Received: 30 May 2022 | Accepted: 29 July 2022

DOI: 10.1111/1365-2656.13795

Journal of Animal Ecology
BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Leveraging Natural History Collections to Understand the Impacts of Global Change

Drivers of Odonata flight timing revealed by natural history collection data

Taylor Woods[1] | **Daniel J. McGarvey**[2]

[1]Department of Ecology and Evolutionary Biology, The University of Tennessee, Knoxville, Knoxville, Tennessee, USA

[2]Center for Environmental Studies, Virginia Commonwealth University, Richmond, Virginia, USA

Correspondence
Taylor Woods
Email: woodstaylorelizabeth@gmail.com

Present address
Taylor Woods, Eastern Ecological Science Center, U.S. Geological Survey, Kearneysville, West Virginia, USA

Handling Editor: Joanne Bennett

Abstract

1. Global change may cause widespread phenological shifts. But knowledge of the extent and generality of these shifts is limited by the availability of phenological records with sufficiently large spatiotemporal extents. Using North American odonates (damselflies and dragonflies) as a model system, we show how a combination of natural history museum and community science collections, beginning in 1901 and extending through 2020, can be leveraged to better understand phenology.
2. We begin with an analysis of odonate functional traits. Principal coordinate analysis is used to place odonate genera within a three-dimensional trait ordination. From this, we identify seven distinct functional groups and select a single odonate genus to represent each group. Next, we pair the odonate records with a list of environmental covariates, including air temperature and degree days, photoperiod, precipitation, latitude and elevation. An iterative subsampling process is then used to mitigate spatiotemporal sampling bias within the odonate dataset. Finally, we use path analysis to quantify the direct effects of degree days, photoperiod and precipitation on odonate emergence timing, while accounting for indirect effects of latitude, elevation and year.
3. Path models showed that degree days, photoperiod and precipitation each have a significant influence on odonate emergence timing, but degree days have the largest overall effect. Notably, the effect that each covariate has on emergence timing varied among functional groups, with positive relationships observed for some group representatives and negative relationships observed for others. For instance, *Calopteryx* sp. emerged earlier as degree days increased, while *Sympetrum* sp. emerged later.
4. Previous studies have linked odonate emergence timing to temperature, photoperiod or precipitation. By using natural history museum and community science data to simultaneously examine all three influences, we show that systems-level understanding of odonate phenology may now be possible.

KEYWORDS
damselflies, degree days, dragonflies, emergence, functional traits, photoperiod, precipitation, temperature

1 | INTRODUCTION

Changes in phenology, or the timing of seasonal life-history events, are increasingly common responses to global change (Cohen et al., 2018; Parmesan, 2006; Parmesan & Yohe, 2003; Renner & Zohner, 2018; Walther et al., 2002). Examples of altered phenology have been reported for mammals (Cohen et al., 2018), terrestrial insects (Altermatt, 2010; Diamond et al., 2011), birds (Crick et al., 1997) and marine fishes (Asch, 2015; Staudinger et al., 2019). These phenological shifts are often caused by environmental perturbations that disrupt life-history cues, such as changes in ambient temperature (McNamara et al., 2011).

Altered temperatures may be particularly disruptive in freshwater ecosystems, where most organisms are ectothermic (Chmura et al., 2019; Cohen et al., 2018; Thackeray et al., 2016). Phenology shifts have been reported in freshwaters for a diverse range of trophic levels and taxonomic groups, ranging from planktonic organisms (Thackeray et al., 2008; Thackeray et al., 2012), to macroinvertebrates (Baranov et al., 2020) and fishes (Warren et al., 2012). Unfortunately, freshwater phenology research has often been constrained to datasets with relatively narrow spatial and/or temporal extents. For example, in a recent review, Woods et al. (2022) found the median numbers of years analysed in lotic and lentic studies were two and three, respectively. These data limitations will constrain research on phenological shifts if the changes are gradual and require long time series to detect (Bates et al., 2022; Doi et al., 2017; Gallinat et al., 2021).

Some of the challenges posed by spatially and temporally limited data can be mitigated with natural history collections (NHCs) (Bates et al., 2022). NHCs aggregate occurrence records across large spatiotemporal extents that dramatically exceed the scope of most individual field studies (Boakes et al., 2010). They also integrate information on large numbers of taxa, providing opportunities to study differing phenological sensitivities of organisms with diverse life histories or functional traits (Chmura et al., 2019). For instance, NHCs have revealed phenological shifts for a broad assortment of flying insects (Duchenne et al., 2020; Fric et al., 2020; Kharouba et al., 2014).

NHCs are, however, prone to several types of sampling bias (Kharouba et al., 2019). Spatial clustering of samples that were collected opportunistically (e.g. along a road network or near a population centre), rather than with a random or standardized site-selection protocol, is often observed in NHC data (Mentges et al., 2020). Temporal sampling bias is also common, with contemporary samples outnumbering historical records, sometimes by large margins (Boakes et al., 2010). Robust statistical tools to account for sampling bias are therefore essential when analysing data from NHCs (Ewers-Saucedo et al., 2021).

In this study, we use NHC data to model odonate phenology throughout North America, focusing specifically on links between phenology and global change. Dragonflies and damselflies (order Odonata) are well-suited to this exercise for at least two reasons. Odonates may be predisposed to phenological shifts because the transition from aquatic larvae to flying adult is strongly influenced by ambient temperature (Hassall & Thompson, 2008); laboratory trials show that odonate development rate generally increases and time to emergence decreases with increasing temperature (e.g. Lutz, 1968; Procter, 1973; Suhling, Suhling, & Richter, 2015). Furthermore, odonates are charismatic insects that have drawn the attention of entomologists, ecologists and the general public for many years (Hassall, 2015; Paulson, 2019; Samways, 2019). This sustained interest has allowed large numbers of historical and contemporary odonate occurrence records to accumulate within NHCs (Kharouba et al., 2014), and more recently, within community or ‘citizen’ science datasets (hereafter included under the NHC label) (Olsen et al., 2020).

Notable examples of the use of NHC data in odonate phenology research have recently been published for European taxa. For instance, records from the British Dragonfly Society database revealed shifts in the annual timing of emergence and adult flight, attributing these shifts to climate change (Hassall et al., 2007) and urban heat islands (Villalobos-Jiménez & Hassall, 2017). Similarly, records from the Dutch Dragonfly Databank showed that earlier odonate flight dates are associated with increasing temperature (Dingemanse & Kalkman, 2008).

Our study is conceptually similar to these European odonate studies but focuses on North America and features three novel methodological components. First, we leverage an exceptionally long time series of odonate records. Prior studies of freshwater phenology have rarely incorporated >20 years of data (Woods et al., 2022) but 120 years of NHC records are included here. We are therefore more likely to detect subtle or gradual changes in phenology.

Second, we use a functional trait analysis to select and then model a subset of odonate genera that are broadly representative of the functional trait space occupied by all North American odonates. We do so because odonates exhibit a variety of traits and life-history strategies that may respond differently to global change (Bybee et al., 2016; Hassall & Thompson, 2008; Rocha-Ortega et al., 2020; Verberk et al., 2008). For instance, in temperate climates, the typical ‘dancer’ (genus: *Argia*) experiences a larval diapause phase (i.e. suspension of growth during short winter days) that synchronizes emergence with warm summer temperatures, effectively creating a univoltine or 1-year life cycle. But in tropical climates, where temperatures are not seasonal, *Argia* have multivoltine life cycles and flying adults can be observed year-round (Pritchard, 1982, 1989). By distinguishing functional subgroups in our analyses, we minimize the risk of conflating phenological inferences for taxa with disparate life histories.

Third, path analysis is used to disentangle the direct effect of temperature on odonate phenology from other environmental influences, including photoperiod, precipitation, latitude and elevation. Photoperiod is of particular interest because it influences diapause and flight patterns in many odonates (Aoki, 1999; Denlinger et al., 2017; Norling, 2018), but unlike temperature, it should not be sensitive to climate change. Path analysis allows us to identify interrelationships among multiple environmental influences and move closer to a systems-level understanding of odonate phenology.

2 | MATERIALS AND METHODS

2.1 | Data collection and preparation

Dates and locations of adult odonate (order: Odonata) observations were retrieved from the Global Biodiversity Information Facility (GBIF, 2021; www.gbif.org) and from iNaturalist (www.iNaturalist.org) in May 2021 (Figure 1a). We queried GBIF odonate records from preserved specimens that occurred within North America and included valid site coordinates and observation dates, using the R package RGBIF (Chamberlain et al., 2021). iNaturalist records were downloaded with the website's application programming interface and were limited to 'research grade' Odonata occurrences from North America. To qualify as research grade, an iNaturalist record must include site coordinates and a clear, in situ photo of the specimen. Taxonomic identify must then be confirmed from the photo by at least two experts. Taxonomic nomenclature was standardized for all specimen records by cross-referencing validated species' names in GBIF, the National Center for Biotechnology Information and the Integrated Taxonomic Information System databases (see Lenoir et al., 2020). Duplicate records (identical scientific name × date × location combinations) were manually identified and removed prior to analysis.

Next, species' names were removed from the data, placing all specimens at genus-level identification. This conservative data preparation step was taken for two reasons. First, it was intended to help minimize the number of potentially erroneous field identifications, particularly in the community science iNaturalist data. Despite the quality assurance process used for research grade records in iNaturalist (photo-based expert confirmation; see above), we assumed some species-level identifications would be incorrect and that genus-level identifications would entail fewer errors. Second, genus-level resolution facilitated a more robust functional trait analysis (see below) because generic-level traits were more readily available than species-level traits (Twardochleb et al., 2021). All subsequent analyses were therefore based on genus-level identification.

