Body colour drives optimal insect phenology via thermoregulation

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Abstract

Phenology, the seasonal timing of life events, is an essential component of biodiversity which partly results from species´ life cycle synchronisation to optimal seasonal moments[1]. The mechanisms involved are, however, complex[2–4] and understudied which limits our ability to predict biodiversity responses to global change drivers[5]. Thermoregulation is crucial for shaping diversity patterns, particularly in ectotherms such as insects. Dark-bodied species are able to inhabit colder areas due to their higher absorbance of solar radiation – a pattern known as Thermal Melanism Hypothesis (TMH). Thermal melanism is well supported to drive spatial variation of insect diversity[6], but whether it also may influence phenological patterns remains unexplored. Here we show, using a unique dataset of thousands of spatio-phenologically explicit dragonfly and damselfly assemblages, that dragonfly body colour lightness patterns respond to seasonal variation of solar radiation, with darker early- and late-season assemblages and lighter mid-season assemblages. This suggests that colour-based thermoregulation can determine insect phenology in relation to optimal seasonal conditions. We also show that the phenological pattern of dragonfly colour lightness advanced significantly over the last 30 years. Together with static nature of solar radiation, our results suggest that global warming may drive flight periods to suboptimal seasonal conditions. Our findings open a new research avenue for a more mechanistic understanding of phenology and spatio-phenological impacts of climate warming on insects and other ectotherms.

Main Text

Improving our capacity to predict biodiversity changes requires a profound understanding of the mechanisms that drive the variation of life in space and time. Over the last decades, ecological research has greatly advanced in documenting spatial patterns of biodiversity at large scales (e.g.[7,8]) as well as their underlying environmental drivers[9–11]. Besides spatial patterns, many taxa show characteristic seasonal replacement of species caused by their particular timing of life events, i.e. species' phenologies. The mechanisms driving phenological patterns of diversity are, compared to those driving spatial diversity, much more complex and poorly understood, which critically limits conclusions about the spatio-temporal changes that underpin species responses to climate change[5].

Insects constitute the vast majority of terrestrial animal species, and their direct dependence on ambient temperature for development, reproduction and activity render them particularly vulnerable to temperature changes. In temperate regions, insects show distinct seasonal timing of their activity periods[12]. Insect phenology results from a complex interaction between developmental constraints and environmental life cycle regulation[2–4], in which life cycles are synchronised to optimal seasonal moments where fitness is maximized – a process named phenological fundamental tracking[1]. Within this system, phenological events such as adult emergence are triggered by environmental cues that link to subjacent drivers of optimal timing[1] (Fig. 1a). For instance, emergence of butterflies may be triggered by certain temperature and photoperiod levels[2] that align to the seasonal appearance of their host plants[13]. Most phenological

research has so far focused on describing species-specific phenological events in response to environmental factors[14], but little is understood about the underlying mechanisms that may determine optimal timing[5,15]. Shifts in species´ phenologies constitute one of the most obvious consequences of climate change[16–18], with many insect groups showing advances in their flight periods. However, we do not understand their consequences for species, which could range from positive to negative – depending on whether species track shifting optimal seasonal conditions[19]. A failure to recognise the mechanisms underlying phenological patterns of diversity is a key knowledge gap in understanding the impact of climate change on natural systems[3,15,20].

Body colour is a key trait for thermoregulation, which is, in turn, a crucial mechanism regulating life cycles and occurrences of ectotherms[21]. Due to their lower reflectance, darker colours absorb more solar radiation than lighter ones[22], making darker bodies heat up faster. As a result, darker individuals and species are able to occur in colder environments than their light-coloured counterparts – a pattern known as Thermal Melanism Hypothesis[6] (TMH). TMH is well supported based on patterns of species' distributions and community composition in a broad range of ectothermic taxa, including reptiles[23] or insects such as ants[24], Lepitoptera[25,26] or dragonflies and damselflies[27,28]. The possible role of thermal melanism in determining insect phenology has never been assessed even though the environmental factors driving the TMH also characterise seasonality.

Here we test whether thermal melanism contributes determining insect phenological patterns of insects. We use Odonata (suborders dragonflies and damselflies) as study system because of their rich natural history record[29]. Odonata is one of the groups where the TMH has been most strongly supported, driving functional community assembly across Europe and North America[27,28]. The strength of thermal melanism in this warm-adapted[30] group is related to their high thermoregulatory requirements. Odonates rely on – energetically costly – flight for all their essential activities (displacement, foraging, reproduction), for which particularly the larger-bodied dragonflies require thoracic temperatures above ambient levels (e.g. 27–36°C[31]). Odonate diversity in temperate latitudes shows characteristic replacement of species´ flight periods over the warm months of the year (Fig. 1d) as a result of environmental regulation of species´ life cycles based on photoperiod and temperature cues together with developmental constraints (Fig. 1c). Whether certain underlying environmental drivers may determine optimal timing of flight periods remains to be understood.

