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RESEARCH ARTICLE

Investigating odonates' response to climate change in Great Britain: A tale of two strategies

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Abstract

Aim: Species are largely thought to maintain broadly static niches over time, an assumption underpinning much theoretical ecology including the implementation of ecological models to project species' current and future distributions. Here, we assess niche conservatism in odonates in Great Britain over the past six decades by simultaneously quantifying changes in species geographic distribution and evaluating temporal trends in species realised climatic niche.

Location: Great Britain.

Methods: Distributional changes were assessed by calculating changes in species distribution centres and deriving occupancy trends. Changes in climatic niches were assessed using a principal component analysis to quantify niche overlap, using information on both climate averages and extremes.

Results: We show that dragonflies and damselflies displayed distinct responses to changing climatic conditions. Dragonflies shifting to higher latitudes maintained, on average, greater consistency in their climatic niches, providing evidence for climate tracking. Greater climate niche flexibility and increased occupancy over time, on the other hand, were more common in damselflies.

Main Conclusions: We unveil evidence for climatic niche divergence in damselflies on a national scale, casting doubt on the relevance of species distribution models for predicting the impacts of climate change on this, and potentially other, groups of species. More broadly, our results call for more multi-species temporal comparisons of spatial distributions and climate niches during recent periods of changes in climatic conditions to improve our ability to contrast species' vulnerability risk to the ongoing climate crisis.

KEYWORDS
biodiversity monitoring, climate change, niche conservatism, niche divergence, range shifts, species' redistribution, wildlife management

1 | INTRODUCTION

Species redistribution is one of the swiftest responses to rapid changes in climatic conditions (Scheffers et al., 2016). As climate changes, species often persist by shifting their geographic range across the landscape to track their ecological niche. The study of the factors underpinning species redistribution is a rapidly developing research area (Bonebrake et al., 2017), with an abundance of evidence that species have already shifted their geographic ranges in response to recent anthropogenic climate change, with potentially profound social and economic impacts (Pecl et al., 2017).

Opportunities for range shifts are known to be influenced by many factors in addition to climate, such as species interactions, dispersal, land use, topography and landscape connectivity. Consequently, many species may not be able to keep pace with climate change, struggling to disperse rapidly enough (Jezkova & Wiens, 2016) or to navigate our increasingly human-modified landscapes. Posed with such challenges, these species may instead shift their ecological niche whilst maintaining a stable geographic distribution–as opposed to maintaining a stable realised niche in environmental space and shifting their geographic range (Wang et al., 2023).

Historically, niche conservatism–the tendency of a species' niche to remain unchanged over time (Pearman et al., 2008)–has largely been assumed when investigating or predicting species biogeographical patterns and informs much theoretical ecology, underpinning in particular ecological niche modelling efforts (Guisan et al., 2014; Jezkova & Wiens, 2016). Nevertheless, studies investigating niche conservatism have found disparate results (Guisan et al., 2014), with evidence suggesting that species' niches can shift across different environments or timescales, rather than remaining static (Jezkova & Wiens, 2016).

Temporal comparisons of climate niches across sets of related species during periods of rapid changes in climatic conditions could represent an effective way to explore how common shifts in species' niche are. This approach, however, has received little attention to date (Lustenhouwer & Parker, 2022), having been largely confined to plants (Wang et al., 2023) and birds (Nadeau & Urban, 2019; Ralston et al., 2017). Comparing responses across species enables researchers to identify the factors shaping species' ability to track or adapt to climate change, which could prove crucial for determining and predicting species risk to ongoing, rapid anthropogenic climate change.

To address this knowledge gap, we investigate species' geographic and climate niche shifts in Great Britain's odonates (dragonflies and damselflies). Great Britain offers a wealth of biological records, with the UK being one of the most densely recorded countries worldwide (Powney & Isaac, 2015). Odonata, in particular, is perceived as a charismatic taxon with a vast repository of species distribution data and well-documented ecologies (Stoks & Córdoba-Aguilar, 2012). It has been recognised as a potential model taxon for investigating responses to climate change (Hassall, 2015), as it is particularly sensitive to environmental change and frequently employed as biological indicators for aquatic, and increasingly terrestrial, environments (Miguel et al., 2017). Research has already indicated that several European species' ranges are shifting or expanding northwards in correlation with recent warming (Olsen et al., 2022). Odonates have been shown to be on the move with climate change in the UK (Pettorelli et al., 2019), with arrivals of new species also documented (Cranston et al., 2023).

Based on the state of current knowledge on odonates, and the known variability in life histories in this taxon, we do not expect all odonates to exhibit niche conservatism over time (H1), with key differences in response to climate change expected between dragonflies and damselflies (Powney & Isaac, 2015). Species that show greater niche flexibility (i.e., higher level of change in their climate niche over time) could be expected to expand their distribution to new geographic areas whilst maintaining occupancy in areas experiencing changes in climatic conditions. As such, we also expect a positive correlation between niche flexibility, changes in overall range size and level of range expansion (Ralston et al., 2017; Tirozzi et al., 2022; Di Cecco & Hurlbert, 2022; H2).

