Running head

Global change and odonate conservation

Title

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

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Data availability statement

Detailed sources of raw data are found at: https://zenodo.org/badge/latestdoi/390123757

Abstract

Critical gaps in understanding how species respond to environmental change limit our capacity to address conservation risks in a timely way. Here, we 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.

Keywords: climate change, damselflies, dragonflies, global change, land use change, land use intensification, macroecology, Odonata, pesticides, range shifts, species persistence

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, we test individual and interactive effects of climate change, land use change, and land use intensification on odonate persistence in the United States. We are particularly interested in testing whether combined effects of climate change and pesticide application on odonate persistence are observable at macroecological scales. We 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. We 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

We 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

We 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). We 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 our data were collected from GBIF (http://gbif.org/) and Canadensys (http://www.canadensys.net/), which are online dataset aggregators, but we 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. We selected species sampled in at least 100 quadrats in both time periods resulting in observation records for 104 species across the USA (Figure 1). We further refined quadrat selection to those that contained a minimum of 15 species observed to remove poorly sampled quadrats while limiting probabilities of including false absences, decreasing probabilities of including bias toward declines. Subsequently, we 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). We allowed a maximum of 15 species between the number of species observed and those estimated by the Chao index, excluding under-sampled quadrats. 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 our models. Sampling intensity change corresponds to the difference in the number of species observed between both time periods. We 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. We maximized the number of unique species observations included in the analysis, while limiting effects of sampling intensity change in the models.

We conducted a preliminary data assessment to estimate range declines among best sampled quadrats and species. As an index of range loss, we 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 our model include change in temperature and precipitation, cropland use, and pesticide application. We used high resolution gridded datasets from the Climatic Research Unit (CRU) as climate change data (available at http://www.cru.uea.ac.uk/data). We downloaded monthly average daily maximum temperature and monthly precipitation across the USA. For both climate variables, we extracted the average values per quadrat, across both time periods, and calculated the difference between the current and historical time period to obtain a single value of change per quadrat.

We 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. We selected agricultural land use as croplands exert larger effects on odonate persistence than livestock grazing or human population density (Goertzen and Suhling 2019). We 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 our first time period and did not increase overall in our second time period across the total study extent.

We 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). We 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, we 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 our main analysis include change in pesticide application (kg), precipitation (ml), monthly average daily maximum temperature (degrees Celsius), cropland use (km^2), and sampling intensity. We verified whether any trends attributed to aspects of environmental change might instead have arisen because of differences in sampling intensity through time. We 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. We explored potential non-independence of predictor variables by plotting all pairwise plots among them and calculating Pearson correlations among them (Appendix S1: Figure S1). These variables were independent.

We identify variables that have a non-zero effect using the credible intervals calculated by the mixed-effects models. We also report 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, we expected low R^2 values. Model parameters were based on 200,000 iterations. We evaluate trace and density figures of all the models that were tested to assess model convergence. We tested for effects of phylogeny on model variance by comparing DIC and pseudo R^2 values of both phylogenetic and non-phylogenetic models.

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. We 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 five furthest observation points from the equator in the historical and current time periods.

Results

Assessment of odonate persistence and decline

We 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, we found a mean quadrat loss of 29% of previously occupied quadrats (Appendix S1: Figure S2). Species declines were found across the entire study extent suggesting the relevance of testing for effects of broad-scale phenomena (Figure 2). It is important to note that species sampled in at least 100 quadrats in both time periods were kept according to our 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 uses decreased, though crop yields rose substantially over the study period (Bigelow and Borchers 2017). The extent of cropland use 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. For this reason, we did not expect to detect strong effects of land use conversions in our model. Monthly average daily maximum temperature increased by a mean of 0.32 ^0C per quadrat, ranging between -0.67 ^0C to 1.33 ^0C 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

We compared six phylogenetic mixed-effects models, outlined in Table 1. We reported the posterior means (Table 2) and credible intervals associated with the predictor variables of the tested models (see Appendix S1: Table 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 (Appendix S1: Figures S3-S8).

Figure 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. We mapped persistence predictions based on this model using raster data of each global change variable for data visualization purposes (Figure 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). 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

We 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). 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). We 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.