We expected the same mechanisms driving ectotherms spatial diversity patterns to contribute to determining insect flight periods. Specifically, we expected (1) colour lightness of odonate assemblages (CL) to follow predictions of the TMH and show phenological variation in response to seasonal changes in solar radiation intensity and temperature. Furthermore, we expected (2) thermal melanism responses to be stronger in the larger dragonflies than in damselflies, based on their higher thermoregulatory requirements[31,32]. Following reported phenological advances in odonate flight periods[33,34], we expected (3) to see advances in the phenological pattern of CL over the last decades.

Recently available massive observational data allowed us to study spatio-phenological diversity patterns at unprecedented detail and extension. We downloaded a database of over one million odonate records for Great Britain[35]. After grouping observations within fine spatio-phenological units and controlling for sampling effort by using rarefaction curves, we obtained unique datasets of 8,159 and 4,134 ecologically meaningful assemblages of dragonflies and damselflies, respectively, between May and October from 1990 to 2020 (see Methods for details). Species´ body colour lightness was obtained from scientific illustrations[36], see[27,28]. To quantify assemblage-level body colour lightness (CL), we used community-weighted means[37], whose deviations from null expectations were then analysed in relation to the seasonal variation of the thermal environment. We also accounted for potential effects of phylogenetic relatedness as well as spatial autocorrelation (see Methods and Supplementary Fig. S3 and Fig. S5). We finally assessed changes in the phenological pattern of CL over the last 30 years to evaluate potential shifts in response to climate change.

We found colour lightness of dragonfly assemblages to vary as expected – both phenologically and with latitude (4th degree polynomial model: n = 8159, $F_{5,8153}$ =1147, R^2 = 0.41, P< 0.001; Fig. 2a, 2d). CL decreased linearly with latitude as predicted by the THM (Lat: t =−29.66, P< 0.001. Figure 2c), but the phenological effect was much stronger, with most explained variance (hierarchical partitioning: 84.8%) depending on the day of the year (Day: t = 15.55, P< 0.001; Day^2: t =−13.8, P< 0.001; Day^3: t = 11.92, P< 0.001; Day^4: t =−10.11, P< 0.001; Fig. 2d, 2e). CL increased from May until mid-June to early July, and then gradually decreased until the end of August from where assemblages remained constantly dark until the end of the season in October (Fig. 2e). The phenological pattern of dragonfly CL was consistent when applying spatially restricted null models (Supplementary Fig. S1) which allows isolating the phenological component (see methods for details). In contrast to dragonflies, CL of damselfly assemblages did not show latitudinal nor phenological patterns (Linear regression: n = 4134, $F_{2,4131}$ =1.5, P= 0.22; Fig. 2b, Supplementary Fig. S2). The observed spatio-phenological patterns of CL of both dragonflies and damselflies were robust to potentially confounding effects of phylogenetic non-independence of traits (see methods and Supplementary Fig. S3). Variation in CL of dragonfly assemblages followed expectations from the TMH as it increased non-linearly with solar radiation received (Fig. 3) (2nd degree polynomial model: n = 7901, $F_{2,7898}$ = 1789, R^2 = 0.31, P< 0.001; radiation: t =−14.92, P< 0.001; $radiation^2$: t = 23.14, P< 0.001). Spatio-phenological components and drivers of dragonfly CL were consistent to alternative definitions of assemblages (Supplementary Table S1).

Independent polynomial models of the phenological pattern of CL for each of the 24 years were consistent in their shape and explained between 34 and 48 percent of CL variation (all P< 0.001; Fig. 4a, Supplementary Fig. S4, Table S2). Phenological CL patterns advanced over years by 3.6 days per decade for the day when CL turned lighter than expected by chance (CL > 0) (Fig. 4b; $F_{1,22}$ =6.12, R^2 = 0.18, P= 0.021), and by 3.8 days per decade for the day when CL peaked (Fig. 4b; $F_{1,22}$ =11.25, R^2 = 0.31, P= 0.003). The day when CL became darker than expected by chance (CL < 0) and the length of the period where CL was lighter than expected by chance did not change over the years (Fig. 4b; $F_{1,22}$ =1.87, P=

0.185 and $F_{1,22}$ =1.34, P = 0.259, respectively). The magnitude of the peak with maximum CL showed a non-significant positive tendency (Fig. 4a, $F_{1,22}$=2.58, R^2 = 0.06, P = 0.122).

Patterns of darker species occurring at colder locations have so far supported thermal melanism as a crucial mechanism driving spatial patterns of ectotherm diversity[6]. Our study based on a uniquely high resolution and comprehensive dataset showed that colour lightness of dragonfly assemblages varied phenologically closely linked to seasonal changes in solar radiation, which provides for the first time support for the fundamental role of thermal melanism as a driver of phenological diversity patterns. Seasonal timing of dragonfly flight periods would therefore be optimized based on the relation between prevailing radiation and species´ thermoregulatory performance driven by body colour lightness. Medium and dark colours seemingly allow early and late flight season species to deal with corresponding intermediate and low radiation, respectively, while light colours enable mid-season species to thermoregulate well under highest seasonal radiation conditions.