2 | METHODOLOGY

2.1 | Species occurrence data

Species occurrence records for odonates in Great Britain between 1961 and 2020 were downloaded from both the Global Biodiversity Information Facility (GBIF, 2023) and the National Biodiversity Network Atlas (British Dragonfly Society Recording Scheme, 2023; NBN Trust, 2023). Occurrence records were prepared using the function clean_coordinates within the R package 'CoordinateCleaner' v.2.0–20 (Zizka et al., 2021); duplicate observations and observations with latitude and longitude values set to zero were removed. Coordinates matching country centroids and biodiversity institutions were also removed using the reference data within the package, as these are likely incorrect records or records of captured individuals.

2.2 | Climate data

Monthly minimum and maximum temperature as well as monthly precipitation were accessed from the Met Office at a 1 km resolution (Hollis et al., 2019), covering the periods 1961–1980 (T1) and 2001–2020 (T2). This data was used to generate a series of 19 bioclimate variables using the biovars function in the R package 'dismo' v.1.3–14 (Hijmans et al., 2021); the variables were calculated for each year and then averaged for each time period. These 19 climate variables were chosen to be biologically meaningful and informative for odonatan distributions (Abbott et al., 2022; Collins et al., 2017), capturing information on annual trends, seasonality and limiting environmental factors.

Despite their potential importance in shaping species distribution (Huang et al., 2017), climate extremes have received little attention when assessing the effects of climate change on biodiversity (Garcia et al., 2014). To address this, we also considered

six indices that capture the intensity and frequency of climate extremes, based on the work from the Expert Team on Climate Change Detection and Indices (ETCCDI). These indices were calculated from daily temperature and precipitation data accessed from the Met Office (Hollis et al., 2019), and included: the maximum of daily maximum temperature (TXx); the minimum of daily minimum temperature (TNn); the number of frost days (FD, daily minimum temperature below 0°C); the number of summer days (SU, daily maximum temperature above 25°C); the number of consecutive dry days (CDD, precipitation below 1 mm) and the maximum 5 days precipitation (Rx5day, maximum precipitation in five consecutive days). As with bioclimate variables, each index was calculated on an annual basis and then averaged for each time period. Calculations were completed using R package 'ClimInd' v.0.1–3 (Reig-Garcia et al., 2021).

2.3 | Assessing distribution and occupancy

The downloaded odonatan occurrence data primarily consists of opportunistically sampled presence-only data whereby sampling effort and probability of detection are not consistent over a given area or across time. Left unaccounted for, such sampling bias can severely distort results when mapping species habitat requirements or investigating species trends (Bird et al., 2014; Johnston et al., 2021). One way to overcome this unevenness of recording–termed by Prendergast et al. (1993) 'the recorder effort problem'–is to model the data collection process (Isaac et al., 2014).

We employed the Frescalo method (FREquency SCAling Local; Hill, 2012) to correct for these data biases and to derive information on odonates distribution in Great Britain, using the Frescalo function within the R package 'sparta' v.0.2.19 (August et al., 2015). In brief, Frescalo relates records of species to a suite of local benchmark species of other odonates that vary between neighbourhoods based on the similarity between record sites. Using this method, the number of species expected to be recorded in each British National Grid hectad (10 km^2 British National Grid Squares) can be estimated, based on the local benchmark species within the neighbourhood and the level of similarity in landcover between sites based on the 2015 UK Land Cover Map data accessed through the R package. Sampling effort is calculated for each British National Grid hectad. By comparing the number of observed species for each period to the value predicted after accounting for variation in recording effort, a subset of adequately sampled hectads can be identified. These adequately sampled hectads are defined as those which reported at least 25% expected species at both T1 (1961–1980) and T2 (2001–2021), following previous research (Hordley et al., 2023). For further details, see Hill (2012).

For the purpose of this study, local benchmark species are defined as the 27% most frequent odonatan species in a given neighbourhood, in accordance with previous research (Eichenberg et al., 2021; Hill, 2012). Time factors (TFactors) were generated to

assess the reporting rate of a focal species at a given time relative to these local benchmark species. As it is advised that benchmark species should be those whose occupancy is relatively stable over time, a re-analysis was conducted, which excluded the 5% most strongly increasing or decreasing species as potential benchmark species (Hill, 2012).

Changes in occupancy, defined as changes in the number of hectads where a given species is expected to be present (Hill, 2012), can be analysed by pooling information over a series of short or long time periods. Here, we compared the outcomes of both approaches. In one approach, TFactors were extracted for each 5 years time periods throughout the duration of the study period (1961–2020) and, from these, occupancy trends were extracted through linear modelling of TFactors. T-tests were applied to determine the significance of any trend in occupancy. In the other, occurrences were pooled into two time periods (T1 and T2) and associated TFactors for these two periods were calculated, with Z-tests applied to determine significant differences. Choosing T1 and T2 as time periods meant that results were directly comparable with those from the distribution and climatic niche analysis. Species were identified as displaying significant trends in occupancy if either the 5 years approach or the two time periods approach yielded significant results.

