimately, range retractions that can be detected across very broad areas (Kerr et al. 2015, Soroye et al. 2020). Understanding determinants of distributions to improve forecasts of species' vulnerabilities under climate change is a priority for freshwater biodiversity conservation (Maasri et al. 2022).

Odonates (dragonflies and damselflies) are sensitive to changing climatic conditions and are a macroecological barometers to those effects (Hassall 2015). Odonates were recently identified as globally threatened due to wetland loss and degradation (IUCN Red list 2021), while facing climate change-related local persistence declines (Sirois-Delisle and Kerr 2021). Odonate species are generally strong dispersers and have shown relatively rapid distributional and temporal responses to climate change (Hickling et al. 2005, Ball-Damerow et al. 2015, Powney et al. 2015, Sirois-Delisle and Kerr 2021). Range losses are expected to vary considerably, from modest to severe, and few odonates are expected to expand their ranges in climate scenarios, even when warming is relatively limited (Maes et al. 2010, Domisch et al. 2013, Simaika and Samways 2015, Li and Park 2020, Boys et al. 2021, Shin et al. 2021).

There is evidence that the increasing frequency and severity of extreme weather contributes to odonate species declines (Sirois-Delisle and Kerr 2021). Temperature variability, marked by exposure to conditions that approach or exceed species' tolerances directly or through their ecological interactions, are associated with odonate population declines and shifts to new environments (Grant et al. 2017, Day et al. 2018, Harris et al. 2018). Extreme climate events also reduce probabilities of establishment in new regions beyond species' historical ranges (Mair et al. 2014, Kerr 2020, Román-Palacios and Wiens 2020). Short-term extreme temperature disturbs the developmental environment of odonate nymphs, rising mortality rates (McCauley et al. 2015). Warming temperatures are related to decreased survival of both eggs and nymphs, and to smaller body sizes in newly emerged adults (Starr and McIntyre 2020).

Land use change and intensification decrease odonate species richness, diversity, and alter community composition (Ball-Damerow et al. 2014, Powney et al. 2015, Villalobos-Jiménez et al. 2016, Goertzen and Suhling 2019). These effects arise partly as a consequence of

odonate species' dependence on vegetation structure and diversity (Goertzen and Suhling 2013). Leaching and spray drift of pesticides also contaminate water bodies and soils, exposing non-target invertebrates such as dragonfly nymphs to bioaccumulate agricultural pollutants (Damalas and Eleftherohorinos 2011, Van Praet et al. 2012). Decreased feeding rates, mobility, emergence probability and immune function, result from exposure to such agricultural pollutants (St Clair and Fuller 2018, Barmentlo et al. 2019, Hashimoto et al. 2019). Impacts of pesticide applications on local extinctions are aggravated by the effects of rising temperature variability that results from anthropogenic climate change (Sirois-Delisle and Kerr 2021). Species may be absent in ecologically suitable areas due to anthropogenic pressures, creating potentially important challenges in our ability to predict species responses to climate change.

The ability to capture species' ecological niche is a necessary first step to identify regions that are climatically suitable for species, a reoccurring goal in species' conservation planning under climate change. In particular, species must be able to maintain net stable or positive population growth rates in an area for them to persist in an existing area or to successfully establish a population in a new one (Hutchinson 1957). Indeed, range limits relate clearly to species' ecological niche limits, and their fitness can decline elsewhere (Hargreaves et al. 2014, Lee-Yaw et al. 2016). Modeling species' ecological niche limits can be helpful to identify species likely to be threatened by global change, areas where many species are at risk of losing suitable habitat, or areas that may act as climate refugia (Elith and Leathwick 2009, Newbold 2018, Sirois-Delisle and Kerr 2018). Species Distribution Models (SDMs) are particularly suited for predictions.

Projecting species distributions under future climate change is among the most common uses of SDMs (Santini et al. 2021). Tests with independent data show that models can improve

predictions of where species are found (in about half of studies reviewed; Lee-Yaw et al. 2022), however, models that are transferred to a new time or place vary considerably in their effectiveness (Sequeira et al. 2018, Yates et al. 2018). Rates of omission and commission – i.e. false absences and false presences respectively – increase in model projections with ecological realism deficiencies (Barry and Elith 2006). Model performance worsens due to species presences in unsuitable regions, which can be caused by vagrant individuals, sink populations or relict populations, and to absences in suitable regions, potentially caused by dispersal limitations restricting abilities to reach suitable habitats, biotic interactions or environmental stochasticity (see review by Lee-Yaw et al. 2022). Models may omit biological requirements for species, causing them to fail in spatial or temporal transferability tests, but still show deceptively high validation metrics calculated using a subset of the current data (Varela et al. 2009). Since human pressures are a major determinant of current biodiversity patterns, SDMs may fail in regions where there is increased human pressures, even if climatic conditions appear completely suitable (Di Marco and Santini 2015, Faurby and Svenning 2015). Significant challenges related to future projections have been known for well over a decade (Dormann 2007, Peterson et al. 2018), yet, studies rarely test models through time with empirical data, and existing tests report highly mixed results (Rapacciuolo et al. 2012, Sofaer et al. 2018). No study describing future odonate distributions also reports transferability tests with temporally independent data, to my knowledge.

Here, I test whether ensemble predictions of odonate range shifts match changes in where species have been observed over time, following a period of rapid climatic and land use-related changes. I identify models that pass these tests of temporal transferability. I then assess whether species for whom models fail to predict range shifts were more likely to have declined within

their historical range. I test whether factors of global change lead model predictions to fail over time (i.e. creating higher rates of commission errors among all species). These tests determine whether anthropogenic pressures prevent species from establishing in otherwise ecologically suitable areas, to better understand anthropogenic threats to odonates. I used a multi-stressor framework to untangle the role of human-caused stressors that hinder species' establishment or persistence in climatically suitable areas, while providing a steppingstone towards better understanding the potential shortcomings of SDMs.

Methods

Occurrence records and study area

I assembled ~1.5 million observation records across the United States of America (area 9,857,306 km^2) collected from 1901 to 2021 (see Supporting Information; Section S1). Records are unique on a species-location-year basis. I assembled data from three dataset aggregators, including the Global Biodiversity Information Facility (http://gbif.org/), Canadensys (http://www.canadensys.net/) and Odonata Central (Abbott 2020). Using data that were not systematically collected can create spatial and temporal biases, but biases are less likely to affect global trends in assessments that include long-term species occurrences over broad geographical areas (Zattara and Aizen 2021). Retaining only the best sampled species and locations for analyses further decreases such risks for presence-only data (Kharouba et al. 2018).

Observations were split according to a historical time period (years 1901 to 1985, inclusively) and a current time period (years 2000 to 2021, inclusively; Figure 4.1). I included as many years as possible in a period preceding effects of rapid climate change to maximise species

detection and known information on habitat suitability used to build the models. Species with less than 150 records in either time period were removed. Observations of the most recent time period were assigned to 100 X 100 km quadrats to maximize probabilities of detecting occupied areas. I removed species if they were observed in fewer than 75 quadrats in either time period, focusing on more common species. Restricting the data to species sampled in more than 50 quadrats, or 100 quadrats, does not change the outcome of my results.

Clusters of observations may cause models to be overfit, where range predictions confirm too closely to the records used to build the model (Veloz 2009, Hijmans 2012, Boria et al. 2014). To limit this issue, I spatially rarefied presence points based on climate heterogeneity using the SDM toolbox in ArcMap 10.8 (Brown 2014). This technique minimizes potential biases that may arise due to spatially autocorrelated occurrence points (Penado et al. 2016) and reduces probabilities of over-fitting based on environmental biases in data collection (Hijmans 2012, Boria et al. 2014).

Environmental variables to build SDMs

To build the models, I used three environmental variables, including monthly average daily maximum temperature in July (degrees Celsius), monthly precipitation (mm), and diurnal temperature range (degrees Celsius), on a 0.5° latitude by 0.5° longitude grid provided by the Climatic Research Unit (available at http://www.cru.uea.ac.uk/data). These variables affect energy and water regimes (Whittaker et al. 2007) and they are least correlated and most representative of climate, since they are not derived from other variables (Brown 2014). Simpler models with fewer predictor variables, as well as those using variables with a maximum absolute Pearson correlation of 0.7, restrict collinearity among predictors (Brun et al. 2020). The variables

selected here are biologically meaningful to odonates at continental scales (Hof et al. 2012, Domisch et al. 2013). Including non-biologically relevant predictors falsely increases accuracy metrics (Fourcade et al. 2018). Incorporating false relationships between predictors and species' presences when building SDMs is problematic, especially in models that project distributions to different times or geographies (Bahn and McGill 2013, Merow et al. 2014).

Building Species Distribution Models

I used historical observation records and environmental conditions to build models, and projected species' distributions to conditions of the current time period. I used two machine learning techniques including Maxent (Phillips et al. 2006) and Random Forest (Breiman 2001), and a parametric regression method, Generalized Additive Models (GAM) (Hastie and Tibshirani 1990). These techniques accommodate presence-only data, in which environmental variables at presence locations are compared to conditions at random pseudo-absence or background points (Guillera-Arroita et al. 2015). Models were run using the *sdm* R package (Naimi and Araújo 2016) with a logistic output, generating a relative probability of occurrence in model projections.