We 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 our results showed smaller direct effects of land use change on these species. First, we 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 though 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). We face limits in the ability to compare land use change effects to pesticide exposure, due to the lack of available pesticides data in previous years. We emphasize 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 habitat, 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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Table 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	**Effect type**	**Model**
Species	Random	1, 2, 3, 4, 5, 6
Pesticides	Fixed	1, 2, 3, 4, 5
Temperature	Fixed	1, 2, 3, 4, 5
Precipitation	Fixed	1, 2, 3, 4, 5
Land use	Fixed	1, 2, 3, 4, 5
Sampling intensity	Fixed	1, 2, 3, 4, 5
Pesticides:Temperature	Fixed	2, 4, 5
Pesticides:Precipitation	Fixed	3, 4
Range expansion	Fixed	6

Table 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

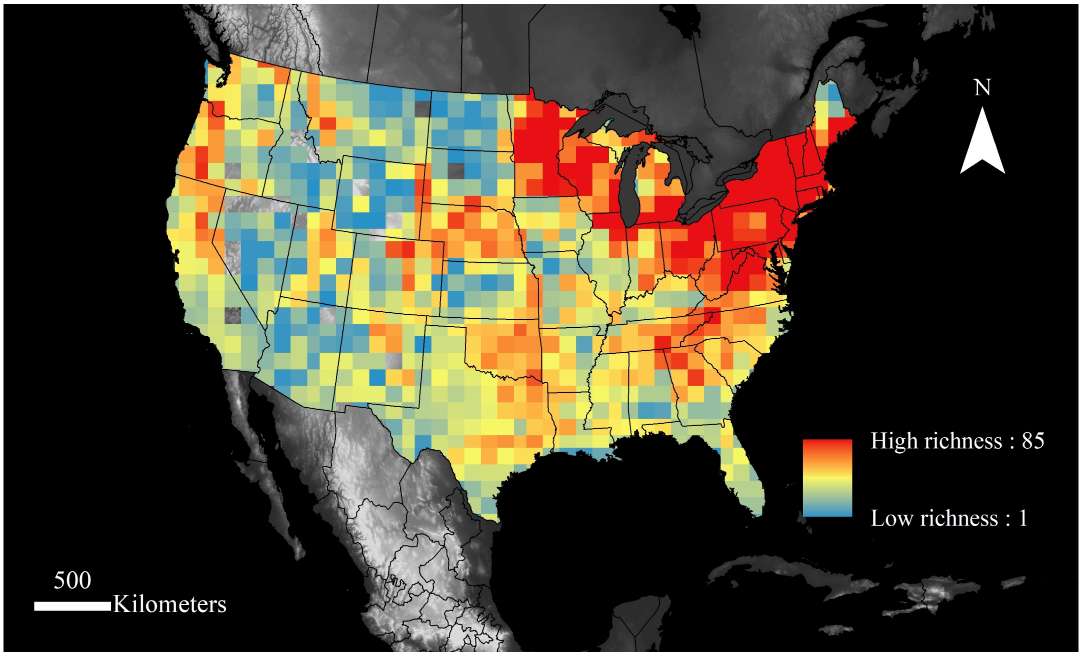

Figure 1: Total distribution and richness of 104 odonate species sampled in the United States of America between 1980 and 2018. Species included here are found in at least 100 quadrats of 100 X 100 km. Warm and cool colors show high and low richness respectively. This map was projected with the Albers Equal Area projection and produced with ArcGIS software version 10.7.1.