2.4 | Geographic distribution change

Species geographic shift was analysed in terms of the change in the geographic centre of species' distribution between periods T1 and T2–a simplistic measure that nonetheless allows for a multidirectional assessment. The mean latitude and longitude for each time period were extracted using QGIS v.3.22.3 from species presence observations at 1-km British National Grid resolution, including only those occurrences within the previously determined adequately sampled hectads. The distance and direction between species centre at T1 and T2 were then determined using R package 'geosphere' v.1.5–18 with the functions distVincentyEllipsoid and bearing, respectively (Hijmans, 2022). This method gives an approximation of species distributional change throughout Great Britain and provides an indication of the distance and rate with which such changes can occur over a 40 years period that can be compared across species. Altitude was derived from the OS Terrain 50 digital terrain model available on the OS OpenData Downloads platform (https://osdatahub.os.uk/downloads/open). Altitude was extracted for each of the species' observations using QGIS and the difference in mean altitude between periods was computed for each species.

Average distances between the central position at T1 and T2, as well as change in altitude, were compared between damselflies and dragonflies using a Mann–Whitney U test. The direction of shift for each species was determined and analysed through a circular statistics approach conducted using the R package 'CircStats' v.0.2–6 (Lund & Agostinelli, 2018). A Watson two-sample test of

homogeneity was calculated to investigate if there was any difference in the direction of species shifts between dragonflies and damselflies; this test is a non-parametric rank-based test that has been recommended for use by Landler et al. (2021) for comparing two samples of circular biological data. In addition, a Rayleigh test of uniformity was applied to determine whether species movements followed a northwards direction (i.e., with an alternative hypothesis specified at mean=0°) and whether dragonflies or damselflies exhibit uniform distributions. The functions circ.mean, circ.disp, r.test, v0.test and watson.two within 'CircStats' were employed for this analysis.

2.5 | Climatic niche change

Species' niche change between the periods considered was determined using an ordination approach, which has been shown to quantify niche overlap more accurately than reciprocal ecological niche models when investigated using virtual species (Guisan et al., 2014). Based on direct species observations, the difference in the climatological attributes of the sites where each species was recorded in each period was compared across the available environmental space (i.e., the climatological conditions throughout the study area across both time periods), as opposed to the geographic space.

To reduce the dimensionality of the available climatic data, a principal component analysis (PCA) was conducted for the 15 temperature and 10 precipitation variables, calibrated with data for the entire study area across both periods. The first two principal components were retained from the PCA, capturing 77.2% of the variability across all climate data. PC1 accounted for 58.7% of the variance and PC2 for 18.5%. For PC1, the highest positive correlation was with precipitation of the driest month (Bio14) and quarter (Bio17) and the highest negative correlation was with Bio5 (maximum temperature of the warmest month) and Bio10 (mean temperature of warmest quarter). This component can thus be understood as contrasting wet conditions from the warmest ones. The second principal component integrates information relative to the coldest conditions within a year with major contributions from seven temperature variables, with strong positive correlations with TNN (minimum of daily minimum temperature), Bio6 (minimum temperature of coldest month) and Bio11 (mean temperature of the coldest quarter) and a strong negative correlation with FD (number of frost days). Further details are provided in Appendix S1 in the (Table S1, Figure S1 and Figure S2).

PCA scores for the entire study area and each species occurrence during both time periods were subsequently projected into a grid of 1000×1000 cells bounded by the maximum and minimum PCA component scores across both periods–that is, the gridded climate space. This methodology–calibrating the PCA with climate data from T1 and T2 combined and subsequently calculating species' PCA scores–means that the differences in position along the principal components discriminate differences between the T1 and T2 climate space, following previous temporal analyses (Ralston

et al., 2017; Sillero et al., 2022; Tirozzi et al., 2022). A smooth kernel density function was applied to estimate the density of species occurrences in each cell of the climate space, correcting for the prevalence of the environments within the species range, as an additional measure to account for sampling bias and to ensure the results remain independent of the resolution of the climate grid chosen (Broennimann et al., 2011).

The niche analysis was conducted in R with the package 'ecospat' v.3.5.1 (Broennimann et al., 2023). To determine niche change over time, Schoener's D index of niche overlap was calculated, chosen for its simplicity and long history of use (Warren et al., 2008). Schoener's D, within the context of this investigation, provides a measurement of the overlap between the climatic niche experienced by each species at T1 and T2 ranging from 0 (no overlap) to 1 (complete overlap). This index is calculated by quantifying, for each grid cell in the climate space, the difference in smoothed kernel densities of species occurrence between periods. The niche comparison between periods was thereupon decomposed into three components to provide additional information about the drivers of niche change (Tirozzi et al., 2022): (i) niche expansion, the proportion of species' niche present at T2 only; (ii) niche contraction (often termed niche unfilling), the proportion of species' niche no longer present at T2 and (iii) niche stability, the proportion of niche present at both time periods. Statistical tests for niche similarity between periods were used to determine whether observed climatic niches at T2 were statistically similar to the observed climatic niches at T1 using the ecospat.niche.similarity function within ecospat. The hypothesis for niche conservatism was tested by comparing observed climatic niches at T1 with random simulations of species' niches at T2 within the available climate space with the same kernel density distribution as T1, following the approach set out by Broennimann et al. (2011). By repeating these simulations 100 times, a null distribution of species overlap values was generated to determine if observed species niche overlaps are more statistically similar (niche conservatism) or not (niche divergence) than random, based on a significance threshold of 0.05. To determine whether there was any significant difference between dragonflies and damselflies in the proportion of species whose niche was conserved over time, a two-proportion Z-test was conducted in R.