Our analysis reveals a novel mechanistic explanation driving optimal timing of insect flight periods. One of the few similar studies showed that phenological changes of body sizes of wild bees in Catalonia (Spain) followed Bergmann´s rule, allowing larger species to deal with cold temperatures in early and late in the year[39]. In our study, radiation was the primary driver of the variation of CL, in line with its direct mechanistic effect on thermoregulation[22] and with previous studies on thermal melanism[23], although others also support the contribution of temperature[27] in combination with radiation[24,28].

The phenological operation of the TMH in dragonflies underlines the well-known dependency of adult odonates on thermoregulation[31]. However, we did not find any support for either spatial or phenological dimensions of the TMH in the suborder of the much smaller damselflies, which could be explained by the generally lower thermoregulatory requirements of small flying insects[32]. Smaller insect species have lower thoracic temperature requirements, possibly because flight is energetically less demanding in those[31]. A similar differential trait response driving phenology depending on group physiology was found in[39] where only the large – more endotherm – bees obey Bergmann's rule and not the small, more thermally conformist species. Previous assemblage-level support for TMH in odonates[27,28] may therefore be mostly driven by the dragonflies. Our contrasting results between taxonomically closely related taxa stresses the importance of accounting for the fundamental physiological difference of taxa in mechanistic ecological studies.

According to our analyses, the phenological pattern of dragonfly CL advanced over the last decades at rates of almost four days per decade, which aligns with previously reported advances of odonate flight periods of 1.5 days per decade in Great Britain[33], or 8.7 in the Netherlands[34]. In the latter, flight period length of species did not change, similarly to our result for the length of the period above average CL. Phenological advances of dragonfly flight periods imply that temperature, whose seasonal patterns are advancing over years[40], plays a primary role for determining dragonfly emergence, either by accelerating development[41] or as environmental cue. This relegates radiation, whose seasonality is static over years[42],

to play only a weak role as an environmental cue triggering dragonfly emergence, even though our analysis suggests that it is the main factor determining optimal flight periods. Poor alignment between the cues triggering seasonal regulation and the drivers of optimal timing may likely prevent species to track shifting seasonal conditions[1]. Altogether, our results suggest that phenological advances may desynchronize dragonfly flight periods from ideal seasonal conditions. Earlier emergence of spring species may expose them to lower radiation than optimal based on body colour lightness, while summer species may be confronted with higher radiation than optimal. Similar results have been suggested for flowering plants (e.g.[43]). Species´ can adjust to seasonal shifts by modifying their phenological responses to environmental cues[1] through either evolutionary adaptation or phenotypic plasticity mechanisms[44,45]. Similarly, species´ body colour lightness may respond to changes in climate or photoperiod, either evolutionarily[46] or via phenotypic plasticity[47,48]. The degree to which these mechanisms would be able to compensate observed and potential future phenological mismatches is, however, unknown (see[49,50]). More research on intraspecific colour variation, plasticity and adaptability in relation to seasonal environmental variation may offer clues about insect´s potential to respond to a changing climate[1].

Our study contributes to filling a gap in the comprehension of the essential but vastly understudied dimension of phenology, by providing support for a phenological extension of the TMH can drive ideal timing of ectotherm´s phenologies. Our results, which rely on key mechanisms regulating species occurrences and life histories, may be representative for a broad spectrum of ectotherm taxa and stress the fundamental ecological importance of colour-based thermoregulation in ectotherms. The complexity of the mechanisms driving phenology make predictive consequences of the phenological component of the TMH which we report in this study far more complex than the direct implications of its spatial operation[28]. However, our results point to body colour as a key trait mediating the mechanisms and repercussions of recent phenological advances, which opens new integrative research avenues that help elucidating general responses of species under global warming both in space and time[51]. We call for more research that does not only report phenological responses to triggering cues and phenological shifts, but addresses mechanisms determining phenology, including the relative contributions of unregulated and regulated phenological tracking as well as mechanisms behind cue systems across taxa. Integrating the growing availability of massive high-resolution species' occurrence and environmental data together with increasingly comprehensive trait datasets opens opportunities for unprecedentedly detailed mechanistic insights into the spatio-temporal variation of diversity – now and in the future.

Methods

Building ecologically meaningful assemblages from occurrence records

We used the publicly available database of occurrence records of Odonata from the British Dragonfly Society Recording Scheme[35] (https://nbnatlas.org). We filtered the database by keeping records of adult individuals between 1990 and 2020. This resulted in 1,047,422 expert-validated records of 56 species across Great Britain between May and October, the flight season of odonates. We used these species-level observations to build ecologically meaningful assemblages, defined as a group of taxonomically related species co-occurring in space and time which are likely to interact[52,53], separately for dragonflies (suborder Anisoptera) and damselflies (suborder Zygoptera). We defined our assemblages based on the following parameters:

- *Spatial resolution (resSp)*, measured as the maximum distance between observations. Should allow observed individuals to have the potential to interact. We considered 0.1 km and 1 km for medium to large-size flying insects like odonates.
- *Phenological resolution* (*resPh*), measured as the maximum difference in days of the year of observations. Should allow individuals observed within this timespan to have the potential to interact. We considered 7 and 14 days based on the phenological turnover of Odonata species.
- *Temporal resolution* (*resTem*), measured as the maximum difference in years between observations. It allows for increasing sampling completeness. We considered strict thresholds of 0 and 3 years to avoid compositional changes over years e.g. due to landcover or climate changes.
- *Sampling effort* (*samEf*), measured as the number of sampling events. We chose a minimum of 4.
- *Sampling coverage* (*samCov*), measured as the percentage of observed richness relative to the estimated richness from rarefaction curves (see below). We chose a conservative threshold of 80%.