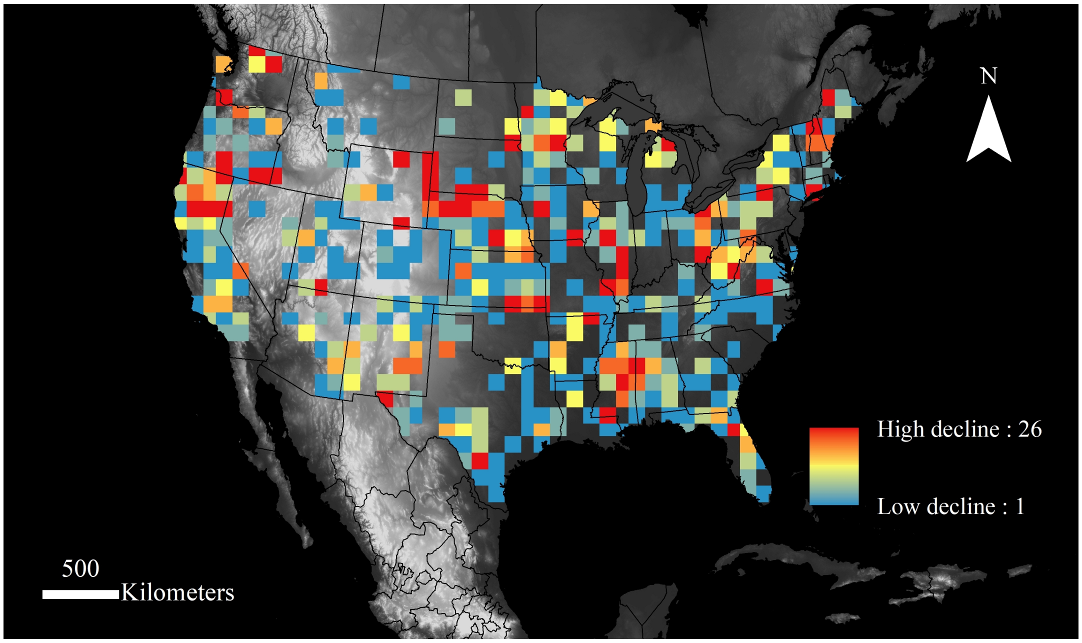

Figure 2: Decline of 104 odonate species richness per quadrat sampled in the USA between the first (1980 – 2002) and the second time period (2008 – 2018), within 100 X 100 km quadrats. Warm and cool colors show high and low numbers of species lost. To measure declines within species historical ranges, we 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.

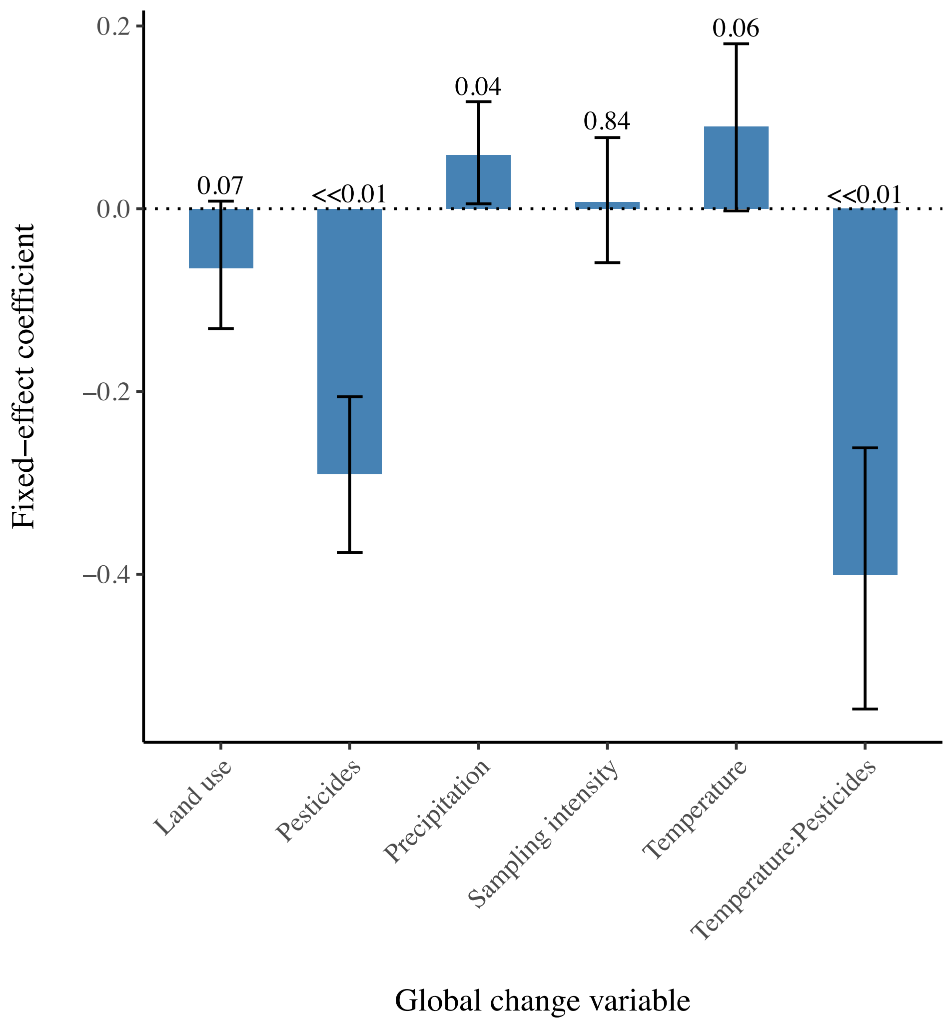

Figure 3: Effect of each Z-scored variable on odonate presence change between historical and current observation records, as determined by MCMCglmm model coefficients (Model 2) and their associated posterior distributions. Probabilities (p-values) for each variable in this model are indicated above the bars for ease of model interpretation.