For each odonate record, the reported Julian date or day-of-year (DOY) was used as an estimate of emergence timing. We assumed all records of winged, adult specimens from GBIF and iNaturalist would be useful in our attempt to summarize the timing of post-emergence flight periods (Kharouba et al., 2019). We also assumed the central tendency of a distribution of flight dates would be a more robust statistical indicator of emergence timing than the first or last date (see 'Caveats and opportunities' in Discussion). Local environmental attributes were then paired with each sample (Figure 1b). Annual climate covariates were downloaded from the ClimateNA database (Wang et al., 2016) and matched to odonate sample locations with the reported geographic coordinates. These covariates included mean annual air temperature (MAT), the annual number of degree days, relative to an 18°C growth threshold (DD18) and mean annual precipitation (MAP). We anticipated that DD18 would be an effective predictor of odonate emergence timing because daily temperature is a key regulator of larval odonate growth (Lutz, 1968;

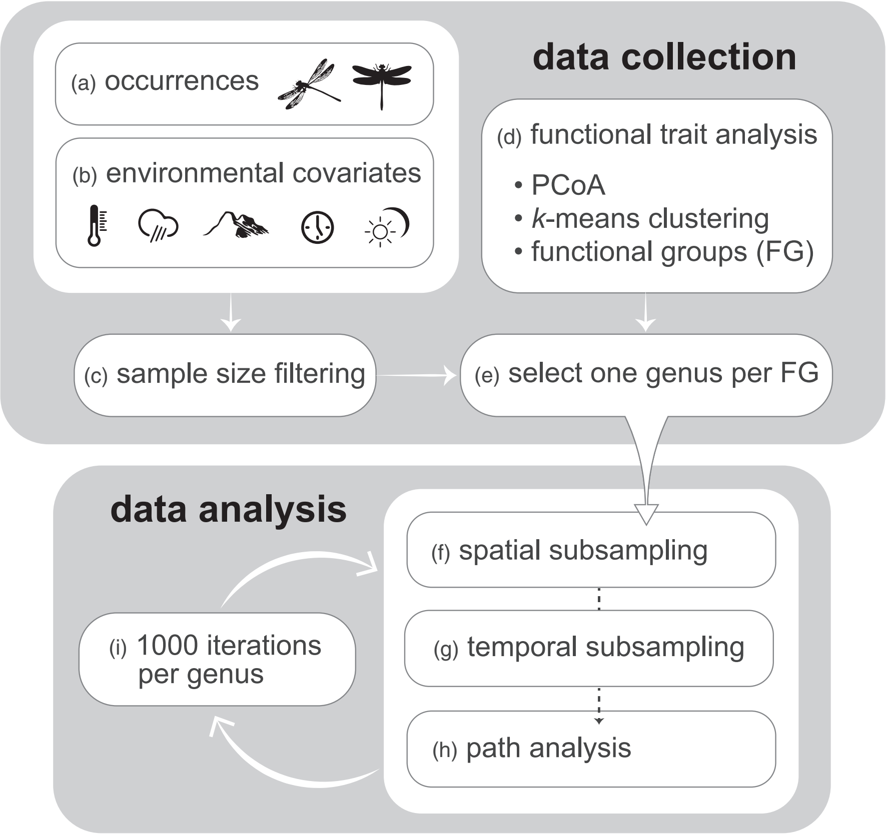

FIGURE 1 Methods workflow diagram. Top panel shows the workflow used for data collection, including: (a) downloading odonate occurrences; (b) downloading environmental covariates; (c) filtering odonate genera to ensure minimum sample size; (d) functional trait analysis, including principle coordinate analysis (PCoA), *k*-means cluster analysis and assignment of functional groups; and (e) selecting a single, representative odonate genera within each FG. Bottom panel illustrates the iterative data analysis process, including: (f) spatial subsampling (by sub-watershed); (g) temporal subsampling (by decadal bin); (h) path analysis using the subsampled data; and (i) 1000 random iterations of the subsampling and path modelling process for each representative genus.

Pritchard & Leggott, 1987; Procter, 1973). Notably, the ClimateNA data are generated and distributed on an annual basis (1901–2020) and could therefore be matched to the specific year of observation for each odonate record. Elevation (ELEV) was obtained from the NASA Shuttle Radar Topography Mission digital elevation data (Farr et al., 2007) and mean annual photoperiod (PHOTO) was obtained from Daymet (Thornton et al., 2020) using Google Earth Engine (Gorelick et al., 2017). Because PHOTO is invariant to climate change (i.e. determined solely by the relative positions of the sun and earth), we selected the most recent complete year of daylength data provided (2014) to calculate average day length. Year and latitude (LAT) were recorded directly from the original sample data.

2.2 | Functional trait analysis

We used a functional trait analysis to identify distinct functional groups (Figure 1c), then selected a single odondate genus within each functional group for modelling. This ensured our results would be broadly representative of the diverse life histories of North American odonates. Odonate samples were matched with their respective genus-level traits from the Freshwater Insects CONUS database (Twardochleb et al., 2021). Trait data included 11 trait groups (generations per year, emergence synchronization, emergence season, female dispersal, adult flying strength, body size, respiration mode, rheophily, thermal preference, habit and feeding style), distributed among four grouping features (life history, dispersal, morphology and ecology; for guidance on functional trait nomenclature, see Schmera et al., 2015). Several traits had uniform values among all odonate genera (e.g. all genera had 'predator' feeding styles); these were uninformative and removed prior to analysis. The final suite of traits provided three functional axes that were useful for delineating odonate groups that may respond differently to changing environments. For example, body size, thermal tolerance, generation time, dispersal ability and habitat use are each known to influence insect phenology (Chmura et al., 2019).

Steps taken in the functional trait analysis are fully detailed in the Supplementary Material (Appendix S1). Briefly, the raw trait group characters were recoded as ordinal integer (e.g. emergence season) or asymmetric binary (e.g. feeding style) variables (see Table S1), then appended to their respective odonate samples. A functional trait matrix (genus × trait) was created from the paired odonate and trait data, then combined with a community matrix (sample site × genus) to calculate Gower dissimilarities among all pairs of odonate genera. The Gower dissimilarity index was used because it is compatible with mixed (e.g. ordinal and binary) data types (Gower, 1971; Podani, 1999). Principal coordinate analysis (PCoA) was then used to build an *n*-dimensional ordination of all genera represented in the Gower matrix. Gower dissimilarities and the PCoA solution were obtained with the FD package in R (Laliberté et al., 2014).

From the functional trait analysis results, we identified distinct functional groups. Scores from the first three PCoA axes were combined with *k*-means cluster analysis and functional group membership was inferred for each odonate genera from the clustering results. *k* was defined as the number of clusters that optimized the within-cluster sum of squares criterion (Hartigan & Wong, 1979; Jackson et al., 2010; Legendre & Legendre, 2012). We calculated the within-cluster sum of squares for a series of potential *k* values ranging from 1 to 20, then estimated *k* as point where a scree plot (*k* × within-cluster sum of squares) approached an asymptote. Visual inspection of the scree plot suggested that seven clusters would be a suitable solution ($k = 7$; see Figure S1). *k*-means clustering was performed with the STATS package in R (R Core Team, 2020).

Next, a sample size criterion was used to select a single representative genus for each of the seven odonate functional groups (Figure 1d). The odonate data were filtered to include only genera with occurrence records in at least 7 of 12 decades, ranging from 1901 to 2020. A minimum of 10 occurrence records was also required within each of the 7–12 sampled decades. This ensured a minimum sample size of 70 occurrences, spanning a minimum time period of 70 years, for each genus. When more than one genus in a functional group met the sample size requirement, we selected the genus with the largest number of occurrence records (Figure 1e). These seven genera were used in subsequent modelling to broadly infer emergence responses to environmental conditions, with the assumption that odonate genera within a common functional group would respond similarly, relative to genera from distinct functional groups.

Characteristic trait values were visually identified for each functional group by plotting trait value distributions against the axis scores for first three PCoA axes (Figures S2–S4) and among the seven functional groups (Figure S5).

2.3 | Path analysis

Phenology was modelled for each of the seven representative, functional group genera with a three-stage process. First, subsampling was used to mitigate the uneven spatiotemporal distribution of odonate records. We began by assigning each sample to its respective sub-watershed from the HydroBASINS database (Pfafstetter level 12 polygons; mean area = 130.2 km^2, SD = 60.7; Lehner & Grill, 2013), then randomly selecting a maximum of three records per sub-watershed for use in modelling (Figure 1f). This reduced the spatial clustering of odonate records within more intensively surveyed areas (Chen & Olden, 2020). Similarly, we assigned each sample to one of 12 decadal bins, ranging from 1901 to 2020, then subsampled records within each decadal bin (Figure 1g). Specifically, we identified the smallest number of records within any of the 12 decadal bins, then randomly selected an equivalent number of records from each of the other bins. By rarefying the data this way, we eliminated the strong temporal bias (i.e. many more contemporary than historical samples; see Table S2) observed among the odonate records.

Second, we used path analysis to test for links between DOY and each of the environmental covariates (Figure 1h). We began with a metamodel (Grace et al., 2010) focusing on the direct influences of degree days and precipitation on phenology, each of which has previously been linked to odonate distributions (Ball-Damerow et al., 2014; Boys et al., 2021; Hassall & Thompson, 2008; Norling, 2018), while controlling for the effects of year and photoperiod (Figure 3). Three exogenous covariates were included: ELEV, LAT and YEAR. Of these, two—ELEV and LAT—have strong influences on MAT, MAP and PHOTO, and are invariant to global change. YEAR is, by definition, a correlate of global change and was therefore used as an index of global change in the path model. The direct path between YEAR and DOY provided a means to detect global change effects on DOY that were not due to altered temperature or precipitation. Prior to modelling, DOY and all covariates were standardized (mean = 0, standard deviation; SD = 1). Path models were then fit with the with the LAVAAN package in R (Rosseel, 2012).