The overall approach–calculating niche overlap, determining niche dynamic indices and testing for niche conservatism through niche similarity testing–was first conducted including the full range of climatic conditions across both time periods. This was to provide a complete picture of the climatic niche changes that have occurred throughout the entirety of Great Britain, including novel climatic conditions and changes between the first and the second time periods. This analysis was then repeated at the intersection of climates between the two time periods, termed the analogue climate analysis, to evaluate species niche dynamics considering only the climatic variability available during both periods thereby excluding niche shifts resulting from variation in the climatic space accessible to species (Tirozzi et al., 2022); subsequent results refer to this method unless specified otherwise.

2.6 | Geographic versus climatic niche shifts

Kendall correlation analyses were conducted to look for any significant relationship between geographic and climatic niche shifts; this type of analysis was deemed an appropriate non-parametric correlation test able to accommodate ties (Tirozzi et al., 2022). Correlation tests were run between species overlap and geographic distribution change, including distance of centroid shift and change in latitude and longitude of these distribution centres. Kendall correlation tests were also employed to determine whether there was any significant correlation between species occupancy trends and niche dynamics, including Schoener's D index of climate niche overlap, expansion and contraction.

3 | RESULTS

Of a total of 37 species of odonates considered, 29 species (78.4%) displayed significant changes in occupancy between 1961–1980 (T1) and 2001–2020 (T2). Sixteen (43.2%) of them showed significant increases in the area they occupy in Great Britain, whilst 13 species (35.1%) showed significant decreases in this parameter. Species' centre of distribution shifted between 3.4 km (*Coenagrion hastulatum* Charpentier, 1825) and 230.8 km (*Leucorrhinia dubia* Vander Linden, 1825) over the study period, equating to a rate of between 0.09 km and 5.8 km a year. Overall species shifts were in an approximately northwards direction (circular mean of $10.5 \pm 25.1°$), ranging primarily from an approximately northwest direction (300.4°, *Somatochlora arctica* Zetterstedt, 1840) to a northeast direction (76.7°, *Lestes dryas* Kirby, 1890), with only one species shifting southwards (220.2°, *Aeshna isosceles* Müller, 1767; Table 1; Figure 1). Rayleigh's test for uniformity supported the presumption that species do have a tendency to shift in a northwards direction ($p < .001$). Both dragonflies and damselflies occurred at higher altitudes on average at T2 than at T1 (with a mean change 3.36 ± 22.2 m and 2.64 ± 17.5 m between periods, respectively), but with high variability between species. Eight damselflies and seven dragonflies had a lower mean altitude at T2 than T1 (40.5% total species).

Our results support the hypothesis that not all odonates in Britain exhibited niche conservatism over the period considered (H1). Sixteen species (43.2%) displayed statistically more similar climate niches between T1 and T2 than expected by chance, indicating niche conservatism; but the remaining 21 species (56.8%) showed signs of niche divergence. When considering the full range of climatic variability across Great Britain, 20 species exhibited niche conservatism (54.1%). Schoener's D index of climate niche overlap between time periods varied from 0.00 (*Aeshna isosceles*) to 0.43 (*Libellula depressa* Linnaeus, 1758). Four species of dragonfly (*Aeshna isosceles*, *Gomphus vulgatissimus* Linnaeus, 1758, *Libellula fulva* Müller, 1764, *Somatochlora metallica* Vander Linden, 1825) and two species of damselfly (*Coenagrion hastulatum*, *Lestes dryas*) had expansion values over 80%. Niche contraction was typically low,

with 21 species (56.8%) having less than 20% niche contraction and 26 species (70.3%) having less than 30% contraction. The species with the highest proportion of niche contraction were *Aeshna isosceles* (100%), *Lestes dryas* (96.6%), and *Coenagrion hastulatum* (66.9%; Figure 2).

As expected, comparing dragonflies and damselflies unveiled several key differences between the two. For example, the 10 species with the greatest distribution shift in terms of distance between distribution centres were all dragonfly species. Dragonflies shifted further than damselflies on average (Mann–Whitney *U* test, $p = 0.02$) with annual mean shifts of 1.9 ± 1.18 km and 1.2 ± 0.49 km, respectively. The distributions of the direction of shift of both dragonflies and damselflies were non-random (Rayleigh test, $p < .001$), but these were not consistent between both groups of species (Watson two-sample test, $p < .01$): dragonflies shifted in a mean northwards direction (357.4°, SD = 22.4°) whilst damselflies shifted, on average, a mean northeast direction (30.3°, SD = 23.4°). However, there was no statistical difference in change of altitude (Mann–Whitney *U* test, $p = .55$) or the proportion of species with divergent niches ($z < 0.001$, $p = 1$) between dragonflies and damselflies.