We build assemblages by aggregating the occurrence records within the spatio-temporal parameters *resSp*, *resPh*, *resTem*, for which we used the British national grid projection (EPSG:27700). To control for sampling representativeness, we then built, for each assemblage, species accumulation curves using the function *spaccum* (R package *vegan*[54]) and estimated predicted richness using the Chao index[55]. We retained assemblages that reached thresholds of *samEf* = 4 and *samCov* = 80%. Resulting point-based assemblages contain all key ecologically meaningful spatial and temporal aspects of assemblages. This approach to build assemblages constitutes a step forward with respect to previous macroecological studies, which typically cluster observations at unadequately large spatial units[56], e.g.[57] or have poor control over sampling representativeness, e.g.[58,59], but see also[60]. Controlling for sampling representativeness reduces the likelihood of false absences resulting from insufficiently sampled assemblages, which may lead to misleading taxonomic and functional patterns[61].

We present our main results using the following parameters: *resSp* = 1km, *resPh* = 14, *resTem* = 3, *samEff* = 4, *SamCov* = 80. Thereby, we aim for a compromise between ecologically meaningful assemblages and representative sample size. We obtained, with this parameter combination, 8,159 dragonfly assemblages in 2,570 locations showing an average species richness of 4.06 +/- 1.95 (SD), and 4,134 damselfly assemblages in 1,613 locations (Fig. 2d) showing an average species richness of 3.58 +/- 1.43. Our dataset contained 27 dragonfly and 19 damselfly species (Fig. 1d) representing all common odonate

species in Great Britain. We also generated alternative sets of assemblages based on combinations of parameter values considered. Consistent results based on those are provided (Supplementary Table S1) to ensure that ecological patterns are robust to assemblage definition[62].

Quantification Of Body Colour Lightness Of Assemblages

We measured body colour lightness of odonate species from illustrations[36] as an average of RGB channels (see[27,28]). As male and female odonates often show different colouration, we focused on males for coherence with previous studies and because most odonatan observational records belong to males due to their more conspicuous behaviour. For each assemblage, we calculated community weighted means[37] of body colour lightness. We measured deviations of assemblage´s colour lightness from null expectations by randomising assemblage composition 100 times from the regional pool of species (all species in our dataset) and using the standard effect size[63]. Thereby we control for inherent biases of community weighted mean estimates[64]. All reported assemblage-level values of body colour lightness (hereafter simply CL) are standard effect sizes. Values of CL > 0 indicate higher colour lightness than expected by chance and values of CL < 0 indicate lower colour lightness than expected by chance.

We also calculated an alternative spatially-constrained CL measure that uses local instead of regional null models to measure standard effect sizes, which allows isolating the deviation in colour lightness corresponding to the phenological (i.e. non-spatial) replacement of species. For this, we divided the study area into quadrats of 100km by 100km, randomised the composition of assemblages based on the species pool within the respective quadrat and used those to quantify CL. For this analysis, we dropped the 326 and 321 assemblages of dragonflies and damselflies, respectively, that belonged to quadrats with less than 50 assemblages to ensure that species pools were in all cases representative. Results on spatially constrained CL are provided (Supplementary Fig. S1).

Species traits carry a phylogenetic signal that may lead to false interpretations of species trait-environment responses, particularly if phylogenetically related species show similar spatio-phenological patterns (see[65]). We used the most up-to-date molecular phylogeny of European odonates[66] and Lynch´s comparative method[67] to partition body colour lightness of species into a phylogenetic (*P*) and a species-specific (*S*) component[28]. *P* represents the phylogenetically predicted part of trait variation, whereas *S* represents the species-specific deviation from this phylogenetic prediction. We calculated CL separately for the *P* and *S* components of body colour (Supplementary Fig. S3). Consistent patterns in the *P* and *S* alternative measures of CL indicated robustness of our results against phylogenetic bias.