Several factors impact model ability to predict species' occurrences. Model type, settings, and parameters, such as the number of presence points, the choice of environmental variables and the dissimilarities between variables at the baseline data and those to which the model is projected, can alter model results; these factors have often been discussed (Wenger and Olden 2012, Vale et al. 2014, Fourcade et al. 2018, Fernandes et al. 2019, Santini et al. 2021). Here, I used a conservative approach throughout the model building process to minimize commission and omission errors that may arise due to novel climatic conditions that occur as a result of

climate change, and to data limitations, similar to previous work (Sirois-Delisle and Kerr 2018). I used a clamping setting, which sets the maximum values of the environmental data in the most recent time period to the maximum training range, due to unknown responses of species facing novel climatic conditions. I used the *buffer* function (distance of 500 km) from the *Raster* R package to build species-specific background grids, from which pseudo-absences were sampled. A large buffer distance was selected to capture boundaries of environmental change. I selected 1000 random background points within this buffer to be used as pseudo-absences. The background sample should be large enough to represent environmental conditions, without creating a "class overlap" where presences and pseudo-absences occur in similar environments (Valavi et al. 2021). Models were replicated using a 10-fold cross-validation method.

I obtained continuous probabilities of occurrence maps in raster format. I extracted the probabilities of presence per 100 X 100 quadrat, and clipped rasters to the background grids, avoiding issues associated with unlimited dispersal assumptions that lead to predictions of presence in unattainable regions for individuals. I retained these continuous maps, but also reclassified them to obtain species-specific presence-absence maps using the probability of occurrence threshold that maximizes the True Skill Statistic (Allouche et al. 2006). TSS is calculated with the following equation:

(TSS = sensitivity + specificity – 1),

where sensitivity is the true positive rate and specificity is the true negative function (Pearson 2008). TSS was calculated using random subsets of observations from the historical time period, so that the function models the absences.

Anthropogenic pressure variables

I used a combination of land cover, land use and temperature variability data to measure whether anthropogenic pressures contribute to commission error rates in projections across the current time period. Even though temperature variability is a climatic factor, it is not used in SDMs that project future distributions, because predictions of extreme temperature events in future years, especially decades into the future, are inconsistent. Regions with greater frequency of commission errors are those in which diversity is predicted to be high according to the models, but where many species failed to establish or persist according to actual occurrence records within these areas.

I downloaded HYDE 3.1 land use data (available at http://www.pbl.nl/hyde). HYDE uses satellite data and statistics of world populations, to create land use maps in 5 arc-minute resolution. I downloaded cropland (km^2 per grid cell), pastureland (km^2 per grid cell) and population density data (inhabitants per km^2 per grid cell) and extracted averages per time period and per quadrat. I calculated the difference in extents of land uses between both time periods.

Pesticide application (kg) was downloaded from the USGS website (available at https://pubs.usgs.gov/ds/752/), which consists of county level estimates of pesticide application (459 compounds) within the conterminous United States. These data are based on the US Department of Agriculture for harvested-crop acreage as well as proprietary Crop Reporting District pesticide use (Thelin, G.P., and Stone 2013). As in Sirois-Delisle and Kerr (2021), I used the total pesticide use per quadrat in each year and averaged those totals across years (2000 to 2018), based on available data. Pesticides applied by seed treatment are excluded from these data

starting from 2015 onwards, so estimates of pesticide applications that represent risks for species may be underestimated (Douglas et al. 2020).

Temperature variability during species' flight season may predict success or failure to persist within species' historical range or to establish in new climatically suitable regions the following year. Using the monthly average daily maximum temperature from CRU, I extracted mean temperature per quadrat in the months of April to October for each year in years 2000 to 2021 inclusively. I calculated the difference between the maximum and minimum values per quadrat across the years of both time periods. I used the difference in variability estimates between both time periods as a spatial measurement of interannual temperature variability per area.

I tested for pairwise Pearson correlations among all predictors and found, as expected, that cropland extent was positively correlated with pesticide application (Pearson coefficient = 0.5) and with temperature variability (Pearson coefficient = 0.3), and negatively correlated with pastureland extent (Pearson coefficient = -0.3). I removed cropland extent from the analysis. All other variables were independent.

Statistical analyses

Models are commonly validated by splitting observation records into a training and testing dataset to calculate the True Skill Statistic (TSS; Allouche et al., 2006) or the Area Under the Curve (AUC; Hanley & McNeil 1982). Split-sample validation, however, tends to be less rigorous and over-optimistic compared to tests of temporal transferability using temporally independent data (Rapacciuolo et al. 2012, Sofaer et al. 2018, Santini et al. 2021). Best practices related to validation metrics and numerous settings throughout modeling processes are

repeatedly ignored due to many studies not adhering to best standards, perpetuating precedence of problematic techniques in new studies (Araújo et al. 2019, Santini et al. 2021). For instance, the AUC metric was deemed outdated and unreliable by several authors (e.g. Lobo et al. 2008, Peterson et al. 2008), but it remains commonly used as a measure of model performance (e.g. Morán-Ordóñez et al. 2017, Charney et al. 2021).

I assess temporal transferability with temporally independent data, using two different approaches; the Continuous Boyce Index (CBI; Boyce et al. 2002), and a binomial Generalized Linear Model (GLM). The Boyce index is a statistic that measures whether continuous probabilities of occurrence predict an independent dataset of actual presence data more accurately than random probabilities. It shows how well model predictions represent observed occurrences, and is fit for validation of models with presence-only data (Boyce et al. 2002). The index varies between -1 and 1, where a value greater than 0 indicates that model performance is better than random probabilities. I also test whether modeled probabilities of presences predict observations in the current time period with a species-specific binomial GLM. The response variable was the state of presence (1) or absence (0) per quadrat in the data collected in current years (2000 to 2021), and the predictor variable was the probability of presence as calculated by each model type.

Model 1: *Current presence ~ Probability of presence*

I report the coefficient estimate, statistical significance of the predictor term ($p < 0.05$) and the variance explained by the model using Nagelkerke R^2 (Nagelkerke 1991). To identify species that perform well across time, I selected a range of values as minimum criteria according to both measures of transferability; I assessed transferability for a CBI value greater than 0.4 and 0.8, and an R^2 value (according to Model 1) greater than 5%, and 30%, from lenient to strict criteria.

The criteria had to be met across all model types. Species that are poorly modeled might decline due to environmental factors that are infrequently included in SDMs, and these species may tend to show greater rates of decline. I measured the relationship between the species' historical range decline according to Sirois-Delisle & Kerr (2021), CBI, and Nagelkerke R^2 (goodness of fit) as calculated in Model 1.

Model 2: *SDM goodness of fit ~ Species historical range loss*

I tested for data non-independence caused by phylogeny among temporal transferability metrics. I assessed whether CBI or the goodness of fit measure of Model 1 contained a phylogenetic signal, using two models of trait evolution: Pagel's lambda and Brownian motion. I would observe a signal here if there were inherited characteristics related to species' ability to fill their ecological niche through space and to persist under factors of global change.

I assessed whether SDMs tend to fail over time as climate and land use change continue to progress in unprecedented and sometimes stochastic ways. I restricted analyses of commission errors to the best sampled quadrats in the current time period, removing quadrats below the 10^{th} percentile sampling intensity. I built a negative binomial regression model, in which the response variable is the number of species with commission errors per quadrat, indicating climatically suitable areas in which species failed to persist or establish. Quadrats identified as those with commission errors included only the quadrats with errors that intersect across all model types. There were 649 unique quadrats included in this analysis. The predictor variables correspond to factors of climate and land use change, as described in the section *Anthropogenetic pressure variables*. A negative binomial model was most appropriate to avoid issues caused by over dispersion, since the variance is much larger than the mean, and the response variable is count data (Ver Hoef and Boveng 2007). I report both the AIC (Akaike's Information Criterion) and

Nagelkerke R^2 (Nakagawa et al. 2017), to ease interpretation of the effect size. Predictors were Z-scored using the *scale* R function for comparison of estimate coefficient weights amongst variables as calculated by the models. The base model is the following:

Model 3: *Number of commission errors ~ Temperature variability + Pastureland + Population density + Pesticide application + Sampling intensity*

To address potential interactions, I tested three models that are the same as the base model (Model 3) but added an interaction term between temperature variability and i; pastureland, ii; population density, or iii; pesticide application. I used the *jtools* R package (Long 2022) to examine the effect of any significant interaction. I selected the best model on the basis of lowest AIC and highest Nagelkerke R^2 values. Sampling intensity, calculated as the number of species sampled per quadrat, was not significant ($p > 0.05$; $R^2 = 0.01$) in any models I tested.

Results

Statistical analysis

I discovered that measures of human pressures predict the number of species' commission errors (Table 4.1). Pesticide application, temperature variability change, and change in pastureland extent, were linked with species' absences in otherwise climatically suitable areas after a period of rapid climate change. I used the minimum criteria of temporal transferability to maximize the number of modeled species to include in this analysis (N = 70), but I also compared results when including all species (N = 132); similar patterns resulted from these analyses, although including only temporally transferable species led to stronger model fit. The best model, identified according to lowest AIC values, contained an interaction between temperature variability and pesticide application ($p < 0.05$). This interaction was examined more closely with the *interact_plot* R function. The positive relationship between pesticide application

and the number of commission errors increases under greater climate variability change. Pastureland extent was also a significant term in the model ($p < 0.05$), but the relationship was negative. Pastureland extent decreased as frequency of commission errors increased. It should be noted that it is unknown whether regions with lower pastureland in the second time period were converted to other land use types with increased land use intensity.

To better understand the interaction between temperature variability and pesticide use, I used land cover data from the Multi-Resolution Land Characteristics Consortium (available at https://www.mrlc.gov/data/type/land-cover) to restrict quadrats in the analysis to those that are most likely to have extensive natural land covers. I reclassified all developed pixels (any built-up lands, hay/pasture, and cultivate crops) and natural land cover types to calculate the percentage of developed pixels per 100 X 100 km quadrat. I incrementally removed the most developed quadrats from the data, according to disturbance rate. Restricting quadrats to those that are most intact revealed that quadrats with approximately 50% of developed land are those driving the observed interaction between pesticides and climate variability.