Third, we repeated the complete path analysis process (subsampling and model fitting) 1000 times for each of the seven odonate genera (Figure 1i). Numbers of samples included in each of the random iterations, for each of the representative genera, are summarized in Table S3. Standardized path coefficients linking covariates, coefficients of determination (R^2) for endogenous covariates, and overall fit statistics were recorded in each iteration, then summarized for each of the modelled genera. A test of significance was performed for each path in the metamodel (Figure 3) by using the mean path coefficient and standard error from 1000 iterations (SE = standard deviation of 1000 coefficients ÷ √1000) to calculate a 95% confidence interval (CI = mean ± 1.96 × SE). Paths with 95% CIs that excluded zero were deemed significant. Overall model fit was assessed with the Standardized Root Mean Squared Residual (SRMR) and the Comparative Fit Index (CFI). Conventional thresholds ($SRMR < 0.09$; $CFI \geq 0.95$) were interpreted as evidence of 'good' model fit (Fan et al., 2016).

3 | RESULTS

The functional trait ordination is shown for all odonate genera, with the seven representative odonate genera highlighted by diamonds in Figure 2. Each of the seven representative genera is listed with key functional traits in Table 1. In general, functional group (FG) 1 consisted of small bodied, univoltine genera with low dispersal and weak flight ability, well-synchronized spring emergence, cool to warm thermal preference and tegument respiration. FG 2 was comprised of semivoltine genera with high dispersal and strong flight ability, well-synchronized spring or summer emergence and cool thermal preference. FG 3 genera were semivoltine with strong flight ability, well-synchronized spring emergence and cool thermal preference. FG 4 genera were semivoltine with low dispersal, strong flight ability, well-synchronized spring emergence and cool thermal preference. FG 5 included a mix of univoltine and multivoltine genera with high dispersal and strong flight ability, poorly synchronized spring emergence and warm thermal preference. FG 6 represented univoltine genera with summer emergence and hot thermal preference. FG 7 genera were univoltine with spring emergence and warm to hot thermal preference.

All path model coefficients are summarized in Table S4. Of the four covariates directly linked to DOY (see Figure 3), DD18 consistently had the strongest effect, as indicated by the relatively large magnitudes of the DD18 path coefficients (Figure 4). Moreover, the path linking DD18 to DOY was significant (95% CI excluding zero) for six of the seven modelled genera (Figure 4a, left panel). Among these, DD18 and DOY were negatively associated (increasing DD18 advanced emergence) for four genera: *Argia* sp. (FG 1), *Calopteryx* sp. (FG 3), *Hetaerina* sp. (FG 4) and *Libellula* sp. (FG 5). DD18 and DOY were positively associated (increasing DD18 delayed emergence) for two genera: *Aeshna* sp. (FG 2) and *Sympetrum* sp. (FG 7). Only *Plathemis* sp. (FG 7) did not exhibit a significant link between DD18 and DOY (Table S4).

MAP had a significant effect on DOY for all seven modelled genera (Figure 4a, right panel). For three genera (*Libellula* sp., *Calopteryx* sp., *Plathemis* sp.), DOY was advanced in wetter years. For the remaining genera, DOY was delayed in wetter years. PHOTO also had a significant effect on DOY for all genera (Figure 4b; Table S4). Three genera (*Argia* sp., *Plathemis* sp., *Sympetrum* sp.) exhibited advanced emergence with increasing day length. YEAR had a significant, positive effect on DOY for all genera. Small path coefficients did, however, indicate the direct effect of YEAR on DOY was modest in comparison to other DOY effects (Figure 4b).

Links between the exogenous and endogenous predictors of DOY also suggested the metamodel (Figure 3) was a useful representation of the key regulators of climate and photoperiod. Each link between an exogenous covariate and MAT, MAP, or PHOTO was significant (Table S4) and across the seven modelled genera, R^2 values were consistently high (>0.7) for MAT and PHOTO (Table 2). R^2 values were more variable for MAP, ranging from 0.09 (mean R^2 for *Aeshna* sp. models) to 0.62 (mean for *Calopteryx* sp. models), and were smallest for DOY (0.05–0.23). Nevertheless, overall model fit was consistently good. For all seven modelled genera, mean SRMR values were below the <0.09 fit threshold (Table 2). Similarly, mean CFI values met or exceeded the ≥0.95 fit threshold for two genera (*Argia* sp., *Libellula* sp.), but were nominally below the threshold (0.93–0.94) for the remaining genera.

4 | DISCUSSION

This study was motivated by previous research on odonate phenology in European freshwaters (Dingemanse & Kalkman, 2008; Hassall et al., 2007), but extends the state of the science in three ways. It compiles and standardizes a NHC database of odonate flight records that is unprecedented in spatiotemporal extent. It uses functional trait analysis to identify unique combinations of traits, potentially representing distinct life-history strategies, and to select odonate genera that are broadly representative of this functional variation. It then uses path analysis to assess the relative importance of several key drivers—degree days, photoperiod and precipitation—for odonate emergence timing and to place them within a systems-level context.

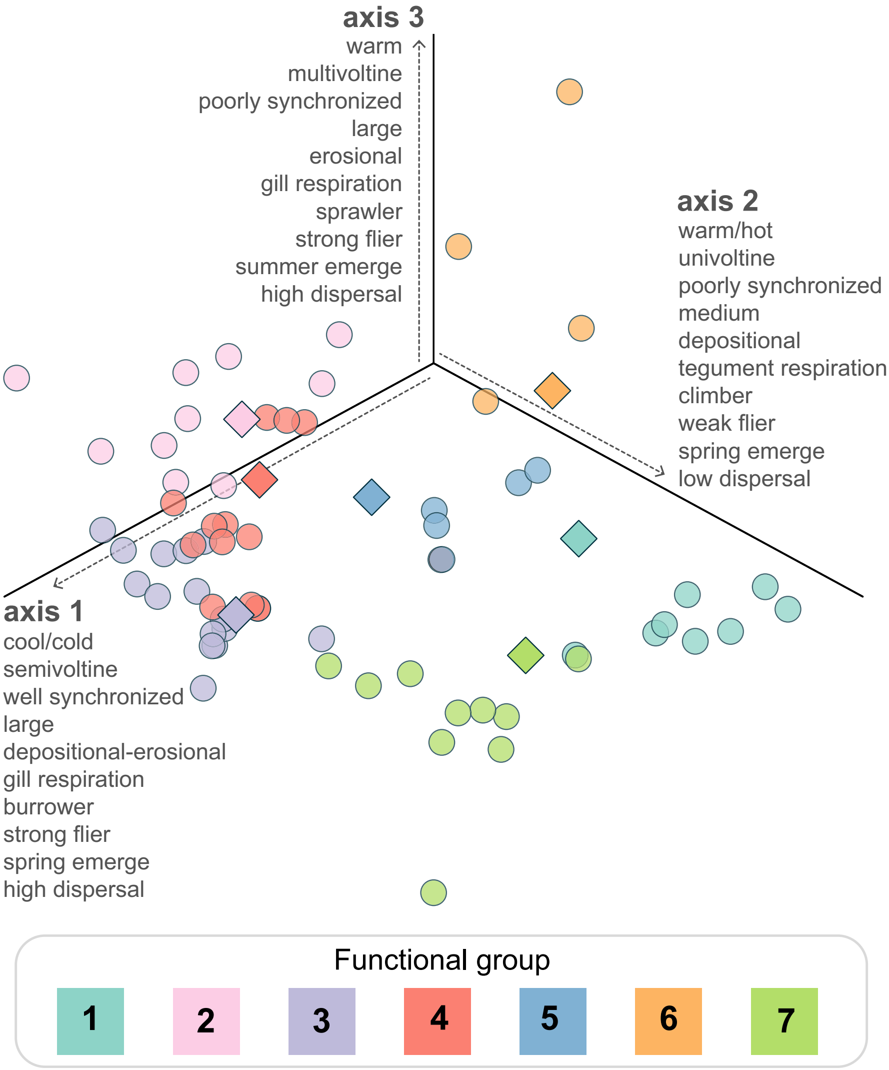

FIGURE 2 Functional trait analysis results. Ordination plot showing the location of each odonate genus included in the study, relative to the first three principal coordinate axes. Traits associated with each axis are listed with the axis labels. Colours indicate membership within the seven functional trait groups, as determined by *k*-means cluster analysis and labelled in the colour legend at bottom. Diamonds show the positions of the seven genera selected to represent the seven functional groups. Each of the representative genera is identified in Table 1.

Of the three innovations, path analysis may be the most important, as it allowed us to disentangle the effects of DD18, PHOTO and MAP from LAT and ELEV. Degree days (Suhling, Suhling, & Richter, 2015), photoperiod (Norling, 2018) and precipitation (McCauley et al., 2018) are each known to influence odonate emergence and/or ecology, but due to their strong covariation with latitude and elevation, it is difficult to isolate their individual effects (Corbet et al., 2006; Hassall, 2013; Śniegula et al., 2016). The meta-model of environmental influences on odonate DOY explicitly accounted for the shared influences of latitude and elevation (Figure 3). Hence, the paths linking DD18, PHOTO and MAP directly to DOY can be interpreted as independent effects (Grace, 2006).

4.1 | Environmental influences on odonate emergence

The strong association between DD18 and DOY that was confirmed for six of seven genera (Figure 4; Table S4), combined with prior work on degree days and the physiology of larval insect development (Cayton et al., 2015; McCauley et al., 2015; McCauley et al., 2018), suggests that odonate phenology may indeed be vulnerable to global change. However, the direction and magnitude of the DD18 versus DOY relationship was highly variable among the seven modelled genera, both in terms of direction and magnitude. A significantly negative DD18 versus DOY relationship, reflecting earlier emergence in warmer years, was observed for four genera but it was not universal. For two genera, emergence occurred significantly later in warmer years.