Spatio-phenological Variation Of Body Colour Lightness And Its Drivers

We quantified the magnitude of variation of CL attributed to spatial and phenological dimensions on dragonflies by using a polynomial model with latitude and day of the year as predictor variables with polynomial terms to accommodate the curvilinear response of CL. We chose a 4th -degree polynomial based on model complexity and fit. For damselflies, CL did not show a curvilinear response to day of the year, therefore we used the linear term together with latitude. We present the latitudinal component of CL of dragonflies by using the residuals of a polynomial model of day of the year (Fig. 2c), and the phenological component (Fig. 2e) by using the residuals of a model with latitude. To evaluate the relative contribution of latitude and phenology to the variation in CL, we employed a hierarchical partitioning[68] analysis (R package *hier.part*). To determine whether CL patterns are a result of TMH, we analysed how much of the variation in CL was explained by environmental conditions of temperature and radiation. We downloaded, for each day of the year between 2004 and 2014, raster maps of surface downwelling shortwave radiation (rsds, hereafter radiation), which account for cloud cover, and near-surface air temperature (tas, hereafter temperature) (Chelsa dataset: w5e5v1.0[69] at 30arcsec (~ 1 km) resolution). We averaged radiation and temperature values for each cell and day of the year across the 10-year period. We extracted values corresponding to the central sampling day and location of assemblages. Then, we used linear models to identify whether radiation or temperature drive the spatio-phenological variation in CL. We carried out model selection by prioritising quadratic effects over interactions[70] and based on BIC criteria[71,72]. The final model included radiation with a quadratic effect and excluded temperature because it had minimal contribution (CL ~ radiation + radiation^2). We validated by using a semivariogram (R package *gstat*[73]), that spatial dependence in CL was weak (Fig. S5). Model assumptions were met in all models.

Change Of The Phenological Pattern Of Body Colour Lightness Over Years

To investigate whether and how the phenological CL pattern changed over the last three decades, we focused on the 97.3% of assemblages at latitudes below 55° N (Fig. 2a, 2b) to reduce variation of CL caused by latitude. We grouped records by year. Every year between 1990 to 1999 contained insufficient data to draw robust individual phenological patterns of CL (i.e. less than 80 days along the flight season). Therefore, we grouped together the years 1990–1993, 1994–1995, 1996–1997, and 1998–1999. For each of the 25 resulting year-groups of assemblages, we built individual polynomial models on variation of CL depending on day of the year, for which we used a 4th -degree polynomial (Fig. S4, Table S2). The model of year group 1996–1997 had much lower explanatory power (R^2: 0.18) than the rest (R^2: 0.34–0.48) due to poorly distributed assemblages over the season, and therefore we did not consider it. We characterised phenological patterns of CL for all other 24 models by extracting five attributes: day when CL turned lighter than expected by chance (CL > 0), day when CL peaked, day when CL became darker than expected by chance (CL < 0), number of days with lighter CL than expected by chance (CL > 0), and maximum CL. We tested whether these five attributes shifted over the period between 1990 and 2020 with linear models, using attributes as response variable and year as the predictor.

Declarations

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The authors declare no competing interests.

Author contributions

RNF: Conceptualization, data curation and analyses, lead writing. SP: trait and phylogenetic data provision, manuscript revisions. DZ: trait data provision, manuscript revisions. RB: trait data provision, manuscript revisions. CH: Conceptualization and manuscript revisions.

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Supplementary Information

Supplementary Figures and Tables are not available with this version.