The best statistical model (Table 4.1), including species that passed tests of SDM temporal transferability, was used to visualize spatial variation in commission error rates (Figure 4.2; Figures 4.3A-4.3B). Error rates were particularly high in the northern continental US, including Montana, parts of South Dakota, areas near the great lakes such as Illinois and Indiana, but also southern Florida. Regions where commission errors were least likely included Washington, North Dakota, Minnesota and Nebraska.

Model performance

I tested whether poorly modeled species also declined within their historical ranges in relation to particular environmental drivers. The degree of species' declines within their historical range predicted temporal transferability, or the degree to which probabilities calculated by the SDMs predicted actual observation records in Model 1. The relationship was negative: species that SDMs skillfully model experienced fewer declines within their ranges ($p < 0.05$). This is true across all three model types. Model 2 showed that species' range declines predicted how well the SDMs performed ($R^2 = 0.10$ for Maxent models, 0.13 for Random Forest models, and 0.05 for General Additive Models). There was also a significant relationship between the Boyce index and the extent of decline of species in Maxent and Random Forest models, although the effect was weaker (Maxent, $R^2 = 1\%$; GAMs, $R^2 = 4\%$). There was no phylogenetic signal among measures of temporal transferability according to two models of trait evolution, Pagel's lambda and Brownian motion ($p > 0.05$).

Model performance was highly variable across the taxon, according to both the Boyce index and to binomial GLM tests of the reliability of the species-specific probability of presences per quadrat (see Appendix S2). Across all models, 51% of species meet fundamental criteria of temporal transferability (CBI > 0.4 and $R^2 > 5\%$), but only 4% of species meet the most stringent criteria (CBI > 0.8 and $R^2 > 30\%$). Across all validation measures and model types, *Ischnura verticalis* and *Lestes rectangularis* were consistently among the most skillfully modeled species (CBI > 0.85, and $R^2 > 45\%$). Species with the lowest validation metrics across all models, included *Aeshna juncea* and *Argia vivida* (CBI < 0.46, and $R^2 < 11\%$).

Maxent models performed better than the other two SDM model types; across all 132 species, coefficient estimates for Model 1 were positive, and p-values were significant ($p < 0.05$). Nagelkerke R^2 varied between 0.01 and 0.65 (mean $R^2 = 0.28$). The mean Boyce index across all species was 0.87, and these values ranged between 0.15 and 0.99 inclusively, where all models performed better than random probability (CBI > 1).

In Random Forest models, probabilities of presence corresponded with observed presences for many species. Coefficient estimates in Model 1 were positive, and p-values significant across all species. Nagelkerke R^2 values ranged between 1% and 66%, with a mean of 23%. However, the Boyce index was lower than for Maxent models overall, where mean Boyce index was of 0.56, and ranged between -0.70 and 0.99 inclusively. Models for 13 species performed poorly where predictions were not consistent with the distribution of the actual occurrences in the current dataset (CBI < 1).

Similarly, GAM model performance was acceptable for many species, but some models performed worse than random probabilities. Coefficient estimates were positive across all species, and, for all except 2 species, the predictor variable was statistically significant. Nalgelkerke R^2 ranged from 0.5% to 64%, with a mean of 23%. CBI ranged from -0.75 to 0.96, with a mean of 0.44. However, SDM predictions for 21 species performed no better, and sometimes worse, than expected by chance (CBI < 0). There are low positive correlations between the Boyce index and R^2 of the binomial GLMs amongst respective model types, as expected.

Discussion

Temperature variability interacts with pesticide applications to hinder dragonfly and damselfly species from occupying their ecological niche across the continental USA, following rapid climate change. Species failed to persist or establish in areas with both high pesticide use and temperature variability, even where climate suitability appeared high in other respects. My results suggest that projections of these, and potentially other, species' distributions over time will often overestimate the benefits of climate change if they do not account for climatic variability and its interactions with land use intensification. Frequencies of extreme temperature events increase with even relatively low levels of mean surface temperature warming (Baker et al. 2018, Lorenz et al. 2019), but the magnitude of these events varies greatly across models, even when they predict similar differences in average conditions (Freychet et al. 2021). The physical processes that drive heat extremes still lack crucial details (Freychet et al. 2021, van der Wiel and Bintanja 2021). The larger the difference between present-day and anticipated future conditions, the lower the reliability of predictions of species' responses to that environmental change. These regions may require more intensive conservation attention because of this elevated uncertainty as well as the expectation that larger biotic responses are likely in areas facing the greatest climatic change (Santini et al. 2021). Uncertainty grows larger still in areas where land use change and intensification can interact with climate change.

Pesticide applications interacted with increasing temperature variability to predict species' losses from historically-occupied areas and their failures to colonize new areas that models predicted to be climatically suitable. Odonates exposed to temperatures that were closer to their apparent thermal limits may be less capable of tolerating the direct or indirect effects of environmental pollutants (Sirois-Delisle and Kerr 2021). Pollutant toxicity and uptake increase

under increased temperatures in aquatic invertebrates (Noyes et al. 2009, Camp and Buchwalter 2016). In the damselfly *Ischnura elegans*, exposure to pesticides decreased the species' upper tolerance limit, due to a decline in aerobic pathways, and a rise in anaerobic metabolic pathways (Op de Beeck et al. 2017). In other words, species' abilities to cope with hot temperature extremes appear to decline under existing pesticide concentrations in the environment (Op de Beeck et al. 2017).

Intact landscapes provide increased habitat availability, the main component for species to establish in new areas, regardless of dispersal abilities (Mair et al. 2014). Contrary to predictions, species were more likely to be absent in areas with smaller pastureland extent (i.e. higher commission error rates for SDMs). While counter-intuitive, some regions in which the extent of pasturelands decreased since the beginning of the 20th century faced increased livestock density over time. Livestock density contributes to decreased species richness and community composition in butterflies (Kasiske et al. 2023), an effect that may extend to odonates. Further, pasturelands may be converted to other land use types with higher land use intensity. In farmland, odonate diversity decreases with the degree of land use intensification, but increases with the size of waterbodies (Nagy et al. 2019). Odonates are also relatively tolerant to pollutants compared to other taxa (Chang et al. 2014) and tolerate a wide range of environmental conditions (e.g. Smith et al. 2007) so it is also possible that some species facing pollutants nearby pasture lands still persist over time.

My results emphasize challenges in predicting how species' geographical ranges will change in the future. It is possible to address part of this challenge by emphasizing tests of temporal transferability for models that are then used to predict future conditions, rather than building those predictions on the basis of a single baseline time period (Sequeira et al. 2018).

Model performance relies on the degree to which modeling assumptions are met (Santini et al. 2021). Models assume that species' distributions are in equilibrium with the environment, but SDMs are commonly fitted using opportunistic data that could not be collected systematically (Guillera-Arroita et al. 2015). Further, species may occupy areas that do not necessarily represent their environmental tolerances and preferences (Guisan and Thuiller 2005). There are biotic constraints including interactions among species, like competition or predation (Soberón and Peterson 2005, Hanspach et al. 2014), intrinsic dispersal abilities (Sirois-Delisle and Kerr 2018), and physical barriers to dispersal, which constrain species to occupy only a part of their potentially habitable ranges. Human pressures can limit species' geographical ranges (Varela et al. 2009, Di Marco and Santini 2015, Faurby and Svenning 2015), which might violate SDM equilibrium assumptions if those areas comprised an environmentally biased subset of their ranges. In a changing world, it may become more challenging to model distributions through time.

It is more difficult to predict range shifts through time among species that are declining. Thus, models may project positive responses to climate change in specific regions, but other human pressures lead to declines or failure to occupy new areas. My results support this suggestion. This likely occurs because declining species are not in equilibrium with the climate, and their presences do not reflect their fundamental niche in the projected time period due to other pressures. When modeling assumptions are violated, accuracy statistics tend to be inflated (Santini et al. 2021), supporting the importance of explicit tests of temporal transferability. Results raise questions about species selection for SDM studies, especially about identifying species more likely to be helpful to model from a conservation perspective while being transferable through time. SDMs may not be used to advise applied conservation practices for

species that are declining under global change, and that occupy highly disturbed regions. Further, it is important to note that future predictions cannot be tested; models that cannot test their predictions with independent data should be regarded as hypotheses, and not published when model accuracy is critical (Lee-Yaw et al. 2022). Research to assess whether projections to various time periods perform equally is the next step.

This work builds on recent findings about anthropogenic factors that negatively affect odonate persistence (Sirois-Delisle and Kerr 2021), extending knowledge about how odonate species occupy their ecological niche more broadly following a period of rapid climate change. I refine knowledge about factors preventing higher numbers of species from persisting or establishing in new areas. Uncertainty underlying predictions of anthropogenic pressures indicates that future distributions are likely overestimated in many regions. However, SDMs are not useless, and have their place in global change biology research. Such models are certainly a useful exercise to predict occurrences under future climate change, taking into consideration species' temporal transferability and challenges related to human pressures. However, SDMs are best used to initiate novel hypotheses regarding regions that could be suitable (Lee-Yaw et al. 2022). An important advantage in using SDMs is that they allow distributional predictions while avoiding overly complex factors like species interactions or other complex specific context dependant factors (Rasmont et al. 2015). In the case of odonates, model transferability was highly variable. When tests using temporally independent data cannot be executed, models cannot be used for informing applied conservation practices, and may not be used to identify species that are at greater risk of climate change. Overestimates of species tolerances can be problematic, as they may lead policy makers and conservation groups to overlook species that are in urgent need of conservation action.