Knowledge of the functional traits and life histories of the seven odonate genera can help explain the disparate DD18 versus DOY relationships. For example, two of the genera with a negative DD18 versus DOY relationship, *Calopteryx* sp. and *Hetaerina* sp., exhibit prototypical Type 1 or spring emergence life cycles (Corbett, 2003). These semivoltine taxa reside in cold to cool environments (see Table 1) where larvae may reach the final (F-0) instar stage by the end of summer but do not emerge as adults until the following year (Suhling, Sahlén, et al., 2015). For these taxa, larval diapause provides a mechanism to ensure overwinter survival, followed by spring metamorphosis and emergence. In this context, a negative DD18 versus DOY relationship is likely to reflect the rapid accumulation of early-year degree days prior to spring emergence.

In contrast to the Type 1 life cycle, one of the genera with a positive DD18 versus DOY relationship, *Aeshna* sp., exhibits a Type 2 or summer emergence life cycle (Corbett, 2003). Type 2 odonates are also semivoltine but do not reach the final instar stage prior to winter diapause; additional time is needed the following spring to complete larval development, with metamorphosis typically occurring in summer. This delayed emergence timing is compatible with a positive association between DD18 and DOY. The other genus with a positive DD18 versus DOY relationship, *Sympetrum* sp., also emerges in mid to late summer, but completes the larval growth process in a single year. The rapid growth rates needed to complete this Type 3, univoltine life cycle are facilitated by warm environments and highly efficient foraging (Corbett, 2003).

A functional trait context is also useful for interpreting differential responses to photoperiod. The strongest negative associations between PHOTO and DOY were exhibited by genera with semivoltine life cycles and cool to cold thermal preferences (*Calopteryx* sp., *Hetaerina* sp.), while positive associations were exhibited by univoltine genera with warm to hot preferences (*Argia* sp., *Sympetrum* sp., *Plathemis* sp.; see Table 1; Figure 4). This functional distinction is intuitive because photoperiod is a key predictor of diapause and as mentioned above, diapause is common to many odonate life cycles (Suhling, Sahlén, et al., 2015). For odonates with Type 1 life cycles, longer days (increasing photoperiod) may allow larvae to reach a mid to late instar stage prior to winter diapause, with rapid development and emergence the following spring (Corbett, 2003). This might account for the negative PHOTO versus DOY relationship observed for *Calopteryx* sp. and *Hetaerina* sp. Alternatively, odonates living in warmer environments may complete their larval development in a single calendar year but emerge at a later Julian date (Type 3 life cycle) than semivoltine taxa exiting winter diapause. This scenario is consistent with a positive PHOTO versus DOY relationship because longer summer days entail greater scope for larval growth.

Explaining the precipitation results is more challenging. As the primary driver of hydrology, precipitation is fundamental to all odonate life histories. However, few studies have directly examined links between precipitation and odonate phenology; most have focused on odonate distribution and richness patterns (Ball-Damerow et al., 2014; Sparrow et al., 2021). We propose that aquatic habitat stability may provide a useful lens for understanding phenological responses to precipitation. Because odonates at temperate latitudes are rarely multivoltine (Suhling, Sahlén, et al., 2015), they will be vulnerable to any hydrologic disturbance that disrupts egg or larval development. Relevant disturbances would include intermittent drying in low precipitation regions or flooding in high precipitation regions. Phenological responses may include strategies to 'sit out' periods of disturbance, such as delayed oviposition (Hassall & Thompson, 2008) or larval diapause (Bêche et al., 2006). Vulnerability to hydrologic disturbance may also vary with functional traits. For instance, taxa with 'climber' and 'clinger' habits are better equipped to persist in high flow conditions than 'sprawler' taxa (Bae & Park, 2016). At

TABLE 1 Functional trait profiles for the seven representative odonate genera. For each genus, the functional group (FG) number and number of species within that genus in our database (in parentheses) is provided with the following traits: female dispersal (DSP), emergence season (EMG), adult flying strength (FLY), habit (HAB), respiration mode (RSP), rheophily (RHP), maximum body size (SIZE), emergence synchronization (SYN), thermal preference (THM) and generations per year or voltinism (VLT). Traits with two values listed indicate genera with multiple dominant trait states per genus. Values in parentheses indicate the breadth metric for each trait, if applicable. See Appendix S1 for complete information on the odonate functional traits.

FG	Genus	DSP	EMG	FLY	HAB	RSP	RHP	SIZE	SYN	THM	VLT
1	*Argia* (8)	Low	Spring (7)	Weak	Clinger, sprawler (2)	Gills, tegument (2)	Depositional-erosional	Large	Well	Warm eurythermal (2)	Univoltine (2)
2	*Aeshna* (5)	High	Summer (6)	Strong	Climber (1)	Gills (1)	Depositional	Large	Well	Warm eurythermal (2)	Semivoltine (2)
3	*Calopteryx* (2)	Low	Spring (8)	Strong	Climber (1)	Gills (1)	Depositional	Large	Well	Cold eurythermal (2)	Semivoltine (2)
4	*Hetaerina* (1)	Low	Spring (8)	Strong	Climber (1)	Gills (1)	Erosional	Large	Well	Cool eurythermal (2)	Semivoltine (3)
5	*Libellula* (8)	High	Spring (7)	Strong	Sprawler (1)	Gills (1)	Depositional	Large	Poor	Warm eurythermal (2)	Univoltine (2)
6	*Sympetrum* (7)	High	Summer (8)	Weak	Sprawler (1)	Gills (1)	Depositional	Large	Well	Hot eurythermal (2)	Univoltine (1)
7	*Plathemis* (1)	—	Spring (3)	—	Sprawler (1)	—	Depositional	—	—	Hot eurythermal (1)	—

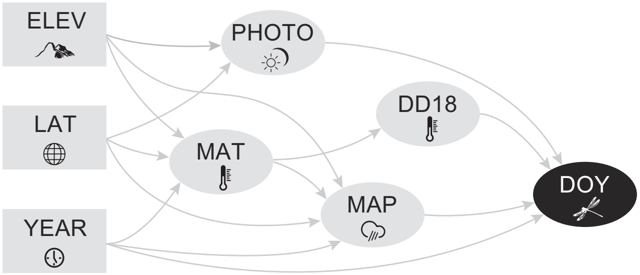

FIGURE 3 Path analysis metamodel. Path diagram showing all links that were included when fitting path analysis models of odonate emergence day-of-year (DOY). The metamodel includes hypothesized, direct links between DOY and mean annual photoperiod (PHOTO), degree days relative to an 18°C threshold (DD18), mean annual precipitation (MAP) and year of observation (YEAR). Covariates with distal effects of DOY include mean annual air temperature (MAT), elevation (ELEV) and latitude (LAT). Exogenous variables are shown as rectangles and endogenous variables are shown as ellipses.

present, we cannot account for the disparate MAP versus DOY relationships observed among the seven odonate genera (Figure 4). But we do suggest the mechanisms proposed here could be tested by combining a subset of odonate records with new, high-resolution data on local hydrologic conditions.

The direct effect of year on DOY is also difficult to interpret. For all modelled genera, a modest but significantly positive relationship was detected between YEAR and DOY (Figure 4). Importantly, this relationship was independent of the intermediate effects of air temperature and precipitation, suggesting that some factor not included in the metamodel (Figure 3) has gradually pushed odonate emergence back to a later Julian date over the past 120 years. A simple explanation may be the pervasive degradation of aquatic habitat in North America. Large scale anthropogenic activities, such as industrial agriculture and urban development, have impacted all types of freshwater environments over the past century (Benke, 1990; Bhagowati & Ahamad, 2019; Brinson & Malvárez, 2002; Carlisle et al., 2011). These changes may in turn delay odonate emergence through multiple pathways. For instance, altered habitat may diminish the abundance of aquatic insect prey (Hershey et al., 2010; Yoshimura, 2012), thereby constraining larval odonate growth and development (Baker, 1982; Lawton et al., 1980). Alternatively, habitat disturbance may increase the distances that adults traverse to locate mates or suitable oviposition sites (Dolný et al., 2014; Nagy et al., 2019). In this way, we suggest the positive YEAR versus DOY effects are a call to expand the scope of odonate phenology research. But we also point out that the YEAR effects on DOY are small, relative to the DD18, PHOTO and MAP effects (Figure 4).

4.2 | Caveats and opportunities

One notable caveat of this study is the relatively low fraction of variation in DOY that each of the path models accounted for. DOY R^2 values were <0.10 for three of seven modelled genera and never exceeded 0.23 (Table 2). Adding new predictors to the path models may increase R^2, as many episodic or local scale factors, such as physicochemical habitat quality, flood events and prey availability can impact the growth and emergence of odonate larvae (Córdoba-Aguilar, 2008). However, natural variation in odonate phenology may be the primary reason for low model precision. Odonate emergence timing can be difficult to predict with a high level of precision (Corbet et al., 2006; Richter et al., 2008) because a single emergence event, or 'emergence curve', will often span a period of weeks or months (Tatarkiewicz, 2012; Wissinger, 1988).

The diffuse timing of emergence events was evident in our data. For instance, the standard deviation of intra-annual DOY values ranged from 6.3–68.7 days for *Argia* sp., with a mean (among 120 years of record) of 40.3 days. Noting that peak activity may occur near the beginning, middle, or end of an emergence event (Lutz & Mcmahan, 1973; Thompson, 2019), we did not wish to use a discrete statistical moment, such as the 5th or 95th percentile (representing the leading and trailing edges of the emergence period; Villalobos-Jiménez & Hassall, 2017), as our response variable. These statistical moments are, in effect, the tails of a distribution of observation dates and are therefore more sensitive to sampling bias than the central tendency. Instead, we took a more general approach: for a given genus, we only assumed that a central tendency would exist within each year of DOY data, and this modal value would be a useful indicator of inter-annual trends in emergence timing. In this way, our continental-scale models emphasized accuracy over precision. But further insight may be gained by adding new response variables, such as the onset and duration of the emergence curve, to the path models. So long as sample sizes are large enough, any number of responses could be included in an expanded path model, allowing researchers to see if different dimensions of emergence timing respond similarly to environmental cues like temperature and photoperiod.