As expected under H2, an overall significant increase in occupancy was correlated with an overall decrease in climatic niche overlap between T1 and T2 for damselflies (Kendall correlation, $\tau = -0.54$, $p = .005$). For that group of species, we moreover found a positive correlation between occupancy trends and climatic niche expansion ($\tau = 0.52$, $p = .007$), which was expected, but also a positive correlation between occupancy trends and contraction ($\tau = 0.43$, $p = .03$), which was less expected. For dragonflies, however, we found no significant correlation between occupancy trends and niche overlap ($\tau = 0.07$, $p = .67$), expansion ($\tau = 0.12$, $p = .44$) or contraction ($\tau = 0.004$, $p = .98$) (Figure 3).

For dragonflies, a Kendall correlation test revealed a significant positive correlation between niche overlap and change in longitude ($\tau = 0.32$, $p = .04$) but no significant correlation with change in latitude ($\tau = 0.07$, $p = .63$), change in altitude ($\tau = -0.22$, $p = .16$), or distance between distribution centres ($\tau = 0.06$, $p = .71$). Whereas considering the full range of climate values and novel climates at T2 revealed a significant positive correlation between niche overlap and change in latitude ($\tau = 0.33$, $p = .03$). Dragonflies with the greatest shifts towards higher latitudes and longitudes thus had the largest consistency in climatic niche between T1 and T2. For damselflies, no Kendall correlation was detected between occupancy trends and distance between distribution centres ($\tau = 0.10$, $p = .59$), nor change in latitude ($\tau = 0.24$, $p = .46$), longitude ($\tau = 0.14$, $p = .22$) or altitude ($\tau = -0.31$, $p = .11$).

4 | DISCUSSION

This study demonstrates for the first time how recent changes in climatic conditions triggered alternative responses by odonates in Great Britain, with some species shifting their geographic distribution to track preferred climatic conditions in space, and others

TABLE 1 Odonates geographic distribution change including annual occupancy trends (ordered from greatest increase in occupancy to greatest decrease, with 0 indicating no significant change detected) and species shift in distribution centre in terms of annual distance and direction of shift.

Species	Suborder	Annual occupancy change (%)	Annual centroid shift: distance (km)	Centroid shift: direction
Anax imperator	Anisoptera	0.75	2.20	22° (N)
Sympetrum sanguineum	Anisoptera	0.60	1.90	18° (N)
Aeshna mixta	Anisoptera	0.53	1.94	353° (N)
Aeshna isoceles	Anisoptera	0.42	0.67	220° (SW)
Libellula depressa	Anisoptera	0.41	2.20	26° (NE)
Orthetrum cancellatum	Anisoptera	0.33	1.70	2° (N)
Brachytron pratense	Anisoptera	0.32	1.97	34° (NE)
Erythromma najas	Zygoptera	0.31	1.06	17° (N)
Libellula quadrimaculata	Anisoptera	0.30	2.16	23° (NE)
Libellula fulva	Anisoptera	0.20	1.38	12° (N)
Somatochlora arctica	Anisoptera	0.19	0.29	300° (NW)
Orthetrum coerulescens	Anisoptera	0.18	2.05	358° (N)
Lestes dryas	Zygoptera	0.15	1.77	77° (E)
Ischnura pumilio	Zygoptera	0.15	0.93	352° (N)
Platycnemis pennipes	Zygoptera	0.14	1.17	27° (NE)
Calopteryx splendens	Zygoptera	0.12	1.62	26° (NE)
Aeshna caerulea	Anisoptera	0.00	1.03	342° (N)
Aeshna cyanea	Anisoptera	0.00	1.30	355° (N)
Aeshna juncea	Anisoptera	0.00	3.36	353° (N)
Calopteryx virgo	Zygoptera	0.00	1.70	56° (NE)
Coenagrion hastulatum	Zygoptera	0.00	0.09	326° (NW)
Coenagrion mercuriale	Zygoptera	0.00	0.71	323° (NW)
Gomphus vulgatissimus	Anisoptera	0.00	1.41	315° (NW)
Somatochlora metallica	Anisoptera	0.00	2.84	337° (NW)
Sympetrum danae	Anisoptera	−0.15	3.52	349° (N)
Ceriagrion tenellum	Zygoptera	−0.24	0.80	71° (E)
Cordulegaster boltonii	Anisoptera	−0.24	1.57	6° (N)
Cordulia aenea	Anisoptera	−0.25	0.90	352° (N)
Lestes sponsa	Zygoptera	−0.29	1.93	11° (N)
Coenagrion pulchellum	Zygoptera	−0.33	1.38	48° (NE)
Sympetrum striolatum	Anisoptera	−0.41	1.75	25° (NE)
Leucorrhinia dubia	Anisoptera	−0.41	5.77	344° (N)
Pyrrhosoma nymphula	Zygoptera	−0.48	1.40	50° (NE)
Enallagma cyathigerum	Zygoptera	−0.51	0.86	71° (E)
Aeshna grandis	Anisoptera	−0.65	0.72	13° (N)
Coenagrion puella	Zygoptera	−0.78	1.55	28° (NE)
Ischnura elegans	Zygoptera	−1.11	0.98	33° (NE)