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Tables and figures

Table 4.1: Assessment of the relationship between the number of commission errors per quadrat and anthropogenic pressures using a negative binomial GLM. 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). Nagelkerke R^2 is reported (Nagelkerke 1991).

	Best modeled species (N = 70)		**All species (N = 132)**	
	Estimate	**p-value**	**Estimate**	**p-value**
Pesticides:T° variability	0.25	< 0.01*	0.21	< 0.01*
Pastureland	-0.15	< 0.01*	-0.13	< 0.01*
Population density	-	-	-	-
Sampling intensity	-	-	-	-
Model evaluation				
AIC	3349		3952	
Null model	3486		4095	
Nagelkerke R^2	20.77%		19.67%	

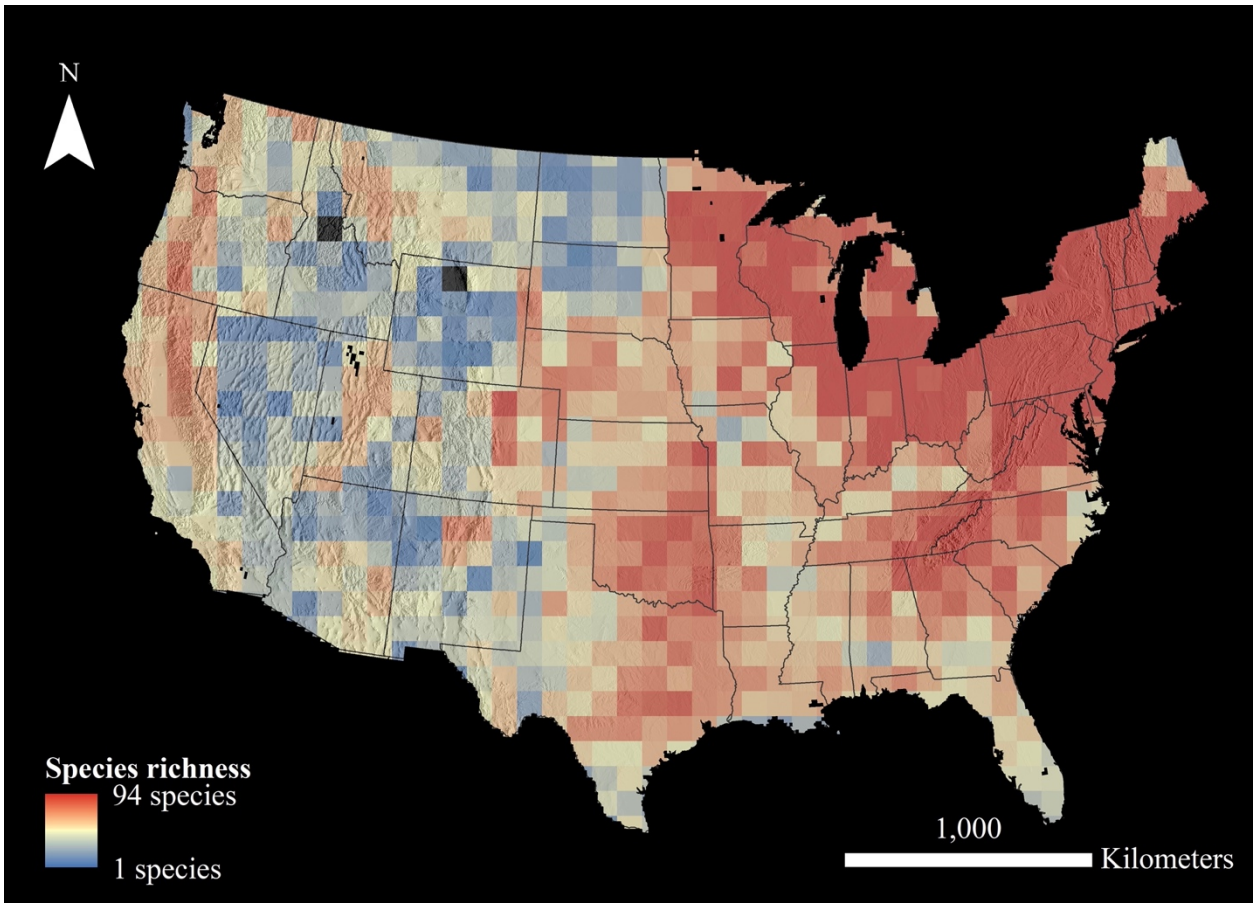

Figure 4.1: Total distribution and richness of 132 odonate species sampled in the United States of America over a historical time period (years 1901 to 1985, inclusively) and a current time period (years 2000 to 2021, inclusively). Species included here are found in at least 75 quadrats of 100 X 100 km in both time periods. Warm and cool colors show high and low richness respectively. This map was produced with ArcGIS software version 10.7.1. High resolution elevation data used for the shaded relief layer originates from the Worldclim 2.1 database (downloaded at https://www.worldclim.org/data/worldclim21.html).

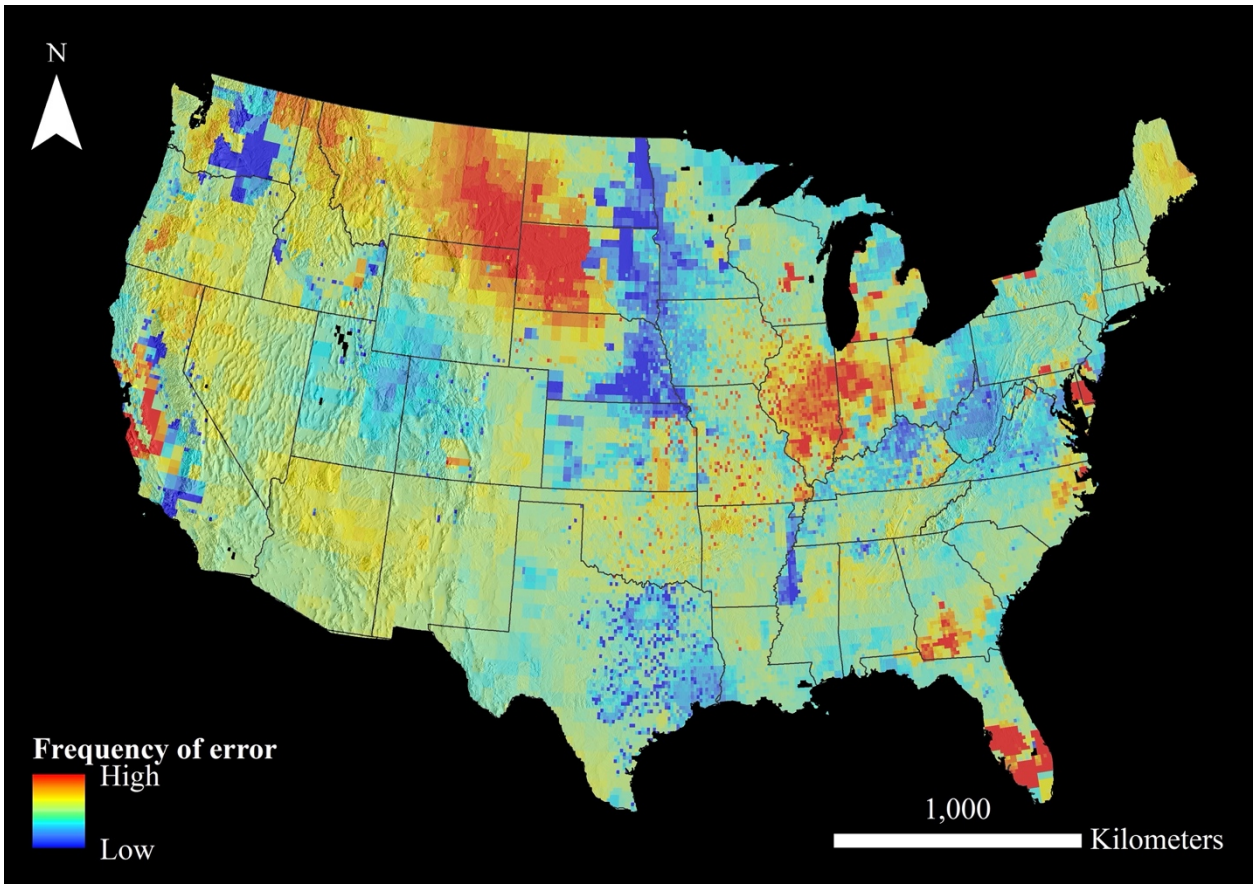

Figure 4.2: Data visualization of the impact of anthropogenic pressures on frequency of commission errors across three different species distribution modeling approaches (maxent, random forest, and GAM), as determined by negative binomial GLM coefficients (see Table 1). Warm and cool colours show areas where the frequency of error is likely to be high or low, respectively, based on the interaction between temperature variability and pesticides, and the extent of pastureland. This map was produced with ArcGIS software version 10.7.1. High resolution elevation data used for the shaded relief layer originates from the Worldclim 2.1 database (downloaded at https://www.worldclim.org/data/worldclim21.html).