Two points of caution are also warranted when interpreting our degree day results. First, an 18°C threshold for larval odonate growth is in line with temperatures reported in some controlled experiments (e.g. Corbet, 1956; Lutz, 1968; Śniegula et al., 2016; Thompson, 2019) but higher than a proposed minimum of ~10°C (Suhling, Sahlén, et al., 2015). Thus, DD18 may underestimate the potential for odonate growth. As a practical matter, this should not affect the path models because DD18 was highly correlated ($r = 0.94$) with the annual number of degree days relative to a 5°C threshold (both thresholds were available from ClimateNA; see Wang et al., 2016). But it emphasizes the limits of degree day estimates when calculated as annual sums, rather than incremental values that can be matched to specific Julian dates. Incremental or cumulative degree day values could be aligned directly with emergence dates, providing a mechanistic link to emergence (Cayton et al., 2015; Finn et al., 2022); this approach would be more powerful than the correlative one used here for DD18 and DOY. Similarly, degree days from the prior year may improve emergence timing models, particularly for semivoltine taxa (Richter et al., 2008).

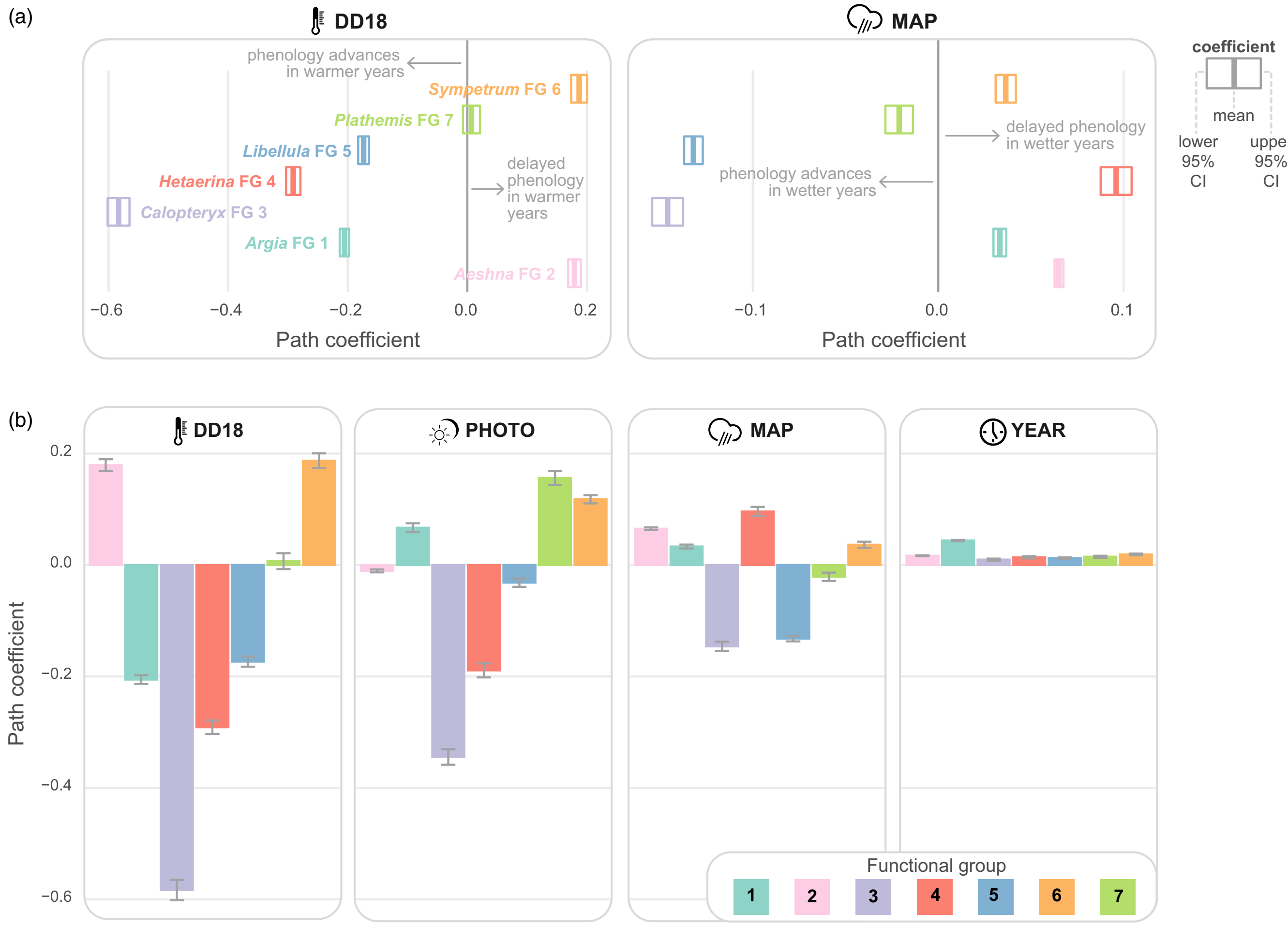

FIGURE 4 Summary of path coefficients for direct links to day-of-year. Panel (a) shows standardized coefficients for model paths linking degree-days (DD18; left panel) and mean annual precipitation (MAP; right panel) to emergence day-of-year. Boxplots summarize coefficients from 1000 path model iterations. Paths were deemed significant when their respective 95% confidence intervals excluded zero. Panel (b) shows mean path coefficients with 95% confidence intervals (error bars) for all four covariates that were linked directly to day-of-year (see Figure 3): DD18, photoperiod (PHOTO), MAP and YEAR. All plots in panel (b) share a common *y*-axis to facilitate direct comparisons of the relative influence of each covariate on emergence. Separate results are provided in each panel for the seven representative functional group genera.

Second, we used air temperature and its associated degree day values as proxies for water temperature. This was prudent because historical air temperatures were readily available from ClimateNA, but it entailed an unknown degree of measurement error. In lotic ecosystems, where a direct association between air and water temperature is well-established (Mohseni et al., 1999), we do not believe this error posed a substantive problem for our continental scale models. However, the air-water temperature relationship is more complex in lentic ecosystems. Lake surface temperature may closely track air temperature (Toffolon et al., 2014), but the relationship can be muted at the subsurface or benthic interface where many odonate larvae reside, particularly during periods of stratification (Robertson & Ragotzkie, 1990). To our knowledge, historical lake temperature records that are comparable in spatiotemporal extent to the air temperature data used here do not exist. But a preliminary assessment of the scope of this issue may be possible by superimposing the georeferenced odonate occurrence records on digital maps of lakes and rivers. A spatial function (e.g. shortest Euclidian distance to a lake or river boundary) could then be used to specify the most likely origin (lake vs. river habitat) of each odonate record. If the air-water temperature relationship is significantly distorted in lentic systems, we would expect DOY models to differ among the two habitat types.

Finally, we recognize that our genus-level records did not account for functional trait or phenological variation at interspecific (within genera) or intraspecific levels. This is important because odonate taxa may exhibit strong inter- and/or intraspecific variation in morphology, physiology and behaviour (e.g. Bybee et al., 2016; Frances et al., 2017). This sub-generic level variation may, in turn, be essential in predicting responses to climate change (Powney et al., 2015; Salo et al., 2020). Accounting for inter- and intraspecific variation is not currently feasible in a whole community, continental scale study such as this, due to the limitations of paired data on species-level traits and distributions (see

TABLE 2 Summary of path model fit statistics. Indicators of overall model fit include the Standardized Root Mean Squared Residual (SRMR) and Comparative Fit Index (CFI). Conventional thresholds to confirm 'good' fit are shown in parentheses for both indices. Coefficients of determination (R^2) are listed for each of the endogenous variables. Values shown are the mean statistics, with 95% confidence intervals (CI), from models independently fit to 1000 subsampling iterations. Results are shown in separate columns for each of the seven representative odonate genera

	Aeshna		*Argia*		*Calopteryx*		*Hetaerina*		*Libellula*		*Plathemis*		*Sympetrum*	
Statistic	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
SRMR (<0.09)	0.06	0.01	0.03	0.01	0.04	0.01	0.03	0.01	0.03	0.01	0.03	0.01	0.03	0.01
CFI (≥0.95)	0.94	0.01	0.95	0.01	0.94	0.02	0.94	0.02	0.96	0.02	0.94	0.02	0.93	0.02
R^2 DOY	0.06	0.04	0.13	0.05	0.23	0.13	0.09	0.05	0.11	0.07	0.10	0.06	0.05	0.04
R^2 DD18	0.48	0.05	0.78	0.02	0.87	0.04	0.75	0.03	0.82	0.03	0.72	0.05	0.79	0.03
R^2 MAP	0.09	0.04	0.18	0.05	0.62	0.10	0.42	0.07	0.31	0.08	0.34	0.11	0.21	0.08
R^2 PHOTO	0.98	<0.01	0.99	<0.01	0.99	<0.01	0.99	<0.01	0.99	<0.01	0.99	<0.01	0.98	<0.01
R^2 MAT	0.72	0.04	0.89	0.02	0.92	0.03	0.85	0.03	0.88	0.02	0.89	0.03	0.86	0.03

Bonada & Dolédec, 2018; Rocha-Ortega et al., 2020; Twardochleb et al., 2021). However, a good starting point may be to focus on a single well-studied region where species-level trait and occurrence data are nearly complete, such as central California, USA (Ball-Damerow et al., 2015).

Addressing the points raised above will further our ability to detect and anticipate global change effects on odonate phenology. We therefore hope that others will be inspired to emulate and extend our work. For the moment, we conclude by crediting the resources that made this study possible. The models presented herein were built entirely with free, open-source data and software. Our time was the sole expense. This is exciting because the availability of open-source data, ranging from opportunistic NHC and community science records (Olsen et al., 2020) to systematic programs like the National Water-Quality Assessment Project (Gilliom et al., 1995) and the National Ecological Observatory Network (Utz et al., 2013), is rapidly increasing. And with this growth will come novel opportunities to dissect and understand aquatic ecosystems. The challenges posed by global change are unprecedented, but so too are the research horizons that are now being revealed by open-source information.

