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Research article

Trait overdispersion in dragonflies reveals the role and drivers of competition in community assembly across space and season

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Our understanding of how biotic interactions influence animal community assembly is largely restricted to local systems due to the difficulty of obtaining ecologically meaningful assemblage data across large spatial extents. Here, we used thousands of spatio-phenologically high-resolution assemblages across three distinct European regions together with a functional diversity approach to understand community assembly of dragonflies and damselflies (Odonata), an insect group characterized by a pronounced competitive reproductive biology. We found that adult dragonfly, but not damselfly, assemblages were consistently composed of species morphologically more different than expected by chance based on the traits that enhance their interspecific reproductive encounters. These results provide consistent evidence for the role of competition in the assembly of animal communities, which we interpret is most likely caused by the territorial reproductive biology of dragonflies. Support for competition varied both spatially and seasonally following theoretical expectations, as it was strongest in locations and seasonal moments with low thermal stress (i.e. warm conditions) and high niche packing. Our study illustrates how spatio-temporal diversity patterns arise from variation in assembly processes.

Keywords: biotic interactions, community assembly, competition, functional diversity, insects, Odonata, phenology

Introduction

Understanding the processes driving community assembly is of central importance for ecological research. From the regional pool, dispersal and environment stress filter (Keddy 1992) the species able to persist in a given location. Then, biotic interactions



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determine which of these species can co-occur. In particular, competition may prevent the coexistence of species using similar resources (Kaplan and Denno 2007). Our understanding of the assembly processes of animal communities is, however, limited to local systems due to the poor availability of reliable community data across large spatial extents, which hinders our ability to draw generalised inferences (Lawton 1999). The role of competition in particular has been a classic (Pianka 1981) and controversial issue (Wiens 2011, Fraterrigo et al. 2014) as it is identified rather rarely and idiosyncratically across studies and taxa. Other assembly processes such as dispersal and environmental filtering are frequently addressed in macroecological approaches; however, the coarse resolution and poor sampling representativeness of those (Gotelli et al. 2010, Barnagaud et al. 2021) impede inferences on biotic interactions, as biotic effects likely define ecological patterns at finer spatial scales (Whittaker et al. 2001, Willis and Whittaker 2002). Fortunately, the recent increasing availability of high-resolution occurrence data promises an unprecedented potential for general understanding of assembly processes across large spatial scales. This is particularly important within the current context of global change, especially because the question of how biotic interactions will modulate the redistribution of species in the face of environment changes still remains largely unexplored (Schleuning et al. 2020).

Functional ecology, which aims to understand ecological processes by focusing on species' traits, is an increasingly used framework in community assembly. Environmental filtering processes cause assemblages to converge on the traits particularly suitable to the prevailing environmental conditions, resulting in lower functional diversity (FD) than expected by chance (Götzenberger et al. 2012). By contrast, competition is expected to promote differentiated ecological niches (Schoener 1974), resulting in trait divergence or higher FD than expected (Götzenberger et al. 2012, de Bello et al. 2021). Research on functional community assembly has a long history in plant ecology but it has only recently been adopted in animal ecology, where predominance of environmental filtering processes is generally identified. Examples of this include studies on birds (Montaño-Centellas et al. 2021), mammals (Belmaker and Jetz 2013), anurans (Schalk et al. 2015), fish (Fitzgerald et al. 2017), or arthropods (Van der Plas et al. 2012, Müller et al. 2022), among others. Conversely, support for the role of competition is uncommon. Ecological theory suggests that competitive effects are most predominant when abiotic stressors are absent or when ecological spaces are filled in species-rich communities (Pianka 1966, Barrio et al. 2013), which has received considerable empirical support (Ding et al. 2021, Jarzyna et al. 2021, Montaño-Centellas et al. 2021).