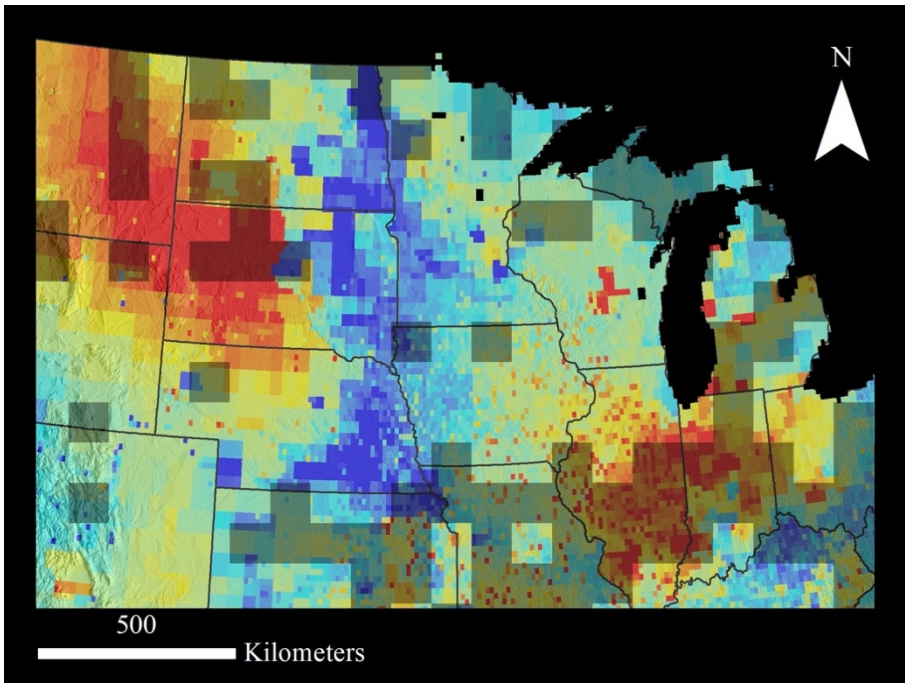

Figure 4.3A: Shaded areas show commission errors – i.e. regions in which the species was not sampled during the second time period, even though all model types (maxent, random forest and GAMs) agree that probabilities of presence are high – for *Lestes unguiculatus*, a species that was well-modeled according to set criteria. Warm and cool colours show areas where the frequency of error is likely to be high or low, respectively, based on the interaction between temperature variability and pesticides, and the extent of pastureland. Shaded areas tend to overlap with warmer colours, indicating that regions likely to lead to commission errors for many species according to anthropogenic pressures tend to match with commission errors in *Lestes unguiculatus* (shaded areas). This map was produced with ArcGIS software version 10.7.1. High resolution elevation data used for the shaded relief layer originates from the Worldclim 2.1 database (downloaded at https://www.worldclim.org/data/worldclim21.html).

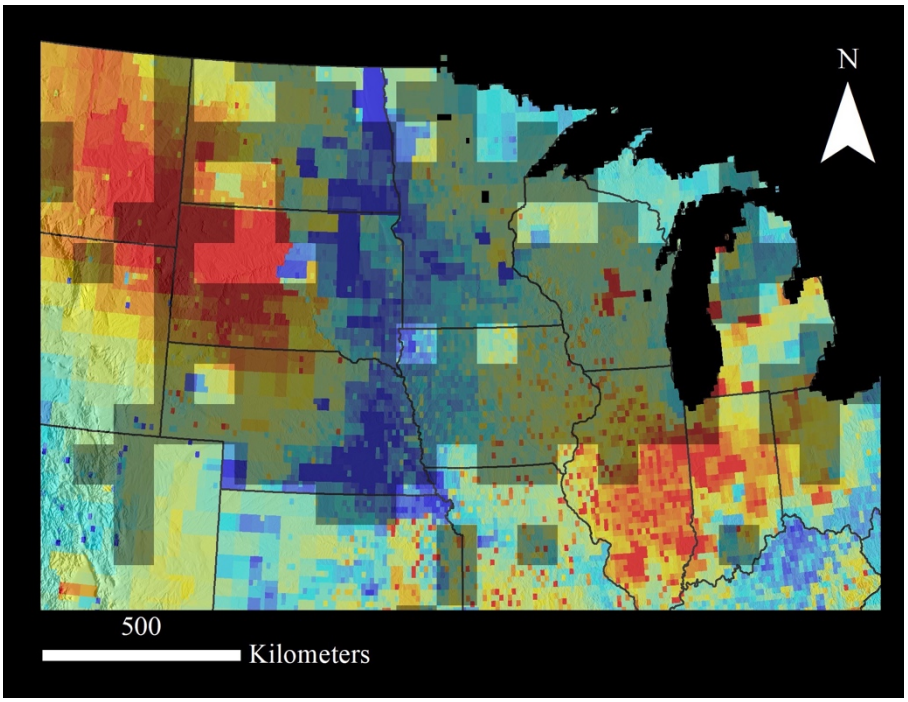

Figure 4.3B: The shaded areas show regions where *Lestes unguiculatus* was present, and where the three model types agree that probabilities of presence are high. Warm and cool colours show areas where the frequency of error is likely to be high or low, respectively, based on the interaction between temperature variability and pesticides, and the extent of pastureland. Shaded areas tend to overlap with cooler colours showing that presences are better captured by SDMs in regions where commission errors are predicted to be low. This map was produced with ArcGIS software version 10.7.1. High resolution elevation data used for the shaded relief layer originates from the Worldclim 2.1 database (available from https://www.worldclim.org/data/worldclim21.html).

Supporting Information for Chapter 4

Section S1: Supplementary Methodology and Species List

Odonate data

The full raw dataset included approximately 1,5 million odonate observation records. I removed inadequate records from the dataset, which included records with incomplete information for species identification, year, or locality, inaccurate georeferenced points, or duplicate records. There were 1,186,263 records from the Global Biodiversity Information Facility (GBIF), 261,857 records from Odonata Central, and 51,536 records from Canadensys. Species' names were modified to match the current name as defined by the Integrated Taxonomic Information System (ITIS); *Tetragoneuria canis* was replaced with *Epitheca canis*, and *Tetragoneuria cynosura*, with *Epitheca cynosura*. I retained 750,000 unique species-location-year observations. I extracted observation records in the continental United States of America (USA), because this region was densely sampled compared to Northern Mexico or Canada, increasing probabilities of producing Species Distribution Models with acceptable temporal transferability metrics. Further, restricting the data to the continental USA allowed me to include pesticide application data in my analyses, due to the accessibility and availability of pesticides data for the region. The following list enumerates 132 odonate species sampled across the USA which follow my criteria for quality observation records for inclusion in the analysis.

Family Anisoptera	**Family Zygoptera**
Aeshna canadensis	*Amphiagrion abbreviatum*
Aeshna constricta	*Amphiagrion saucium*
Aeshna eremita	*Archilestes grandis*
Aeshna interrupta	*Argia apicalis*
Aeshna juncea	*Argia fumipennis*
Aeshna palmata	*Argia lugens*
Aeshna umbrosa	*Argia moesta*
Anax junius	*Argia nahuana*

Basiaeschna janata
Boyeria vinosa
Celithemis elisa
Celithemis eponina
Celithemis fasciata
Cordulegaster diastatops
Cordulegaster dorsalis
Cordulegaster maculata
Cordulia shurtleffii
Didymops transversa
Dorocordulia libera
Epiaeschna heros
Epitheca canis
Epitheca cynosura
Epitheca princeps
Erpetogomphus designatus
Erythemis collocata
Erythemis simplicicollis
Erythrodiplax berenice
Erythrodiplax minuscula
Erythrodiplax umbrata
Gomphus exilis
Hagenius brevistylus
Helocordulia uhleri
Ladona deplanata
Ladona exusta
Ladona julia
Leucorrhinia frigida
Leucorrhinia glacialis
Leucorrhinia hudsonica
Leucorrhinia intacta
Leucorrhinia proxima
Libellula auripennis
Libellula cyanea
Libellula forensis
Libellula incesta
Libellula luctuosa
Libellula pulchella
Libellula quadrimaculata
Libellula saturata
Libellula semifasciata
Libellula vibrans
Macromia illinoiensis
Macromia taeniolata
Nannothemis bella
Ophiogomphus severus
Pachydiplax longipennis
Paltothemis lineatipes
Pantala flavescens
Pantala hymenaea
Perithemis tenera
Argia plana
Argia sedula
Argia tibialis
Argia translata
Argia vivida
Calopteryx aequabilis
Calopteryx maculata
Chromagrion conditum
Coenagrion interrogatum
Coenagrion resolutum
Enallagma annexum
Enallagma antennatum
Enallagma basidens
Enallagma boreale
Enallagma carunculatum
Enallagma civile
Enallagma ebrium
Enallagma exsulans
Enallagma geminatum
Enallagma hageni
Enallagma praevarum
Enallagma signatum
Hetaerina americana
Ischnura cervula
Ischnura denticollis
Ischnura hastata
Ischnura perparva
Ischnura posita
Ischnura ramburii
Ischnura verticalis
Lestes congener
Lestes disjunctus
Lestes dryas
Lestes eurinus
Lestes forcipatus
Lestes rectangularis
Lestes unguiculatus
Lestes vigilax
Nehalennia gracilis
Nehalennia irene
Telebasis salva

Phanogomphus exilis
Plathemis lydia
Progomphus obscurus
Rhionaeschna californica
Rhionaeschna multicolor
Somatochlora albicincta
Somatochlora cingulata
Somatochlora elongata
Somatochlora minor
Somatochlora williamsoni
Stylurus plagiatus
Sympetrum ambiguum
Sympetrum corruptum
Sympetrum costiferum
Sympetrum danae
Sympetrum illotum
Sympetrum internum
Sympetrum obtrusum
Sympetrum pallipes
Sympetrum rubicundulum
Sympetrum semicinctum
Sympetrum vicinum
Tramea lacerata
Tramea onusta

Section S2: Supplementary Results (Table 4.S1)

Table 4.S1: Assessment of the relationship between probabilities of presence according to three SDM model types (Maxent, random forest, and GAM), and temporally independent observation records, in 132 modeled odonate species in the USA. I report the Continuous Boyce Index (CBI), and results of Model 1, to identify which species showed satisfactory temporal transferability. The "*" symbol shows that the predictor variable was statistically significant in Model 1 results.