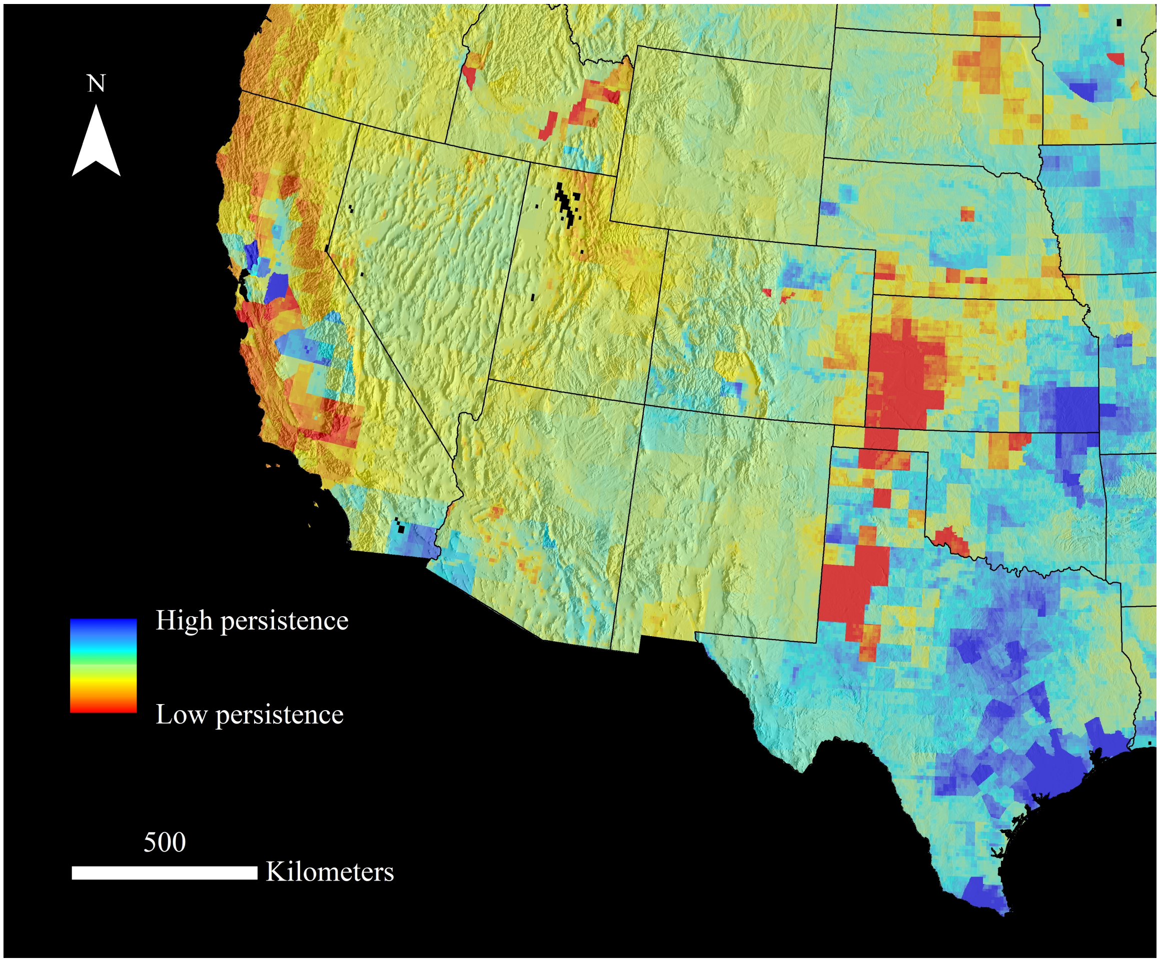

Figure 4: Data visualization of the impact of global change on odonate presence change between historical and current observation records, as determined by MCMCglmm model coefficients (Model 2). Coefficient values and statistical significance are shown in Figure 3. Warm and cool colors show areas where 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).