shifting their realised climatic niche. Contradictory to previous assumptions that species niches remain consistent over time, we found evidence that several odonates have not retained statistically similar realised climatic niches in Great Britain during a period of recent climate change. For damselflies, species with greater differences in their realised climatic niche between periods correlated positively with an increase in species' occupancy, suggesting that niche flexibility underpinned the dispersion of damselflies into new geographic areas. For dragonflies, species distributional changes towards higher latitudes and longitudes enabled those species to maintain a greater climatic niche overlap between periods, providing evidence for climate tracking. Overall, this research provides a framework for assessing multidirectional distribution shifts alongside climate niche dynamics.
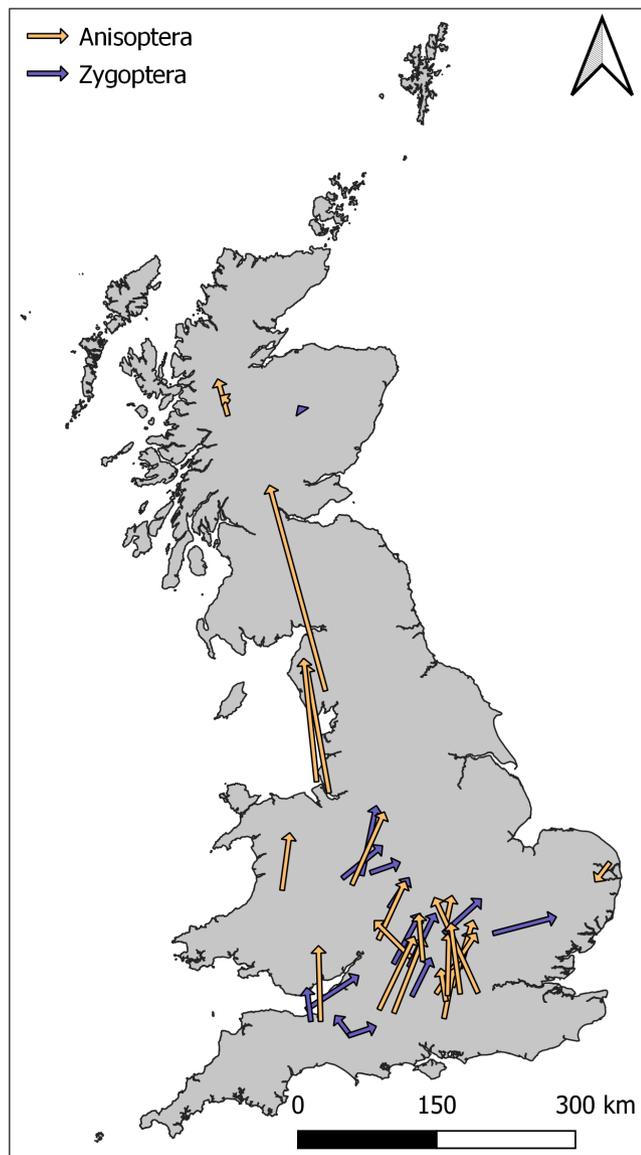
FIGURE 1 Shifts in dragonflies (Anisoptera) and damselflies (Zygoptera) distribution centre between periods T1 (1961–1980) and T2 (2001–2020).

FIGURE 2 Kendall correlation between species occurrence trends and species climatic niche dynamics (namely Schoener's D overlap index on the top, niche expansion in the middle and niche contraction on the bottom).