				Binomial GLM (Model 1) results					
	CBI			Coefficient est.			Nagelkerke R^2		
Species	**MaxEnt**	**RF**	**GAM**	**Maxent**	**RF**	**GAM**	**Maxent**	**RF**	**GAM**
Aeshna canadensis	0.987	0.589	0.754	9.443*	11.172*	55.769*	0.521	0.466	0.491
Aeshna constricta	0.92	0.518	0.02	5.502*	11.192*	27.796*	0.303	0.356	0.272
Aeshna eremita	0.99	0.496	0.607	3.98*	4.023*	25.887*	0.121	0.097	0.088
Aeshna interrupta	0.991	0.966	0.906	4.66*	5.173*	25.918*	0.152	0.173	0.13
Aeshna juncea	0.331	0.462	0.16	1.249*	3.371*	24.336*	0.01	0.026	0.02
Aeshna palmata	0.992	0.99	0.797	4.492*	6.606*	22.781*	0.168	0.19	0.152
Aeshna umbrosa	0.988	0.919	0.829	6.795*	7.127*	33.875*	0.317	0.355	0.345
Amphiagrion abbreviatum	0.984	0.797	0.604	5.425*	6.397*	26.225*	0.198	0.137	0.166
Amphiagrion saucium	0.889	0.776	0.807	6.819*	9.566*	29.38*	0.414	0.345	0.383
Anax junius	0.88	0.804	0.643	5.809*	5.906*	18.494*	0.236	0.29	0.191
Archilestes grandis	0.935	0.282	0.267	3.638*	5.743*	21.039*	0.104	0.091	0.074
Argia apicalis	0.671	0.338	-0.061	9.389*	12.647*	31.406*	0.392	0.395	0.346
Argia fumipennis	0.952	0.876	0.858	5.57*	6.531*	17.852*	0.322	0.404	0.281
Argia lugens	0.713	-0.038	-0.411	4.315*	5.448*	14.632*	0.054	0.023	0.022
Argia moesta	0.799	0.572	0.129	6.324*	8.413*	21.653*	0.327	0.398	0.27
Argia nahuana	0.743	-0.704	-0.651	4.956*	3.969*	18.228*	0.128	0.029	0.062
Argia plana	0.594	-0.008	-0.467	2.999*	7.539*	9.024*	0.089	0.058	0.028
Argia sedula	0.779	-0.271	0.04	4.633*	6.746*	14.4*	0.182	0.166	0.105
Argia tibialis	0.702	-0.055	0.177	10.161*	14.6*	42.22*	0.561	0.461	0.501
Argia translata	0.911	0.512	0.637	3.367*	4.655*	29.316*	0.08	0.039	0.064
Argia vivida	0.148	0.341	-0.751	4.046*	6.737*	10.214*	0.11	0.108	0.028
Basiaeschna janata	0.814	0.136	0.4	6.504*	9.649*	26.912*	0.3	0.288	0.224
Boyeria vinosa	0.927	0.482	0.194	9.092*	10.887*	30.312*	0.436	0.347	0.404

Calopteryx aequabilis	0.974	0.54	0.433	5.116*	10.468*	30.437*	0.268	0.296	0.217
Calopteryx maculata	0.959	0.721	0.776	12.69*	13.482*	37.862*	0.655	0.658	0.637
Celithemis elisa	0.986	0.874	0.694	10.815*	13.202*	46.319*	0.622	0.564	0.589
Celithemis eponina	0.96	0.741	0.686	5.74*	7.707*	16.41*	0.396	0.392	0.284
Celithemis fasciata	0.862	0.036	0.607	7.694*	13.471*	58.571*	0.492	0.34	0.504
Chromagrion conditum	0.977	0.351	0.848	7.511*	15.024*	34.32*	0.42	0.379	0.385
Coenagrion interrogatum	0.775	0.595	-0.23	4.64*	11.263*	87.769*	0.06	0.029	0.022
Coenagrion resolutum	0.805	0.54	0.836	4.614*	6.982*	49.967*	0.133	0.161	0.123
Cordulegaster diastatops	0.973	0.65	0.937	9.42*	27.791*	63.354*	0.428	0.442	0.427
Cordulegaster dorsalis	0.81	0.6	0.306	6.223*	15.904*	24.643*	0.315	0.288	0.312
Cordulegaster maculata	0.928	0.944	0.872	6.123*	8.635*	36.893*	0.347	0.248	0.327
Cordulia shurtleffii	0.992	0.96	0.709	5.588*	7.194*	33.969*	0.254	0.246	0.221
Didymops transversa	0.945	0.646	0.44	8.666*	12.06*	45.867*	0.465	0.42	0.435
Dorocordulia libera	0.984	0.306	0.515	11.707*	25.415*	68.069*	0.547	0.426	0.428
Enallagma annexum	0.993	0.835	0.714	5.82*	6.136*	33.229*	0.187	0.206	0.174
Enallagma antennatum	0.645	0.001	-0.139	5.273*	5.694*	12.865*	0.242	0.14	0.186
Enallagma basidens	0.777	0.391	-0.084	3.032*	5.966*	7.86*	0.081	0.145	0.039
Enallagma boreale	0.957	0.966	0.743	4.017*	4.88*	20.405*	0.096	0.139	0.111
Enallagma carunculatum	0.967	0.957	0.815	5.625*	6.134*	17.834*	0.198	0.242	0.151
Enallagma civile	0.911	0.921	0.517	5.959*	7.301*	17.09*	0.286	0.363	0.202
Enallagma ebrium	0.93	0.818	0.58	5.809*	7.71*	22.193*	0.325	0.331	0.256
Enallagma exsulans	0.934	0.662	0.852	7.529*	9.631*	19.552*	0.383	0.476	0.3
Enallagma geminatum	0.952	0.744	0.951	7.013*	10.214*	32.549*	0.405	0.362	0.355
Enallagma hageni	0.96	0.617	0.795	6.731*	8.195*	26.629*	0.369	0.367	0.304
Enallagma praevarum	0.648	-0.176	0.014	5.355*	7.321*	20.456*	0.077	0.045	0.023
Enallagma signatum	0.637	0.817	0.031	8.263*	11.292*	27.66*	0.426	0.488	0.306
Epiaeschna heros	0.867	0.423	-0.212	7.939*	10.773*	38.543*	0.544	0.465	0.411
Epitheca canis	0.979	0.115	0.467	8.806*	12.452*	62.185*	0.468	0.321	0.443
Epitheca cynosura	0.98	0.792	0.621	7.346*	7.284*	26.45*	0.434	0.406	0.338
Epitheca princeps	0.889	-0.081	0.606	9.254*	15.755*	57.289*	0.396	0.397	0.349
Erpetogomphus designatus	0.891	0.657	0.853	4.288*	7.083*	16.811*	0.211	0.182	0.158

Erythemis collocata	0.678	0.099	0.442	2.907*	5.088*	11.345*	0.057	0.089	0.047
Erythemis simplicicollis	0.976	0.838	0.779	5.454*	6.343*	12.83*	0.333	0.379	0.27
Erythrodiplax berenice	0.784	0.706	0.79	4.081*	4.859*	18.702*	0.188	0.143	0.169
Erythrodiplax minuscula	0.654	0.557	-0.257	3.887*	5.417*	4.185*	0.179	0.11	0.05
Erythrodiplax umbrata	0.916	0.317	0.276	2.052*	2.005*	2.616*	0.062	0.013	0.012
Gomphus exilis	0.837	0.22	0.53	7.546*	6.818*	20.572*	0.22	0.134	0.168
Hagenius brevistylus	0.929	0.13	0.764	8.279*	14.804*	50.538*	0.41	0.295	0.33
Helocordulia uhleri	0.964	0.46	0.699	6.527*	14.871*	48.262*	0.309	0.204	0.254
Hetaerina americana	0.883	0.877	0.11	4.296*	4.832*	10.845*	0.156	0.175	0.12
Ischnura cervula	0.981	0.924	0.424	5.206*	4.779*	7.361*	0.16	0.091	0.032
Ischnura denticollis	0.796	0.753	0.639	5.038*	3.535*	16.897*	0.062	0.023	0.025
Ischnura hastata	0.955	0.625	0.783	5.746*	8.05*	27.541*	0.326	0.295	0.318
Ischnura perparva	0.896	0.959	0.769	6.27*	7.941*	16.17*	0.154	0.202	0.107
Ischnura posita	0.846	0.53	0.032	6.378*	8.07*	16.623*	0.318	0.351	0.231
Ischnura ramburii	0.909	0.149	0.457	2.988*	4.313*	8.011*	0.12	0.106	0.06
Ischnura verticalis	0.989	0.941	0.947	9.006*	8.076*	23.037*	0.497	0.535	0.456
Ladona deplanata	0.897	0.04	0.425	7.732*	4.814*	34.176*	0.441	0.066	0.394
Ladona exusta	0.795	0.395	0.023	9.512*	16.773*	24.927*	0.308	0.311	0.085
Ladona julia	0.957	0.928	0.403	8.24*	14.353*	54.259*	0.537	0.509	0.505
Lestes congener	0.99	0.744	0.728	5.621*	7.91*	32.309*	0.249	0.288	0.25
Lestes disjunctus	0.979	0.91	0.964	3.757*	3.712*	18.18*	0.131	0.138	0.146
Lestes dryas	0.969	0.784	0.899	4.126*	5.446*	23.471*	0.182	0.21	0.218
Lestes eurinus	0.992	0.453	0.541	8.829*	13.792*	49.164*	0.466	0.29	0.362
Lestes forcipatus	0.973	0.882	0.488	4.214*	5.788*	17.128*	0.229	0.178	0.155
Lestes rectangularis	0.99	0.888	0.866	9.288*	10.271*	26.347*	0.539	0.535	0.477
Lestes unguiculatus	0.922	0.975	0.951	5.08*	7.354*	25.291*	0.248	0.302	0.25
Lestes vigilax	0.894	0.44	0.315	6.363*	12.072*	30.742*	0.35	0.267	0.3
Leucorrhinia frigida	0.947	0.609	0.744	9.946*	17.415*	60.741*	0.566	0.518	0.438
Leucorrhinia glacialis	0.931	0.79	0.775	5.387*	6.847*	51.58*	0.256	0.237	0.239
Leucorrhinia hudsonica	0.991	0.832	0.935	6.221*	5.107*	42.124*	0.248	0.163	0.218
Leucorrhinia intacta	0.991	0.989	0.387	6.091*	9.199*	24.833*	0.362	0.437	0.355
Leucorrhinia proxima	0.903	0.795	0.91	5.789*	7.455*	46.891*	0.28	0.226	0.288