AUTHOR CONTRIBUTIONS

Taylor Woods and Daniel J. McGarvey conceived and designed the study. Taylor Woods collected and prepared the odonate dataset and Daniel J. McGarvey prepared the functional trait data and analysis. Taylor Woods and Daniel J. McGarvey analysed the data. Taylor Woods and Daniel J. McGarvey interpreted results and wrote the manuscript.

ACKNOWLEDGEMENTS

We extend our sincere gratitude to the many researchers, community scientists and agencies who contributed data and made our study possible. Helpful comments from the Associate Editor and two anonymous reviewers substantially improved the quality of our analysis and manuscript. D.J.M. was supported by the U.S. National Science Foundation (DEB-1553111, DEB-2032146). Ethics approval was not required for this study.

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.5hqbzkh8k (Woods & McGarvey, 2022).

ORCID

Taylor Woods https://orcid.org/0000-0002-6277-1260
Daniel J. McGarvey https://orcid.org/0000-0002-1218-5896

REFERENCES

Altermatt, F. (2010). Climatic warming increases voltinism in European butterflies and moths. *Proceedings of the Royal Society B: Biological*

Sciences, *277*(1685), 1281–1287. https://doi.org/10.1098/rspb.2009.1910

Aoki, T. (1999). Larval development, emergence and seasonal regulation in *Asiagomphus pryeri* (Selys) (Odonata: Gomphidae). *Hydrobiologia*, *394*, 179–192. https://doi.org/10.1023/A:1003626011117

Asch, R. G. (2015). Climate change and decadal shifts in the phenology of larval fishes in the California Current ecosystem. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(30), E4065–E4074. https://doi.org/10.1073/pnas.1421946112

Bae, M. J., & Park, Y. S. (2016). Responses of the functional diversity of benthic macroinvertebrates to floods and droughts in small streams with different flow permanence. *Inland Waters*, *6*(3), 461–475. https://doi.org/10.1080/IW-6.3.891

Baker, R. L. (1982). Effects of food abundance on growth, survival, and use of space by nymphs of *Coenagrion resolutum* (Zygoptera). *Oikos*, *38*(1), 47–51.

Ball-Damerow, J. E., M'Gonigle, L. K., & Resh, V. H. (2014). Local and regional factors influencing assemblages of dragonflies and damselflies (Odonata) in California and Nevada. *Journal of Insect Conservation*, *18*(6), 1027–1036. https://doi.org/10.1007/s10841-014-9709-6

Ball-Damerow, J. E., Oboyski, P. T., & Resh, V. H. (2015). California dragonfly and damselfly (Odonata) database: Temporal and spatial distribution of species records collected over the past century. *ZooKeys*, *482*, 68–89. https://doi.org/10.3897/zookeys.482.8453

Baranov, V., Jourdan, J., Pilotto, F., Wagner, R., & Haase, P. (2020). Complex and nonlinear climate-driven changes in freshwater insect communities over 42 years. *Conservation Biology*, *34*(5), 1241–1251. https://doi.org/10.1111/cobi.13477

Bates, J. M., Fidino, M., Nowak-Boyd, L., Strausberger, B. M., Schmidt, K. A., & Whelan, C. J. (2022). Climate change affects bird nesting phenology: Comparing contemporary field and historical museum nesting records. *Journal of Animal Ecology*. https://doi.org/10.1111/1365-2656.13683

Bêche, L. A., McElravy, E. P., & Resh, V. H. (2006). Long-term seasonal variation in the biological traits of benthic-macroinvertebrates in two Mediterranean-climate streams in California, USA. *Freshwater Biology*, *51*(1), 56–75. https://doi.org/10.1111/j.1365-2427.2005.01473.x

Benke, A. C. (1990). A perspective on America's vanishing streams. *Journal of the North American Benthological Society*, *9*(1), 77–88.

Bhagowati, B., & Ahamad, K. U. (2019). A review on lake eutrophication dynamics and recent developments in lake modeling. *Ecohydrology & Hydrobiology*, *19*(1), 155–166. https://doi.org/10.1016/j.ecohyd.2018.03.002

Boakes, E. H., McGowan, P. J. K., Fuller, R. A., Chang-Qing, D., Clark, N. E., O'Connor, K., & Mace, G. M. (2010). Distorted views of biodiversity: Spatial and temporal bias in species occurrence data. *PLoS Biology*, *8*(6), e1000385. https://doi.org/10.1371/journal.pbio.1000385

Bonada, N., & Dolédec, S. (2018). Does the Tachet trait database report voltinism variability of aquatic insects between Mediterranean and Scandinavian regions? *Aquatic Sciences*, *80*, 7.

Boys, W. A., Siepielski, A. M., Smith, B. D., Patten, M. A., & Bried, J. T. (2021). Predicting the distributions of regional endemic dragonflies using a combined model approach. *Insect Conservation and Diversity*, *14*(1), 52–66. https://doi.org/10.1111/icad.12444

Brinson, M. M., & Malvárez, A. I. (2002). Temperate freshwater wetlands: Types, status, and threats. *Environmental Conservation*, *29*(2), 115–133. https://doi.org/10.1017/S0376892902000085

Bybee, S., Córdoba-Aguilar, A., Duryea, M. C., Futahashi, R., Hansson, B., Lorenzo-Carballa, M. O., Schilder, R., Stoks, R., Suvorov, A., Svensson, E. I., Swaegers, J., Takahashi, Y., Watts, P. C., & Wellenreuther, M. (2016). Odonata (dragonflies and damselflies) as a bridge between ecology and evolutionary genomics. *Frontiers in Zoology*, *13*(1), 1–20. https://doi.org/10.1186/s12983-016-0176-7

Carlisle, D. M., Wolock, D. M., & Meador, M. R. (2011). Alteration of streamflow magnitudes and potential ecological consequences: A multiregional assessment. *Frontiers in Ecology and the Environment*, *9*(5), 264–270. https://doi.org/10.1890/100053

Cayton, H. L., Haddad, N. M., Gross, K., Diamond, S. E., & Ries, L. (2015). Do growing degree days predict phenology across butterfly species? *Ecology*, *96*(6), 1473–1479. https://doi.org/10.1890/15-0131.1

Chamberlain, S., Barve, V., McGlinn, D., Oldoni, D., Desmet, P., Geffert, L., & Ram, K. (2021). *rgbif: Interface to the global biodiversity information facility API*. https://cran.r-project.org/package=rgbif

Chen, K., & Olden, J. D. (2020). Threshold responses of riverine fish communities to land use conversion across regions of the world. *Global Change Biology*, *26*(9), 4952–4965. https://doi.org/10.1111/gcb.15251

Chmura, H. E., Kharouba, H. M., Ashander, J., Ehlman, S. M., Rivest, E. B., & Yang, L. H. (2019). The mechanisms of phenology: The patterns and processes of phenological shifts. *Ecological Monographs*, *89*(1), e01337. https://doi.org/10.1002/ecm.1337

Cohen, J. M., Lajeunesse, M. J., & Rohr, J. R. (2018). A global synthesis of animal phenological responses to climate change. *Nature Climate Change*, *8*(3), 224–228. https://doi.org/10.1038/s41558-018-0067-3

Corbet, P. S. (1956). Environmental factors influencing the induction and termination of diapause in the Emperor Dragonfly, *Anax imperator* Leach (Odonata: Aeshnidae). *Journal of Experimental Biology*, *33*(1), 1–14. https://doi.org/10.1242/jeb.33.1.1a

Corbet, P. S., Suhling, F., & Soendgerath, D. (2006). Voltinism of odonata: A review. *International Journal of Odonatology*, *9*(1), 1–44. https://doi.org/10.1080/13887890.2006.9748261

Corbett, P. S. (2003). A positive correlation between photoperiod and development rate in summer species of Odonata could help to make emergence date appropriate to latitude: A testable hypothesis. *Journal of the Entomological Society of British Columbia*, *100*, 3–17.

Córdoba-Aguilar, A. (2008). *Dragonflies and damselflies: Model organisms for ecological and evolutionary research*. Oxford University Press.

Crick, H., Dudley, C., Glue, D., & Thomson, D. (1997). UK birds are laying eggs earlier. *Nature*, *388*(6642), 526.

Denlinger, D. L., Hahn, D. A., Merlin, C., Holzapfel, C. M., & Bradshaw, W. E. (2017). Keeping time without a spine: What can the insect clock teach us about seasonal adaptation? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1734), 20160257. https://doi.org/10.1098/rstb.2016.0257

Diamond, S. E., Frame, A. M., Martin, R. A., & Buckley, L. B. (2011). Species' traits predict phenological responses to climate change in butterflies. *Ecology*, *92*(5), 1005–1012. https://doi.org/10.1890/10-1594.1

Dingemanse, N. J., & Kalkman, V. J. (2008). Changing temperature regimes have advanced the phenology of Odonata in the Netherlands. *Ecological Entomology*, *33*(3), 394–402. https://doi.org/10.1111/j.1365-2311.2007.00982.x

Doi, H., Gordo, O., Mori, T., & Kubo, M. T. (2017). A macroecological perspective for phenological research under climate change. *Ecological Research*, *32*(5), 633–641. https://doi.org/10.1007/s11284-017-1480-1

Dolný, A., Harabiš, F., & Mižičová, H. (2014). Home range, movement, and distribution patterns of the threatened dragonfly *Sympetrum depressiusculum* (Odonata: Libellulidae): A thousand times greater territory to protect? *PLoS ONE*, *9*(7), e100408. https://doi.org/10.1371/journal.pone.0100408

Duchenne, F., Thébault, E., Michez, D., Elias, M., Drake, M., Persson, M., Rousseau-Piot, J. S., Pollet, M., Vanormelingen, P., & Fontaine, C.