Figures

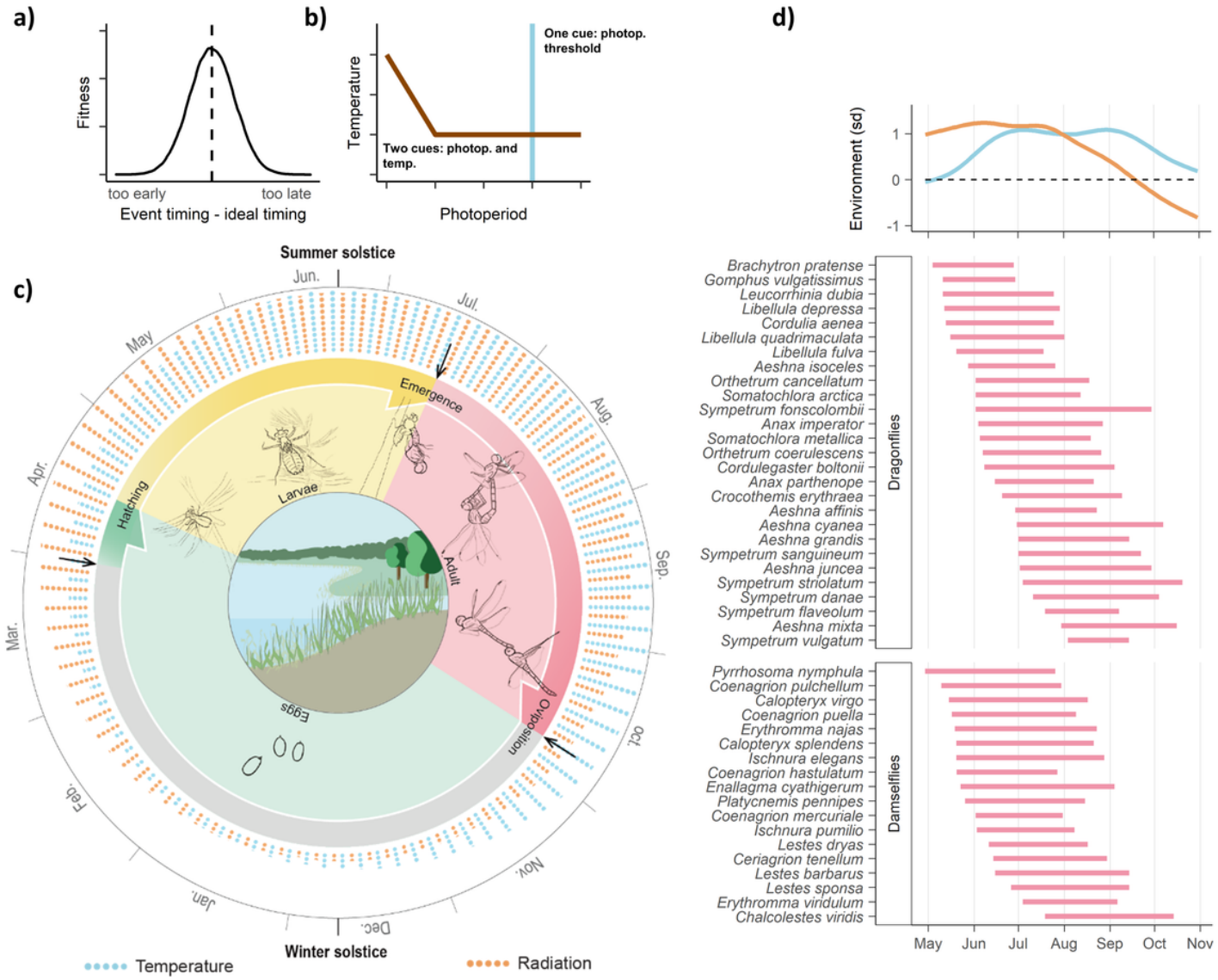

Figure 1

Phenology of Odonata in relation to seasonal environmental conditions. (a) Phenological fundamental tracking synchronises species´ phenology to optimal seasonal moments; (b) phenological tracking operates by triggering species' phenological responses to environmental cues of temperature or photoperiod that link to – unknown – underlying drivers of optimal timing (a and b adapted from[1]). (c) Example of the life cycle of the dragonfly *Sympetrum striolatum* which is regulated by seasonal environmental conditions. Arrows note phenological events triggered by environmental cues. After oviposition in October, cold temperatures induce a diapause in embryonic development until spring when it resumes triggered by photoperiod and temperature cues[38]. Larvaes hatch and develop for two to four months, depending on water temperature. Last instar larvaes emerge, again triggered by photoperiod and temperature cues. Adults complete maturation and reproduce[38]. Alternatively, if oviposition occurs earlier, eggs can develop directly, larvaes hatch in autumn and enter diapause until spring where development resumes[38]. Other temperate odonates have different regulated or unregulated life cycles varying in duration, from less than a year to several years[38]. (d) Percentile 5-95 of dragonfly and damselfly flight

periods in Great Britain, together with the seasonal change in radiation and temperature (upper panel). The dashed line represents average annual values. *Coenagrion scitulum* is not shown because it is very rare and records do not allow to derivate a representative flight period.