Libellula auripennis	0.52	-0.585	0.012	3.489*	4.485*	11.025*	0.15	0.067	0.091
Libellula cyanea	0.986	0.615	0.535	10.48*	15.131*	31.862*	0.529	0.452	0.418
Libellula forensis	0.982	0.983	0.909	4.044*	11.269*	14.584*	0.113	0.191	0.1
Libellula incesta	0.753	0.734	0.517	7.969*	16.336*	33.377*	0.464	0.522	0.429
Libellula luctuosa	0.979	0.979	0.763	8.895*	8.804*	25.82*	0.521	0.557	0.443
Libellula pulchella	0.987	0.843	0.617	8.81*	8.397*	32.198*	0.444	0.495	0.421
Libellula quadrimaculata	0.985	0.945	0.736	5.741*	5.486*	31.184*	0.269	0.249	0.259
Libellula saturata	0.522	0.983	-0.253	5.168*	7.157*	21.517*	0.21	0.167	0.137
Libellula semifasciata	0.951	0.796	0.421	4.501*	8.72*	16.74*	0.261	0.209	0.23
Libellula vibrans	0.947	0.876	0.676	7.708*	12.856*	43.591*	0.479	0.387	0.467
Macromia illinoiensis	0.466	-0.493	-0.309	6.695*	9.857*	35.437*	0.331	0.246	0.273
Macromia taeniolata	0.604	-0.469	-0.341	6.247*	8.399*	23.523*	0.333	0.165	0.139
Nannothemis bella	0.955	0.122	-0.328	4.985*	13.679*	29.289*	0.178	0.153	0.095
Nehalennia gracilis	0.991	0.206	-0.215	5.831*	9.517*	33.705*	0.257	0.114	0.115
Nehalennia irene	0.985	0.648	0.894	7.422*	10.334*	42.271*	0.428	0.415	0.42
Ophiogomphus severus	0.969	0.81	0.793	6.112*	10.456*	43.688*	0.255	0.227	0.2
Pachydiplax longipennis	0.945	0.983	-0.035	5.486*	5.591*	12.001*	0.339	0.376	0.272
Paltothemis lineatipes	0.88	0.699	0.78	3.114*	5.77*	7.648	0.025	0.052	0.005
Pantala flavescens	0.987	0.818	0.094	3.806*	6.761*	15.312*	0.147	0.218	0.074
Pantala hymenaea	0.87	0.158	0.716	2.62*	3.845*	14.765*	0.065	0.066	0.066
Perithemis tenera	0.951	0.583	0.79	6.276*	7.408*	17.919*	0.399	0.415	0.335
Phanogomphus exilis	0.916	-0.264	0.432	9.029*	19.682*	69.318*	0.434	0.352	0.414
Plathemis lydia	0.927	0.94	0.127	8.069*	9.162*	26.846*	0.459	0.519	0.412
Progomphus obscurus	0.917	0.23	0.558	6.204*	7.959*	21.246*	0.348	0.283	0.284
Rhionaeschna californica	0.948	0.98	0.739	5.105*	11.972*	17.371*	0.222	0.238	0.181
Rhionaeschna multicolor	0.946	0.897	0.738	6.751*	8.587*	20.664*	0.217	0.197	0.126
Somatochlora albicincta	0.42	0.572	0.612	2.024*	2.735*	28.828*	0.02	0.015	0.025
Somatochlora cingulata	0.745	0.551	0.643	2.756*	4.644*	14.993	0.041	0.022	0.012
Somatochlora elongata	0.861	0.421	0.182	8.036*	15.936*	52.87*	0.261	0.162	0.18
Somatochlora minor	0.874	0.692	0.38	3.038*	5.901*	43.698*	0.062	0.038	0.053
Somatochlora williamsoni	0.836	0.311	0.289	4.526*	10.699*	38.746*	0.149	0.072	0.096

Stylurus plagiatus	0.464	-0.396	-0.461	3.937*	5.549*	13.964*	0.188	0.079	0.103
Sympetrum ambiguum	0.973	0.135	-0.501	8.833*	16.164*	25.534*	0.492	0.377	0.212
Sympetrum corruptum	0.782	0.471	-0.164	4.304*	4.39*	14.876*	0.17	0.151	0.152
Sympetrum costiferum	0.975	0.904	0.758	5.85*	7.397*	43.235*	0.23	0.241	0.211
Sympetrum danae	0.973	0.951	0.554	4.344*	5.41*	33.512*	0.105	0.106	0.092
Sympetrum illotum	0.615	0.919	0.686	3.357*	9.247*	24.48*	0.037	0.147	0.064
Sympetrum internum	0.954	0.953	0.558	4.56*	5.28*	24.894*	0.158	0.196	0.167
Sympetrum obtrusum	0.921	0.974	0.279	6.914*	8.688*	26.824*	0.335	0.375	0.316
Sympetrum pallipes	0.982	0.97	0.591	5.601*	8.515*	21.836*	0.183	0.18	0.131
Sympetrum rubicundulum	0.969	0.83	0.803	6.838*	6.933*	15.079*	0.421	0.386	0.363
Sympetrum semicinctum	0.96	0.899	0.663	6.088*	7.932*	28.243*	0.285	0.313	0.245
Sympetrum vicinum	0.974	0.911	0.888	7.197*	7.939*	25.597*	0.422	0.461	0.382
Telebasis salva	0.811	0.514	0.4	6.77*	8.652*	35.657*	0.216	0.163	0.185
Tramea lacerata	0.648	-0.342	-0.605	5.462*	7.31*	19.069*	0.198	0.151	0.114
Tramea onusta	0.993	0.961	-0.29	3.623*	5.838*	14.954*	0.115	0.094	0.058

Chapter 5: General conclusions and synthesis

Climate change effects on global insect declines are difficult to measure, due to challenges related to data availability. There can be biases towards certain taxa and geographical regions, and species face several other threats simultaneously (Halsch et al. 2021). However, climate change-related local extinctions are underway (Kerr et al. 2015, Soroye et al. 2020, Halsch et al. 2021) and will likely increase substantially in the future (Urban 2015, Newbold 2018, Sirois-Delisle and Kerr 2018). This work helps identify effects of climate change and land use intensification on odonate species' persistence within their ranges (Chapter 2). I tested species' spatial and temporal responses to such changes at continental scales and assessed potential mechanisms that contribute to these responses (Chapter 3). I also tested models commonly used for predicting species distributions under future climate change and identify factors that could reduce species' capacities to establish or maintain populations in areas that appear suitable for them (Chapter 4). This thesis adds specific knowledge regarding global change impacts on species and points to new research trajectories for future work, while highlighting the changing vulnerabilities of many insect species to an array of anthropogenic threats.

Responses to global change

I untangled impacts of various drivers of global change on odonate decline and found that rising surface temperatures and applications of pesticides interact to predict these declines (Chapter 2). I found that temperature variability and pesticide applications interact also to predict species absences across areas that are otherwise climatically suitable, according to species modeled climatic niches (Chapter 4). Interactions between land use intensification and climate

change have emerged in other research as important drivers of species decline in some groups (Fox et al. 2014, Bowler et al. 2017, Ganuza et al. 2022, Neff et al. 2022). Effects of land use change varied. It may be the intensity of land use, rather than the change in land use itself, that leads to greater impacts on persistence or establishment in new regions, especially across landscapes that were heavily modified in the baseline time period. Odonates are strong fliers and can disperse relatively well across fragmented landscapes if they have access to suitable habitats, including freshwater habitats and terrestrial landscapes rich in resources, maintaining and restoring odonate populations in areas that have been modified from their natural state (Raebel et al. 2012, Husband and McIntyre 2021). Multi-stressor frameworks are essential in studies identifying risks related to global change.

I discovered a significant and convergent relationship between phenology and range shifts across Europe and North America (Chapter 3). Species showing stronger range limit shifts towards higher latitudes also advanced their emergence phenologies towards earlier spring seasons more strongly. Many species (41% of assessed species) shifted towards both higher latitudes and earlier emergence dates, indicating that these species could be tracking climate change, potentially decreasing climate debt. While I did not measure climate debt, this is an area for future research. Perhaps some species are "universal winners" in terms of their responses to climate change, responding strongly both spatially and temporally. As a group, odonates may fare better than other invertebrates that respond slowly or negatively to climate and land use-related changes observed to date (e.g. Kerr et al. 2015). However, I observed strong interspecific variation. About 10% of species' ranges shifted in directions opposite to expectations, both spatially and temporally. Some species might tolerate both past and present environmental changes, but many are susceptible to declines that are related to increasingly unsuitable climates.