Species distribution shifts with climate change have been widely documented for a range of species, including odonates. Several European species have been reported to shift northwards with recent climatic warming (Olsen et al., 2022), with odonates being among the taxa showing the strongest polewards range expansions (Bybee et al., 2016). Our centroid change analyses showed that species shifted up to 5.8 km annually, which is comparable to previous studies (Hickling et al., 2005). Species exhibiting niche fidelity between periods–with statistically similar climatic niches between periods and a large proportion of niche overlap–might be concluded to be tracking climatic change across the landscape, if there is any evidence of a distributional change. Yet it might not always be the case that the species with the greatest shift or the greatest change in latitude and longitude have the most consistent climatic niche as species' specific climatic tolerances might not always necessitate
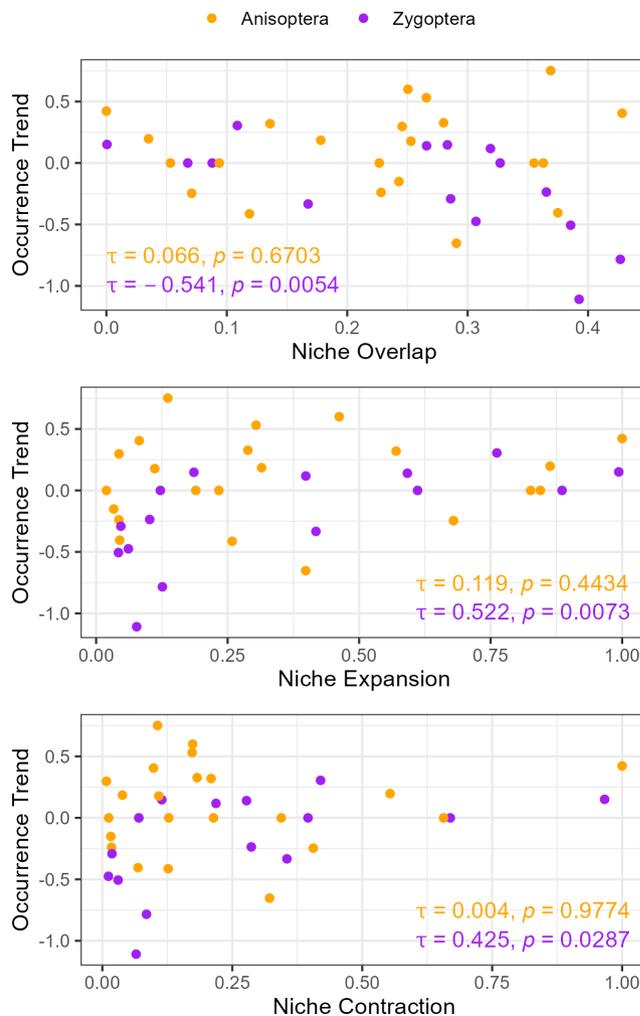
large distributional change. Species on the move with climate change might therefore be classified as any species with a statistically similar niche during a period of climatic change that has had a significant positive trend over the same period or whose distribution centre has altered to a certain degree.

Dragonflies shifted greater distances than damselflies on average, likely because they are typically larger, faster and more robust than damselflies (Cancellario et al., 2022; Olsen et al., 2022). Dispersal capacity has been previously found to constrain species ability to geographically track climate change (Littlefield et al., 2019; Thomas et al., 2010) and might similarly substantiate an important consideration for climatic niche change analyses. Whilst species with greater dispersal abilities might have greater capacity to shift into newly available climatic space, those with lower dispersal ability, such as damselflies, may not be able to shift geographically in pace with climatic change and may instead be left behind in unsuitable climate. Considering these geographic and climatic niche changes alongside change in species occupancy allows
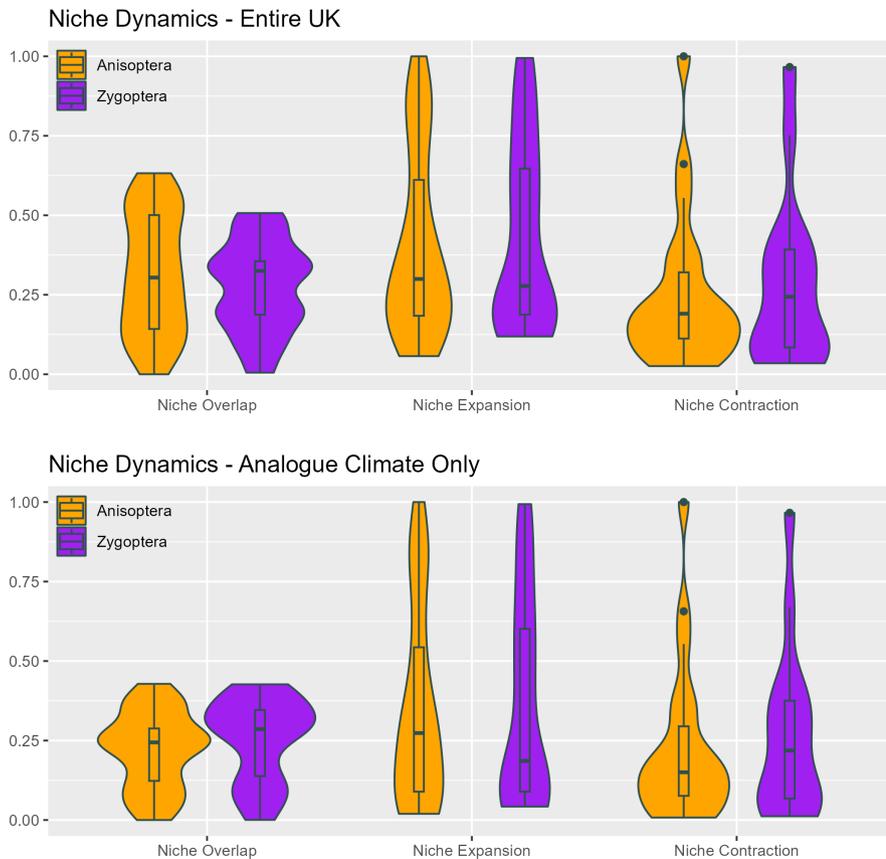
an examination of which species are experiencing the greatest increase or decline in their distribution in Great Britain and an assessment of the relative success of their varying responses. Overall, our results imply that the best dispersers may be more able to maintain consistent climatic niches over time, whilst species with narrow thermal tolerances and low dispersal ability may be more likely to display climatic niche flexibility.