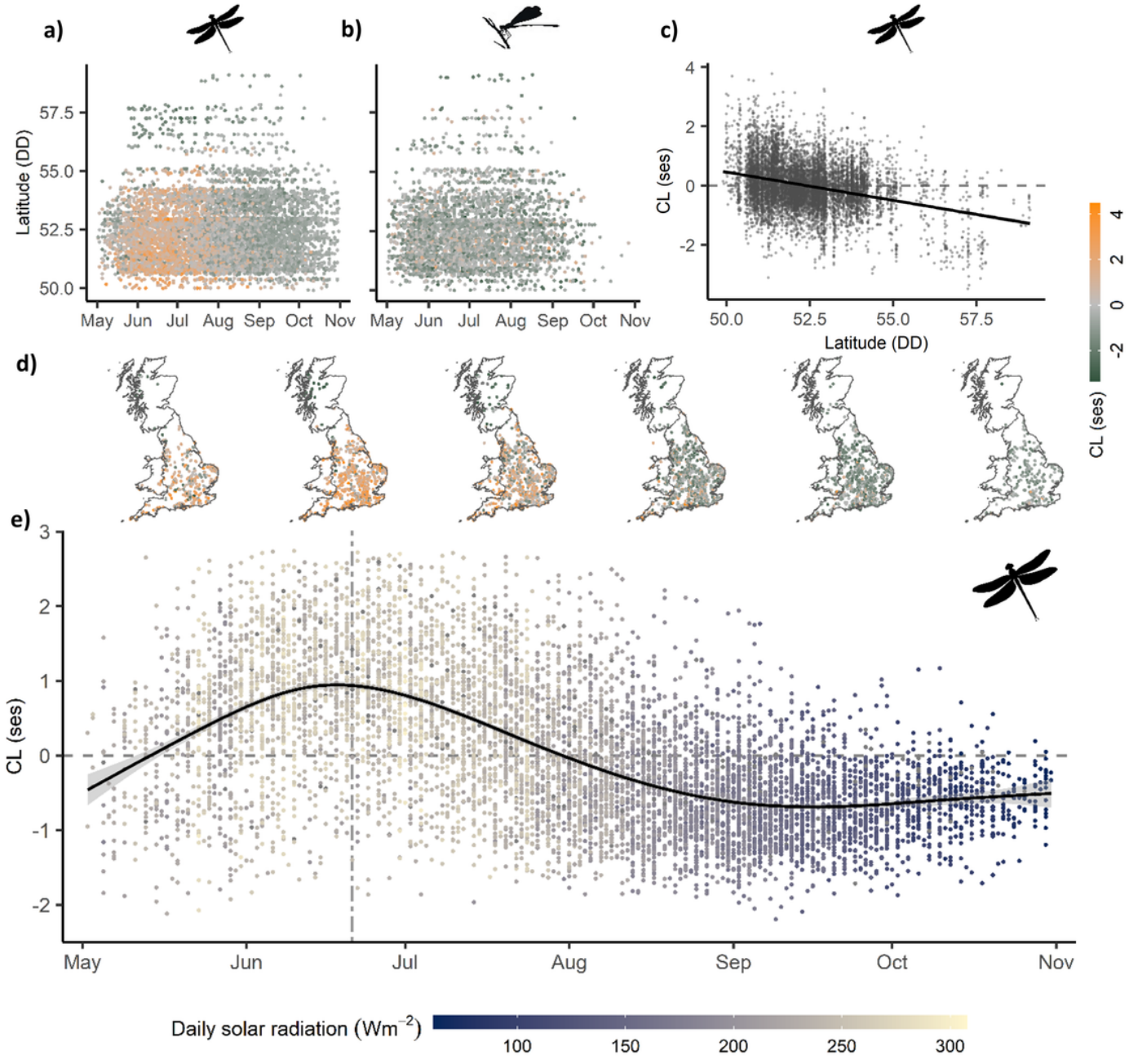

Figure 2

Spatio-phenological variation of body colour lightness (CL) of dragonfly (a, c, d, e) and damselfly (b) assemblages in Great Britain. Variation of CL of dragonfly **(a)** and damselfly **(b)**assemblages along latitude and season. **(c)** Residual CL variation of dragonfly assemblages with latitude, after removing the seasonal component. **(e)** Residual CL variation of dragonfly assemblages along the season after removing the latitudinal component. Black curve indicates LOESS regression; point colour indicates solar radiation intensity received on the specific day of the year at the assemblage location; the vertical dashed

line indicates summer solstice. CL is measured as community-weighted mean of body colour lightness in standard effect size units, i.e. as deviation of observed values from those of random assemblages (see Methods). CL values above zero (marked by the horizontal dashed line) indicate lighter assemblages than expected by chance, CL values below zero indicate darker assemblages than expected by chance.