Insects are the most diverse group of animals, yet the assembly processes of insect assemblages are comparatively understudied (Wong et al. 2019). Besides spatial patterns of community assembly, many insect groups show a particular replacement of species over the season or phenological patterns (Wolda 1988) which result from complex and

poorly understood mechanisms. The phenological dimension of diversity is, in fact, often neglected (Forrest and Miller-Rushing 2010, Ponti and Sannolo 2022) despite its importance in understanding the distribution of biological phenomena (Woods et al. 2022). Odonata (with suborders dragonflies: Anisoptera, and damselflies: Zygoptera) is an insect order with a rich natural history record, particularly of adults, that may be uniquely useful for understanding animal competitive interactions. The adult life of this warm-adapted group is characterised by competitive encounters over limited reproductive aquatic habitats (Moore 1964), whereby males of many species, most particularly the larger and more active dragonfly subgroup (Crabot et al. 2022), allocate much of their adult time to protect territories (Corbet 2004a). Odonata's competitive reproductive encounters are targeted towards conspecifics, but occur frequently – sometimes as intensely – interspecifically, particularly between morphologically similar species in body size, body proportions, and colour, likely due to visual recognition errors (Corbet 2004a, Worthen and Phillips 2014). Odonate interspecific encounters are known to interfere with reproductive behaviour (Rehfeldt and Hadrys 1988), and modify habitat use (Moore 1964, Worthen and Jones 2007, Khelifa et al. 2013), but their consequences on community assembly have received little attention (Grether et al. 2023).

In this study, we use a functional diversity approach and fine-scale and ecologically meaningful 5694 and 1806 assemblages of adult dragonflies and damselflies respectively across Great Britain (United Kingdom), Bavaria (Germany), and Catalonia (Spain) to better understand Odonata community assembly. If competition has a predominant role, we expect 1) functional overdispersion in the traits describing species' overall morphology and enhancing competitive interspecific encounters. We furthermore expect 2) functional overdispersion to increase under low abiotic stress based on temperature, the most critical factor driving odonatan activity, and with increasingly filled niches of species-rich assemblages. Odonata assemblages show characteristic patterns of species replacement over the flight season whose underlying ecological drivers are largely unexplored. We expect 3) support for competition to change seasonally and be stronger during the seasonal moments with lower thermal stress. Finally, we expect 4) stronger support for competitive interactions in dragonflies than in damselflies due to their stronger territoriality. We discuss the implications of our findings for a better understanding of the role of competitive interactions in shaping animal communities under climate change.

Material and methods

Occurrence data

We used databases of occurrence records of Odonata for three study regions in northern (Great Britain, United Kingdom), central (Bavaria, Germany), and southern Europe (Catalonia, Spain). For Great Britain (GB) we used the database from

the British Dragonfly Society ([British Dragonfly Society Recording Scheme 2021](#)), for Bavaria the database Bayerische Artenschutzkartierung (www.lfu.bayern.de/natur/artendaten), and for Catalonia the database from Institutió Catalana d'Història Natural (<https://blogs.iec.cat/ichn/>) was used. These databases agglutinate observations from different sources and do not follow any systematic collection protocol. From each database we retained occurrence records of adult odonates with species-level identification, high spatial resolution ($\sim < 100$ m), and exact date. This resulted in 1 047 422 records in GB and 137 421 in Bavaria between 1990 and 2020, and 29 046 records in Catalonia between 1990 and 2012. All three databases had expert-validated species identification. Note that we only use adult observations based on our hypothesised competition mechanisms.

Building assemblages from occurrence records

We used each database on species-level observations to build presence/absence multi-species assemblages of dragonflies and damselflies. For this, we followed a method that pools observations within ecologically meaningful spatio-temporal dimensions and controls for the sampling representativity of these assemblages (Novella-Fernandez et al. 2023). We first bear in mind the concept of assemblage as a set of taxonomically related species co-occurring in space and time and likely to interact (Fauth et al. 1996, Stroud et al. 2015). Based on this, we define ecologically meaningful assemblages by using the following six parameters related to spatio-temporal dimensions and sampling representativeness. As we specifically aim to infer competition, we emphasize parameter choices that enable recovering realistic species' co-occurrences between adults. We consider one or two values for each parameter and built alternative assemblage datasets:

- *Spatial resolution (resSp)*. Maximum spatial distance among observations within an assemblage. Should be finer than observed individuals' movement ranges for them to have the potential to interact. Overly large thresholds increase the likelihood of generating false positive co-occurrences. We considered 100 m because Odonata are medium- to large-sized flying insects.
- *Phenological resolution (resPh)*. Maximum days of the year separating observations within an assemblage. To recover realistic co-occurrences among adults it should be finer than patterns of replacement of adult flight periods. Overly large thresholds increase the likelihood of false adult co-occurrences due to unrealistic possibilities of interaction, and ultimately pooling larval and adult stages in an assemblage. We considered 14 and 30 days based on the phenological turnover of Odonata flight periods.
- *Temporal resolution (resTem)*. Maximum years of difference among observations within an assemblage. Larger values allow increasing sampling completeness, therefore reducing likelihood of false absences but increases the likelihood of false positive co-occurrences due to temporal compositional changes. We considered strict thresholds of 0 and 3 years.
- *Sampling effort (samEf)*. Minimum number of sampling days within an assemblage. Reduces the likelihood of false absences caused by insufficient sampling. We considered a minimum of four days.
- *Sampling coverage (samCov)*. Minimum percentage of observed richness relative to estimated richness based on rarefaction curves (see below). Reduces the risk of false absences caused by insufficient sampling. We chose a conservative threshold of 80%.
- *Richness minimum (Smin)*. Minimum species richness required to constitute an assemblage. We considered three and four species based on fieldwork experience on Odonata and to allow for minimally reliable assemblage-level metric calculations.

We built assemblages by pooling point-based occurrence records within the spatio-temporal parameters *resSp*, *resPh*, *resTem*. To account for sampling representativeness, we built – with each spatio-temporally explicit pool of records – species accumulation curves (*specaccum*, R package 'vegan', www.r-project.org, Oksanen et al. 2022), and used them to estimate predicted richness based on Chao's index (Chao 1987). Finally, those pools of records not reaching the thresholds of *samEf*, *samCov* and *Smin* were filtered out and the rest were regarded as ecologically meaningful assemblages. We followed this process to build alternative datasets of assemblages for each study region using all eight combinations of parameters considered. We chose the following parameter combination for the main analysis to balance between fine spatio-temporal resolution and reasonable assemblage sample size across study regions: *resSp*=0.1 km, *resPh*=30, *resTem*=3, *samEf*=4, *samCov*=80 and *Smin*=4. Study regions with resulting assemblages are shown in Fig. 1. Additionally, we used the occurrence dataset of GB to build a dataset with higher phenological resolution adequate to analyse changes in assembly processes over the flight season of Odonata (May–October). To achieve this, we replaced from the previous parameter selection, *resPh*=14 and *resTem*=0, and relaxed *Smin*=3 to obtain a reasonable sample size. Additionally, in this case we focused on the assemblages located below 55°N (99% of all assemblages) to reduce potential confounding effects between latitudinal variation and phenology. Assemblage datasets for main and phenological analysis are described in Table 1. Note that our operational definition of assemblage is restricted to the adult life-stage although both larvae and adults are part of the Odonata community of a location. This is because only co-occurrences between species within the same life stage can be interpreted as a result of competition since adult and larval dragonflies live in different media (air and water) and occupy separated niches. We discuss the possible contribution of larval stage assembly processes in the Discussion section. Similarly, we built separated assemblages of dragonflies and damselflies because competition is only likely to occur within suborders given the markedly distinct morphology and ecological niches between them (see the Supporting information for species included). We built presence/absence