(2020). Phenological shifts alter the seasonal structure of pollinator assemblages in Europe. *Nature Ecology and Evolution*, *4*(1), 115–121. https://doi.org/10.1038/s41559-019-1062-4

Ewers-Saucedo, C., Allspach, A., Barilaro, C., Bick, A., Brandt, A., Fiege, D., Füting, S., Hausdorf, B., Hayer, S., Husemann, M., Joger, U., Kamcke, C., Küster, M., Lohrmann, V., Martin, I., Michalik, P., Reinicke, G.-B., Schwentner, M., Stiller, M., & Brandis, D. (2021). Natural history collections recapitulate 200 years of faunal change. *Royal Society Open Science*, *8*(4), 201983. https://doi.org/10.1098/rsos.201983

Fan, Y., Chen, J., Shirkey, G., John, R., Wu, S. R., Park, H., & Shao, C. (2016). Applications of structural equation modeling (SEM) in ecological studies: An updated review. *Ecological Processes*, *5*, 19. https://doi.org/10.1186/s13717-016-0063-3

Farr, T., Rosen, P., Caro, E., Crippen, R., Duren, R., Hensley, S., Kobrick, M., Paller, M., Rodriguez, E., Roth, L., Seal, D., Shaffer, S., Shimada, J., Umland, J., Werner, M., Oskin, M., Burbank, D., & Alsdorf, D. (2007). The shuttle radar topography mission. *Reviews of Geophysics*, *45*(2), RG2004. https://doi.org/10.1007/3-540-44818-7_11

Finn, D. S., Johnson, S. L., Gerth, W. J., Arismendi, I., & Li, J. L. (2022). Spatiotemporal patterns of emergence phenology reveal complex species-specific responses to temperature in aquatic insects. *Diversity and Distributions*. https://doi.org/10.1111/ddi.13472

Frances, D. N., Moon, J. Y., & McCauley, S. J. (2017). Effects of environmental warming during early life history on libellulid odonates. *Canadian Journal of Zoology*, *95*(6), 373–382.

Fric, Z. F., Rindoš, M., & Konvička, M. (2020). Phenology responses of temperate butterflies to latitude depend on ecological traits. *Ecology Letters*, *23*(1), 172–180. https://doi.org/10.1111/ele.13419

Gallinat, A. S., Ellwood, E. R., Heberling, J. M., Miller-Rushing, A. J., Pearse, W. D., & Primack, R. B. (2021). Macrophenology: Insights into the broad-scale patterns, drivers, and consequences of phenology. *American Journal of Botany*, *108*(11), 2112–2126. https://doi.org/10.1002/ajb2.1793

GBIF. (2021). Occurrence Download [Data set]. The Global Biodiversity Information Facility. https://doi.org/10.15468/DL.TSJ7Z8

Gilliom, R. J., Alley, W. M., & Gurtz, M. E. (1995). *Design of the National Water-Quality Assessment Program: Occurrence and distribution of water-quality conditions*. United States Geological Survey, Circular 1112.

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., Thau, D., & Moore, R. (2017). Google earth engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*, *202*, 18–27. https://doi.org/10.1016/j.rse.2017.06.031

Gower, J. (1971). A general coefficient of similarity and some of its properties. *Biometrics*, *27*(4), 857–871. https://doi.org/10.2307/2528823

Grace, J., Anderson, T., Olff, H., & Scheiner, S. (2010). On the specification of structural equation models for ecological systems. *Ecological Monographs*, *80*(1), 67–87.

Grace, J. B. (2006). *Structural equation modeling and natural systems*. Cambridge University Press.

Hartigan, J. A., & Wong, M. A. (1979). A *K*-means clustering algorithm. *Applied Statistics*, *28*(1), 100–108.

Hassall, C. (2013). Time stress and temperature explain continental variation in damselfly body size. *Ecography*, *36*(8), 894–903. https://doi.org/10.1111/j.1600-0587.2013.00018.x

Hassall, C. (2015). Odonata as candidate macroecological barometers for global climate change. *Freshwater Science*, *34*(3), 1040–1049. https://doi.org/10.1086/682210

Hassall, C., & Thompson, D. J. (2008). The effects of environmental warming on odonata: A review. *International Journal of Odonatology*, *11*(2), 131–153. https://doi.org/10.1080/13887890.2008.9748319

Hassall, C., Thompson, D. J., French, G. C., & Harvey, I. F. (2007). Historical changes in the phenology of British Odonata are related to climate. *Global Change Biology*, *13*(5), 933–941. https://doi.org/10.1111/j.1365-2486.2007.01318.x

Hershey, A. E., Lamberti, G. A., Chaloner, D. T., & Northington, R. M. (2010). Chapter 17 – Aquatic insect ecology. In J. H. Thorp & A. P. Covich (Eds.), *Ecology and classification of North American freshwater invertebrates* (3rd ed., pp. 659–694). Academic Press.

Jackson, D. A., Walker, S. C., & Poos, M. S. (2010). Cluster analysis of fish community data: "New" tools for determining meaningful groupings of sites and species assemblages. *American Fisheries Society Symposium*, *73*, 503–527.

Kharouba, H. M., Lewthwaite, J. M. M., Guralnick, R., Kerr, J. T., & Vellend, M. (2019). Using insect natural history collections to study global change impacts: Challenges and opportunities. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *374*(1763), 20170405. https://doi.org/10.1098/rstb.2017.0405

Kharouba, H. M., Paquette, S. R., Kerr, J. T., & Vellend, M. (2014). Predicting the sensitivity of butterfly phenology to temperature over the past century. *Global Change Biology*, *20*(2), 504–514. https://doi.org/10.1111/gcb.12429

Laliberté, E., Legendre, P., & Shipley, B. (2014). Measuring functional diversity (FD) from multiple traits, and other tools for functional ecology. R package version 1.0-12.

Lawton, J. H., Thompson, B., & Thompson, D. J. (1980). The effects of prey density on survival and growth of damselfly larvae. *Ecological Entomology*, *5*(1), 39–51. https://doi.org/10.1111/j.1365-2311.1980.tb01122.x

Legendre, P., & Legendre, L. (2012). *Numerical Ecology* (3rd ed.). Elsevier.

Lehner, B., & Grill, G. (2013). Global river hydrography and network routing: Baseline data and new approaches to study the world's large river systems. *Hydrological Processes*, *27*(15), 2171–2186.

Lenoir, J., Bertrand, R., Comte, L., Bourgeaud, L., Hattab, T., Murienne, J., & Grenouillet, G. (2020). Species better track climate warming in the oceans than on land. *Nature Ecology and Evolution*, *4*(8), 1044–1059. https://doi.org/10.1038/s41559-020-1198-2

Lutz, P. E. (1968). Effects of temperature and photoperiod on larval development in *Lestes eurinus* (Odonata: Lestidae). *Ecology*, *49*(4), 637–644.

Lutz, P. E., & Mcmahan, E. A. (1973). Five-year patterns of emergence in *Tetragoneuria cynosura* and *Gomphus exilis* (Odonata). *Annals of the Entomological Society of America*, *66*(6), 1343–1348.

McCauley, S. J., Hammond, J. I., Frances, D. N., & Mabry, K. E. (2015). Effects of experimental warming on survival, phenology, and morphology of an aquatic insect (Odonata). *Ecological Entomology*, *40*(3), 211–220. https://doi.org/10.1111/een.12175

McCauley, S. J., Hammond, J. I., & Mabry, K. E. (2018). Simulated climate change increases larval mortality, alters phenology, and affects flight morphology of a dragonfly. *Ecosphere*, *9*(3), e02151. https://doi.org/10.1002/ecs2.2151

McNamara, J. M., Barta, Z., Klaassen, M., & Bauer, S. (2011). Cues and the optimal timing of activities under environmental changes. *Ecology Letters*, *14*(12), 1183–1190. https://doi.org/10.1111/j.1461-0248.2011.01686.x

Mentges, A., Blowes, S. A., Hodapp, D., Hillebrand, H., & Chase, J. M. (2020). Effects of site-selection bias on estimates of biodiversity change. *Conservation Biology*, *35*(2), 688–698. https://doi.org/10.1111/cobi.13610

Mohseni, O., Erickson, T. R., & Stefan, H. G. (1999). Sensitivity of stream temperatures in the United States to air temperatures projected under a global warming scenario. *Water Resources Research*, *35*(12), 3723–3733. https://doi.org/10.1029/1999wr900193

Nagy, H. B., László, Z., Szabó, F., Szőcs, L., Dévai, G., & Tóthmérész, B. (2019). Landscape-scale terrestrial factors are also vital in shaping Odonata assemblages of watercourses. *Scientific Reports*, *9*, 18196. https://doi.org/10.1038/s41598-019-54628-7

Norling, U. (2018). Constant and shifting photoperiods as seasonal cues during larval development of the univoltine damselfly *Lestes sponsa* (Odonata: Lestidae). *International Journal of Odonatology*, *21*(2), 129–150. https://doi.org/10.1080/13887890.2018.1462263

Olsen, K., Holm, T. E., Pape, T., & Simonsen, T. J. (2020). Natural history museum collection and citizen science data show advancing phenology of Danish hoverflies (Insecta: Diptera, Syrphidae) with increasing annual temperature. *PLoS ONE*, *15*(5), 5–8. https://doi.org/10.1371/journal.pone.0232980

Parmesan, C. (2006). Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics*, *37*, 637–669. https://doi.org/10.1146/annurev.ecolsys.37.091305.110100

Parmesan, C., & Yohe, G. (2003). A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, *421*(6918), 37–42. https://doi.org/10.1038/nature01286

Paulson, D. (2019). *Dragonflies and damselflies - A natural history*. Princeton University Press.