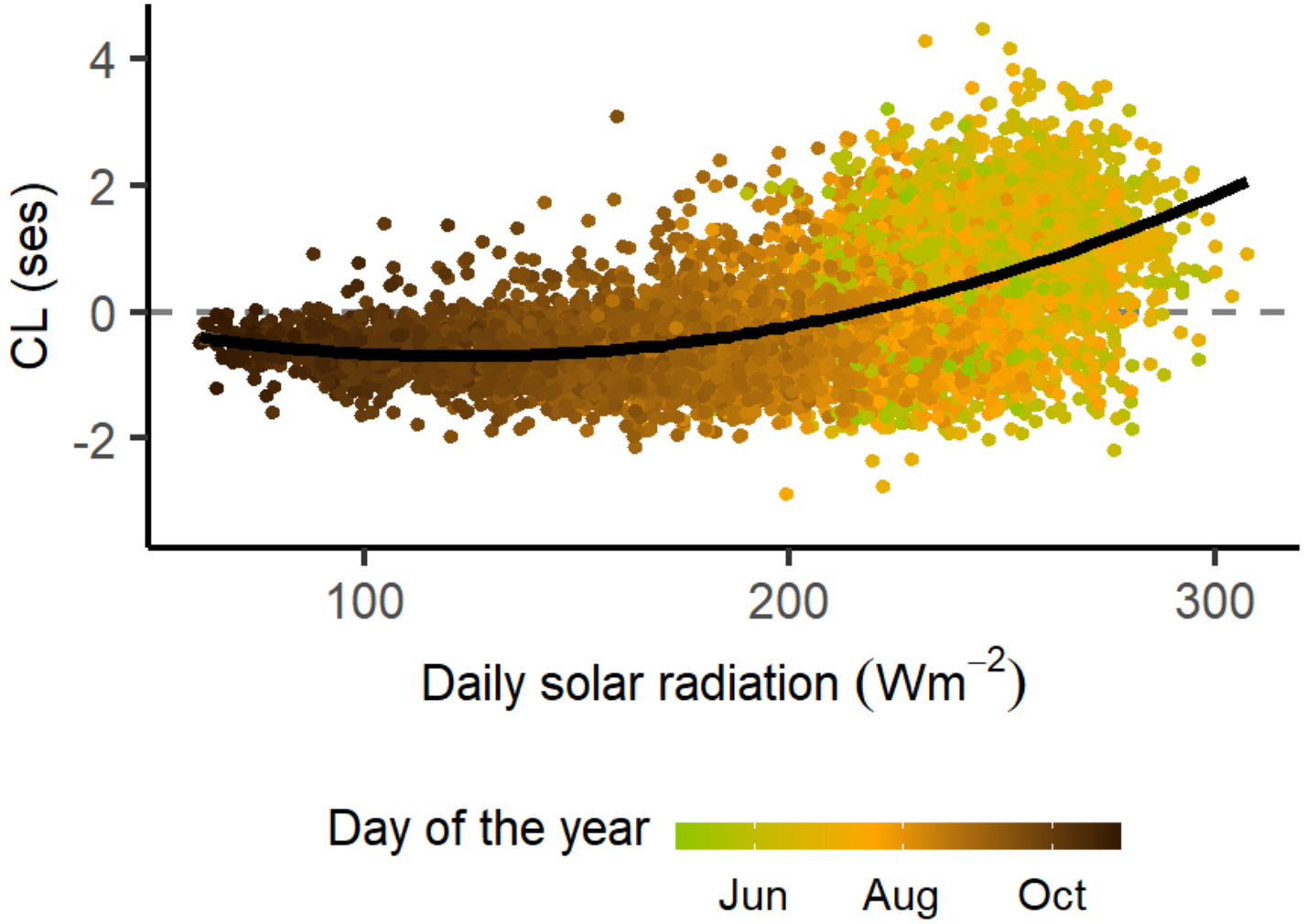

Figure 3

Body colour lightness (CL) of dragonfly assemblages in relation to solar radiation. Each point represents an assemblage. CL is measured as community-weighted mean of body colour lightness in standard effect size units, i.e. as deviation of observed values from those of random assemblages (see Methods). Point colour indicates the day of the year during dragonfly flight season (May to October). Solar radiation is measured as the average solar radiation received on the specific day of the year at the assemblage location. The black curve indicates the regression line of a 2nd-degree polynomial model.

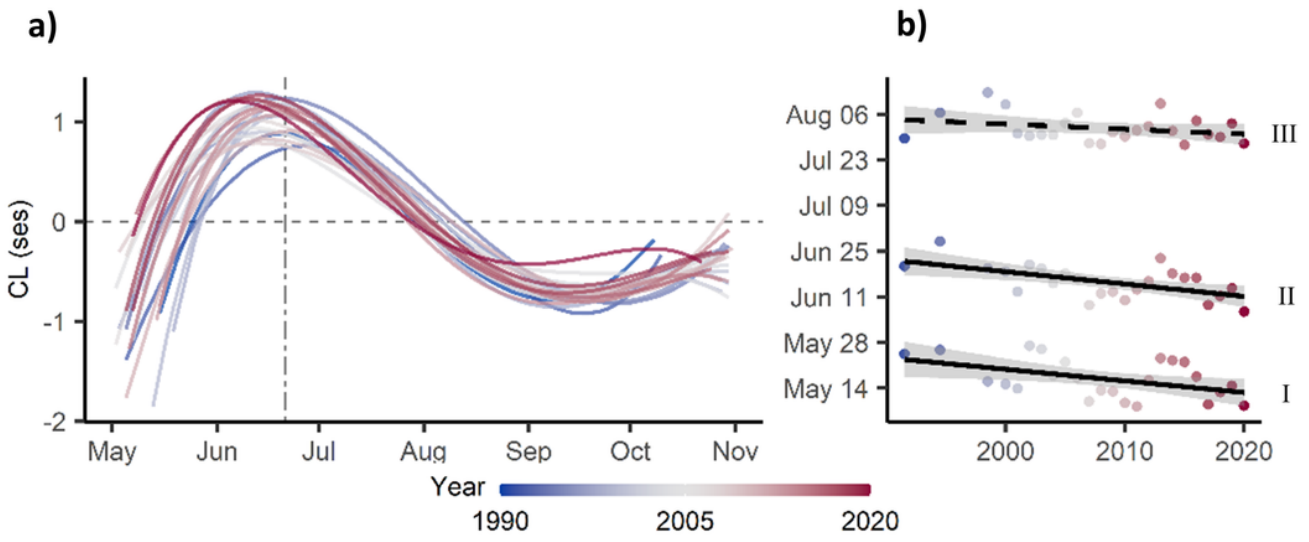

Figure 4

Variation of the phenological pattern of body colour lightness (CL) of dragonfly assemblages between 1990 and 2020. (a) Coloured lines represent regression lines of phenological models (4th-degree polynomial) of CL variation from 1990 (blue) to 2020 (red) (see Supplementary Fig. S4 for a depiction of the raw data for each year and Table S2 for statistical details); the vertical dashed line represents summer solstice. **(b)** Shift of attributes of phenological CL patterns over the 30-year period, specifically: (I) day of the year when CL turned lighter than expected by chance (CL > 0), (II) day of the year when CL peaked (maximum lightness), (III) day of the year when CL became darker than expected by chance (CL < 0); solid lines represent significant models (P <0.05).