This study refers to species realised climatic niche based on the climate variables throughout species geographic distribution within Great Britain, and so all values refer to species' niche dynamics on a national scale and are not informative of species' climatic niche within their wider distribution. As such, species which have not exhibited a statistically similar niche between periods within Great Britain, could have exhibited niche conservatism overall had their entire geographic distribution been considered beyond this national boundary. To aid the interpretation of these national findings, species realised niche conservatism was computed considering an analogue climate analysis–including only the climatic variability available during both time periods examined. Thereby, even though species might occupy a broader climatic range outside of Great Britain, any changes of species' niche within a given limited set of climatic conditions theoretically available to species can be established. Furthermore, our findings indicate differences in species niche dynamics within a geographically isolated landmass and these results are relevant to national-level studies, a scale that distribution models and climate change assessments are often applied.

Our results may have important ecological and conservation consequences as they cast doubt on typical assumptions underpinning species distribution modelling and other investigations where species climate niche is thought to remain broadly stable over time at national scales. They also suggest that efforts to theorise future species distributions based on vectors of climate change might prove to be an inappropriate basis for allocating conservation efforts, without prior consideration as to whether species climatic niche can change over time. Such findings are in accordance with other investigations that have found shifts in the realised climatic niches of plants, birds, reptiles, amphibians and mammals during recent climate change (Enriquez-Urzelai et al., 2019; Sillero, 2021; Sillero et al., 2022; Wolf et al., 2016). Broennimann et al. (2011) advocated for avoiding the projection of niche models outside the calibration area unless niche overlap is high (Schoener's $D \approx 1$) and tests for niche equivalency could not be rejected; here even those 16 species which exhibited statistically similar niches over time had low niche overlap (maximum 0.43) and would not meet such requirements to adequately project future distributions within Great Britain under continued climate changes. The application of SDMs for predicting odonatan distributions based on similar bioclimatic data using national scale occurrence information such as from the British Dragonfly Society, should therefore be implemented with care; whether species are exhibiting niche flexibility under climatic change, or whether national distribution data is inadequate in defining species' climatic niche, projections may not be accurate for Odonata and potentially other species. SDMs based

on climatic and environmental data calibrated with national occurrence data within Great Britain have been previously employed for Odonates (Geary & Von Hardenberg, 2020), other invertebrates (Bourhis et al., 2023; Giannini et al., 2012; Oliver et al., 2012), as well as plants, birds, reptiles, amphibians and mammals (Buxton et al., 2021; Oliver et al., 2012; Rapacciuolo et al., 2014; Rodríguez-Roy et al., 2023); including species of conservation concern (the grey long-eared bat *Plecotus austracius*; Razgour et al., 2011) and invasive species (Reeve's muntjac deer *Muntiacus reevesi*; Freeman et al., 2022). Further temporal analyses of climatic niche changes within broader geographic and temporal scales would be advantageous to further evaluate niche conservatism.

It should also be emphasised that differences here refer to species realised climatic niche that is restricted by historical and biotic factors and is a subset of the broader environmental conditions that species could potentially occupy–the fundamental niche (Jezkova & Wiens, 2016). Isolating these aspects would provide a greater understanding of species response to climate change; however, this has proved problematic to date (Guisan et al., 2014). The reported niche shifts experienced by some species may indicate a change in fundamental niches resulting from evolutionary adaptation to climate change. But these shifts could also be due to species being unable to keep pace geographically to remain within their optimal climate conditions. Alternatively, it may also be the case that species displaying changes in their climate niches over the period considered are simply not limited by these climatic factors within their Great British distribution. Further research into the specific climatic tolerance of the species considered in this study would enable a greater understanding of the mechanisms underpinning our findings.

Although odonatan suborders demonstrated significantly different responses to climate change, we found a noticeable level of variability between species in each suborder, in line with previous reports on species redistribution (Angert et al., 2011; Hill et al., 2002). For example, niche conservatism and niche divergence were both found among dragonfly and damselfly species, corroborating trends found in other temporal assessments of realised climatic niches (Tirozzi et al., 2022). This level of interspecific variation, and the lack of congruence in responses across phylogenetically similar groups, calls for more research across a wider set of taxa on the factors promoting niche conservatism or niche divergence in response to climate change. Such knowledge will be key to inform wildlife management as our climate continues to alter.

CONFLICT OF INTEREST STATEMENT
None declared.

PEER REVIEW
The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13816.

DATA AVAILABILITY STATEMENT
The data that support the findings of this study are openly available on Dryad, at https://doi.org/10.5061/dryad.v41ns1s3h

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BIOSKETCH

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Author contributions: D.O. collected and analysed the data; D.O. and N.P. led the writing; all authors contributed to the writing of the manuscript.

SUPPORTING INFORMATION

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