Species whose northern range limits are retracting *away* (i.e. toward the south) from their historic limits could be threatened if their southern range margins have remained stable or shifted to the north over the observation period. Such range retractions, especially if accompanied by abundance declines, expose species to higher risks of extinction (Lenoir et al. 2020). Further, even though warmer conditions associated with climate change drive shorter development rates and longer reproductive periods, emergence periods that intersect with environmental temperatures similar to those projected for the next century are related to higher rates of mortality in odonates (Hassall and Thompson 2008, McCauley et al. 2015). In other words, phenology shifts can be maladaptive (Zettlemoyer and Peterson 2021), which may explain why some species showed strong phenological responses but still experienced substantial range losses along their historic northern range limits.

Mechanisms underlying global change responses

It is essential to understand mechanisms driving species' responses to global change to improve predictions of these responses and better inform conservation actions. All chapters support the hypothesis that increasing temperatures and temperature variability, especially coupled with land use changes and intensification, increase odonate range losses and consequently could hinder shifts. In Chapter 3, I found that, regardless of species' ecological traits, conditions to which species are exposed may facilitate or hinder range shifts. In other words, it is where they are, rather than their unique set of traits, that most commonly governs species' abilities to establish and persist in new areas. Indeed, southern species and those exposed to lower temperature variability change over time showed greater rates of range shift to the north. Highly variable climates may decrease population growth and abundance in odonates if extreme temperatures exceed limits defined by species' climatic niche, increasing risks of local

extinction. These results are supported by findings of Chapter 2 and Chapter 4. Higher rates of surface temperature change led to higher rates of decline across the US (Chapter 2), while northern latitudes see greater rates of surface temperature increases (IPCC 2021). Therefore, northern species can have lower capacities to shift at their northern range limits (Chapter 3), since stable or positive population trends is critical for range shifts to occur (Mair et al. 2014). Further, areas with the largest increases in temperature variability also had larger numbers of species that failed to persist or establish in new regions over time, despite the relative suitability of those areas when measured using average conditions (Chapter 4). Species facing greater temperature variability change also showed greater rates of range retractions from their northern range limits (Chapter 3). Mechanisms underlying phenology shifts were less clear but were not related to temperature variability or range geography. Aquatic microclimates provide refugia for climate change, as shown in urban environments (Husband and McIntyre 2021), which may explain the lack of consistent effects of temperature variability on species' emergence phenologies.

Species relatedness and ecological traits appear to affect how, but not how much, each species responds to climate change and to emerging variability in climatic conditions. Models were improved in Chapter 2 when phylogeny was included in models, indicating that closely related species showed similar responses locally (Chapter 2). However, neither range shifts nor phenological shifts were linked with species' shared evolutionary histories, which was not surprising given the absence of effect in any of the ecological traits that I assessed (Chapter 3). It is possible that species with shared phylogeny have divergent thermal tolerances. Selection may drive differentiation of thermal sensitivities of species that coexist in one region, while species that are geographically isolated could adapt to different local climates (Schuetz et al. 2019).

Traits may matter in some ways, but the trends that may arise from traits, especially across broad geographical extents, can be masked by unique environmental changes related to climate change and land use intensification, other global change factors, and interactions between them.

Species conservation

Species that are unlikely to track their ecological needs through time and space may be at greater risk of extinction. Effective conservation planning takes into account that biodiversity shifts through time and space under rapid environmental change (Pressey et al. 2007). Conservation practices that increase the likelihood of successful colonisations in new areas, and that help species maintain stable or positive population growth rates, are needed for insect species that are especially susceptible to climate change-driven decline (Sirois-Delisle and Kerr 2018). Even though urban ponds can be heavily disturbed by surrounding conditions (e.g. groundwater, land use, and eutrophication, or decreasing diversity of aquatic invertebrates), they may serve as "stepping stones" to increase landscape connectivity, which can improve metapopulation persistence (De Meester et al. 2005, Villalobos-Jiménez et al. 2016) and also facilitate range shifts in response to climate change. Dispersal corridors can help maximise climate connectivity and facilitate movement across the landscape and improve population persistence (Carroll et al. 2018, Littlefield et al. 2019). Managed relocation may also be a useful practice for some species to establish in areas they will require in the future (Wang et al. 2019, Butt et al. 2021, Twardek et al. 2023). This technique involves the translocation of individuals to areas that are adjacent to their current range, excluding introductions across biogeographical boundaries, to increase probabilities of survival and avoid potentially irreversible consequences such as extinctions (e.g. Hoegh-Guldberg et al. 2008, Thomas 2011). Developing small-scale managed relocation trials to research population and community-level outcomes, monitoring

protocols, and programs for political and public support, is essential (Wang et al. 2019, Butt et al. 2021, Twardek et al. 2023). To estimate habitat suitability and identify best regions for translocations, distribution models may be useful (Willis et al. 2009).

SDM results used to predict future climatic suitability should be interpreted with great caution, however (Chapter 4). Models that cannot be tested temporally should only be used to generate hypotheses and cannot be used when model accuracy is critical (Lee-Yaw et al. 2022). While predictions of future distributions remain very common in the literature (Santini et al. 2021), my results suggest that these predictions overestimate species' likely ranges in the future when they face other anthropogenic threats. Regions with high climate variability, and high pesticide applications, relate to greater model uncertainty. Probabilities of extreme events are projected to continue to increase in the future (IPCC 2021), and omission of such trends cause models to identify areas incorrectly as suitable for many species. Extreme weather events differ strongly across different climate scenarios and modelers (Freychet et al. 2021), so they cannot be predicted with certainty in SDMs. Consequently, there are large uncertainties in predictions of species' persistence and the capacity of species to establish populations in such areas. Newer model types that are used for similar objectives as SDMs, such as dynamic occupancy models (DOMs) consider rates of extinction and colonization, using time series of occurrence data. Tests of such models show that, as with my results, predictive performance statistics can be high even though empirical data shows that range changes are poorly predicted by models (Briscoe et al. 2021). While SDMs, or other model types such as DOMs, remain useful to create novel hypotheses regarding species' occurrences, these projections are not reliable as guidance for policy makers tasked with generating conservation recommendations.

Locally, landscape management may help diminish interactive and individual impacts of climate change and land use intensification factors. Water and habitat management are important odonate population trend drivers (Tang and Visconti 2021). Preventing the degradation and promoting the restoration of natural wetlands are among priorities for sustainable landscape management; conservation of these habitats would benefit several other taxa, as well as odonates (IPBES 2019). Constructed wetlands, which are artificial ecosystems that usually use biogeochemical processes similar to natural wetlands for water purification, may increase biodiversity of vegetation, invertebrates, fish, and birds (Herrmann 2012, Johnson et al. 2013, Green and Elmberg 2014) with proper management intervention, aiming to imitate natural wetlands (Zhang et al. 2020). Landscape management can promote the creation of climate refugia, even in the most heavily disturbed areas, such as cities (Husband and McIntyre 2021). Microclimate heterogeneity improves survival at species' distribution edges, where they are more vulnerable to other threats due to decreased fitness, and where species' population growth is most important for range expansions (Hargreaves et al. 2014, Lawson et al. 2014, Mair et al. 2014). Creating and managing freshwater bodies near agricultural areas where pesticides may leach in freshwater bodies might support many species, but ensuring that these habitats include floating and submerged vegetation as well as buffers around them will increase both water quality and species richness further (Raebel et al. 2012).

Future research and concluding remarks

As the Anthropocene continues (Crutzen 2006, Syvitski et al. 2020), and global climate changes imperil species and ecosystems, alter ecosystem functions, and ecosystem services (Grant et al. 2017, Day et al. 2018, Harris et al. 2018, Román-Palacios and Wiens 2020), it is evident that further research and greater conservation efforts are essential to preserving Earth's

flora and fauna (IPBES 2019). Much research remains to enable understanding of the impacts that climate change has on invertebrates, especially through increasingly frequent and several instances of extreme weather, land use change and intensification, and interactions among such factors. It is critical to increase monitoring of species' abundance changes over time. Citizen science can contribute vitally to this goal (Bried et al. 2020). Understanding the drivers of population trends among odonate species, such as through effects of water and habitat management, is imperative to report accurate assessments of their status and to predict how such trends will vary (Tang and Visconti 2021). This imperative extends to insect taxa more generally. Synergistic and additive drivers of population and distribution changes at different scales need to be further researched (Suhling and Suhling 2013). Combining qualitative and quantitative approaches to study global change-related impacts at the community and global levels, including short-term and long-term temporal extents, is needed for future work (Tang and Visconti 2021).

A precautionary approach is also needed. Scientific uncertainty should not excuse delays in action to protect species when there is the possibility for irreversible losses of populations or species (IPBES 2019). High-impact studies reporting an "insect apocalypse" earned massive public attention, from both academics and the media (Montgomery et al. 2020, Saunders et al. 2020), but controversy over potentially extravagant claims of global insect declines can distract from urgent conservation decisions for which evidence is stronger. Many insect species certainly are in decline and this conservation challenge is not limited geographically to just a few places (Sánchez-Bayo and Wyckhuys 2019). My results consistently demonstrate that many insect species are not tracking rapid shifts in their ecological niches either spatially or temporally, increasing extinction risks for some of them. Conservation planning for insects needs to consider the urgency of insect decline and become part of inclusive discussions that engage representative

cross-sections of economic, social, and political interests if we hope to avoid further species extinctions.

"Think it over, think it under."

"Winnie-the-Pooh", A.A. Milne

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