Podani, J. (1999). Extending Gower's general coefficient of similarity to ordinal characters. *Taxon*, *48*(2), 331–340. https://doi.org/10.2307/1224438

Powney, G. D., Cham, S. S. A., Smallshire, D., & Isaac, N. J. B. (2015). Trait correlates of distribution trends in the Odonata of Britain and Ireland. *PeerJ*, *3*, e1410.

Pritchard, G. (1982). Life history strategies in dragonflies and the colonization of North America by the genus Argia (Odonata: Coenagrionidae). *Advances in Odonatology*, *1*, 227–241.

Pritchard, G. (1989). The roles of temperature and diapause in the life history of a temperate-zone dragonfly: *Argia vivida* (Odonata: Coenagrionidae). *Ecological Entomology*, *14*(1), 99–108. https://doi.org/10.1111/j.1365-2311.1989.tb00759.x

Pritchard, G., & Leggott, M. (1987). Temperature, incubation rates and origins of dragonflies. *Advances in Odonatology*, *3*(1), 121–126.

Procter, D. L. C. (1973). The effect of temperature and photoperiod on larval development in Odonata. *Canadian Journal of Zoology*, *51*(11), 1165–1170. https://doi.org/10.1139/z73-169

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.r-project.org

Renner, S. S., & Zohner, C. M. (2018). Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annual Review of Ecology, Evolution, and Systematics*, *49*(1), 165–182. https://doi.org/10.1146/annurev-ecolsys-110617-062535

Richter, O., Suhling, F., Müller, O., & Kern, D. (2008). A model for predicting the emergence of dragonflies in a changing climate. *Freshwater Biology*, *53*(9), 1868–1880. https://doi.org/10.1111/j.1365-2427.2008.02012.x

Robertson, D. M., & Ragotzkie, R. A. (1990). Changes in the thermal structure of moderate to large sized lakes in response to changes in air temperature. *Aquatic Sciences*, *52*(4), 360–380. https://doi.org/10.1007/BF00879763

Rocha-Ortega, M., Rodríguez, P., Bried, J., Abbott, J., & Córdoba-Aguilar, A. (2020). Why do bugs perish? Range size and local vulnerability traits as surrogates of Odonata extinction risk. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1924), 20192645. https://doi.org/10.1098/rspb.2019.2645

Rosseel, Y. (2012). Lavaan: An R package for structural equation modeling. *Journal of Statistical Software*, *48*(2), 1–36. https://doi.org/10.18637/jss.v048.i02

Salo, T., Mattila, J., & Eklöf, J. (2020). Long-term warming affects ecosystem functioning through species turnover and intraspecific trait variation. *Oikos*, *129*(2), 283–295. https://doi.org/10.1111/oik.06698

Samways, M. J. (2019). *Insect conservation: A global synthesis*. CABI.

Schmera, D., Podani, J., Heino, J., Erős, T., & Poff, N. L. (2015). A proposed unified terminology of species traits in stream ecology. *Freshwater Science*, *34*(3), 823–830. https://doi.org/10.1086/681623

Śniegula, S., Gołąb, M. J., & Johansson, F. (2016). Time constraint effects on phenology and life history synchrony in a damselfly along a latitudinal gradient. *Oikos*, *125*(3), 414–423. https://doi.org/10.1111/oik.02265

Sparrow, D. J., De Knijf, G., & Sparrow, R. L. (2021). Diversity, status and phenology of the dragonflies and damselflies of Cyprus (Insecta: Odonata). *Diversity*, *13*(11), 532. https://doi.org/10.3390/d13110532

Staudinger, M. D., Mills, K. E., Stamieszkin, K., Record, N. R., Hudak, C. A., Allyn, A., Diamond, A., Friedland, K. D., Golet, W., Henderson, M. E., Hernandez, C. M., Huntington, T. G., Ji, R., Johnson, C. L., Johnson, D. S., Jordaan, A., Kocik, J., Li, Y., Liebman, M., … Yakola, K. (2019). It's about time: A synthesis of changing phenology in the Gulf of Maine ecosystem. *Fisheries Oceanography*, *28*(5), 532–566. https://doi.org/10.1111/fog.12429

Suhling, F., Sahlén, G., Gorb, S., Kalkman, V. J., Dijkstra, K.-D. B., & van Tol, J. (2015). Chapter 35 - Order odonata. In J. H. Thorp & D. C. Rogers (Eds.), *Thorp and Covich's freshwater invertebrates* (4th ed., pp. 893–932). Academic Press.

Suhling, F., Suhling, I., & Richter, O. (2015). Temperature response of growth of larval dragonflies – An overview. *International Journal of Odonatology*, *18*(1), 15–30. https://doi.org/10.1080/13887890.2015.1009392

Tatarkiewicz, D. (2012). Analysis of the emergence of the scarce chaser *Libellula fulva* O.F. Müller, 1764 (Odonata: Libellulidae). *Aquatic Insects*, *34*(3–4), 173–193. https://doi.org/10.1080/01650424.2013.800556

Thackeray, S. J., Henrys, P. A., Hemming, D., Bell, J. R., Botham, M. S., Burthe, S., Helaouet, P., Johns, D. G., Jones, I. D., Leech, D. I., Mackay, E. B., Massimino, D., Atkinson, S., Bacon, P. J., Brereton, T. M., Carvalho, L., Clutton-Brock, T. H., Duck, C., Edwards, M., … Wanless, S. (2016). Phenological sensitivity to climate across taxa and trophic levels. *Nature*, *535*(7611), 241–245. https://doi.org/10.1038/nature18608

Thackeray, S. J., Henrys, P. A., Jones, I. D., & Feuchtmayr, H. (2012). Eight decades of phenological change for a freshwater cladoceran: What are the consequences of our definition of seasonal timing? *Freshwater Biology*, *57*(2), 345–359. https://doi.org/10.1111/j.1365-2427.2011.02614.x

Thackeray, S. J., Jones, I. D., & Maberly, S. C. (2008). Long-term change in the phenology of spring phytoplankton: Species-specific responses to nutrient enrichment and climatic change. *Journal of Ecology*, *96*(3), 523–535. https://doi.org/10.1111/j.1365-2745.2008.01355.x

Thompson, A. L. (2019). *The life history of Anax junius (Drury) in Minnesota: Determining instars, growth development pathways, emergence phenology, and the effect of temperature on development (Odonata: Aeshnidae)*. University of Minnesota.

Thornton, M. M., Shrestha, R., Wei, Y., Thornton, P. E., Kao, S., & Wilson, B. E. (2020). *Daymet: Daily surface weather data on a 1-km grid for North America, version 4*. ORNL DAAC. https://doi.org/10.3334/ORNLDAAC/1840

Toffolon, M., Piccolroaz, S., Majone, B., Soja, A.-M., Peeters, F., Schmid, M., & Wüest, A. (2014). Prediction of surface temperature in lakes with different morphology using air temperature. *Limnology and Oceanography*, *59*(6), 2185–2202. https://doi.org/10.4319/lo.2014.59.6.2185

Twardochleb, L., Hiltner, E., Pyne, M., & Zarnetske, P. (2021). Freshwater insects CONUS: A database of freshwater insect occurrences and traits for the contiguous United States. *Global Ecology and Biogeography*, *30*(4), 826–841. https://doi.org/10.1111/geb.13257

Utz, R. M., Fitzgerald, M. R., Goodman, K. J., Parker, S. M., Powell, H., & Roehm, C. L. (2013). The National Ecological Observatory Network: An observatory poised to expand spatiotemporal scales of inquiry in aquatic and fisheries science. *Fisheries*, *38*(1), 26–35. https://doi.org/10.1080/03632415.2013.748551

Verberk, W. C. E. P., Siepel, H., & Esselink, H. (2008). Life-history strategies in freshwater macroinvertebrates. *Freshwater Biology*, *53*(9), 1722–1738. https://doi.org/10.1111/j.1365-2427.2008.02035.x

Villalobos-Jiménez, G., & Hassall, C. (2017). Effects of the urban heat island on the phenology of Odonata in London, UK. *International Journal of Biometeorology*, *61*(7), 1337–1346. https://doi.org/10.1007/s00484-017-1311-7

Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J.-M., Hoegh-Guldberg, O., & Bairlein, F. (2002). Ecological responses to recent climate change. *Nature*, *416*(28), 389–395.

Wang, T., Hamann, A., Spittlehouse, D., & Carroll, C. (2016). Locally downscaled and spatially customizable climate data for historical and future periods for North America. *PLoS ONE*, *11*(6), e0156720. https://doi.org/10.1371/journal.pone.0156720

Warren, D. R., Robinson, J. M., Josephson, D. C., Sheldon, D. R., & Kraft, C. E. (2012). Elevated summer temperatures delay spawning and reduce redd construction for resident brook trout (*Salvelinus fontinalis*). *Global Change Biology*, *18*(6), 1804–1811. https://doi.org/10.1111/j.1365-2486.2012.02670.x

Wissinger, S. A. (1988). Life history and size structure of larval dragonfly populations. *Journal of the North American Benthological Society*, *7*(1), 13–28.

Woods, T., Kaz, A., & Giam, X. (2022). Phenology in freshwaters: A review and recommendations for future research. *Ecography*, *2022*(6), e05564. https://doi.org/10.1111/ecog.05564

Woods, T., & McGarvey, D. J. (2022). Data from: Drivers of Odonata flight timing revealed by natural history collection data. *Dryad Digital Repository*, https://doi.org/10.5061/dryad.5hqbzkh8k

Yoshimura, M. (2012). Effects of forest disturbances on aquatic insect assemblages. *Entomological Science*, *15*, 145–154. https://doi.org/10.1111/j.1479-8298.2011.00511.x

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Woods, T., & McGarvey, D. J. (2022). Drivers of Odonata flight timing revealed by natural history collection data. *Journal of Animal Ecology*, *00*, 1–14. https://doi.org/10.1111/1365-2656.13795