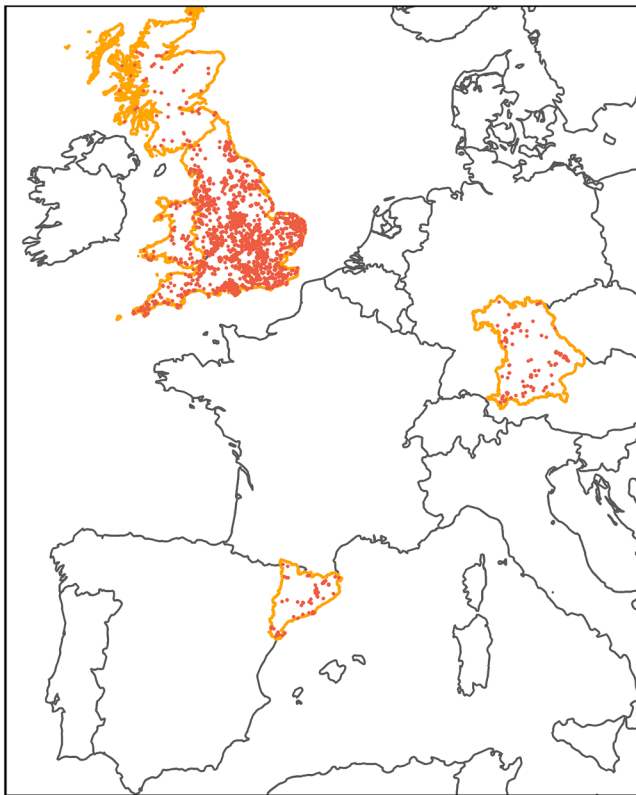


Figure 1. Location of dragonfly and damselfly assemblages within the three complementary study regions of Great Britain (United Kingdom), Bavaria (south-east Germany), and Catalonia (north-east Spain).

assemblages because species' abundance was not systematically reported in the databases. This necessary simplification does not allow for assessing the density-dependent processes involved in community assembly, but is common in large-extent community ecology studies. Our assemblages overcome limitations of macroecological studies that typically use unsuitably large (Willis and Whittaker 2002) spatial units, e.g. 50 km (Fraser et al. 2017), or ignore species' phenology (Zeuss et al. 2014, Pinkert et al. 2017). In addition, we reduced the likelihood of false absences resulting from insufficiently sampled assemblages by controlling for sampling representativeness. This is rarely considered in macroecological studies (Cooper et al. 2008, Ovaskainen et al. 2016), but see Marta et al. (2021), even though it can result in misleading interpretations of taxonomic and functional patterns (Si et al. 2018).

Functional trait data

Using FD inferences to assess community assembly processes requires a trait choice that reflects species' ecological niches (de Bello et al. 2021). Body size is recognised as the most important trait characterising an animal's performance and ecological niches (Schmidt-Nielsen and Knut 1984, Peters and Peters 1986). Odonata wing size affects gliding and dispersal, and together with abdomen length influences flight manoeuvrability (Wootton 1991, Sacchi and Hardersen 2013). Abdomen and body colour contributes to Odonata thermoregulatory physiology (May 1976, Corbet 2004b). Besides influencing species' ecological niches, these traits link to Odonata interspecific competition (de Bello et al. 2021). Odonate species similar in body size, morphology, and colour are more prone to engage in interspecific competitive reproductive encounters because they are more likely to mistake each other as co-specifics (Corbet 2004a, Anderson and Grether 2010, Worthen and Phillips 2014). We estimated body volume from Dijkstra et al. (2006) as described in Zeuss et al. (2017), and used it as a proxy for body size. We obtained absolute values of hindwing length, abdomen length, and body length from Dijkstra et al. (2006). Because all morphological measurements depend on body size, we calculated ratios of hindwing length to body length (wing length), and relative abdomen length to body length (abdomen length). Separate colour estimates for the red, green, and blue (RGB) channels were calculated from scientific illustrations (Dijkstra et al. 2006) as previously described (Zeuss et al. 2014, Pinkert et al. 2017). All considered traits for dragonflies and damselflies had low collinearity ($r < |0.7|$) except for the blue and green colour channels (Supporting information), which we allowed because they both contribute to colour.

Functional diversity quantification

We computed multi-trait measures of functional diversity (FD) because they should provide more informative representation on species' ecological niches than single-trait FD measures (de Bello et al. 2021). Our main multi-trait measure of FD included all four traits: body size, abdomen length, wing length, and the three RGB colour channels. However, because trait choice is a critical yet difficult to justify aspect of functional ecology analyses (de Bello et al. 2021), we computed all possible alternative multi-trait FD sets (Supporting information) that include body size, together with two alternative traits: abdomen length and

Table 1. Description of dragonfly (dr) and damselfly (da) assemblages across analyses and study regions. Number of species (S), number of assemblages (n) and locations, and average richness \pm SD. GB, Great Britain.

Analysis	Study region	S		n		Locations		Richness	
		dr	da	dr	da	dr	da	dr	da
Main	GB	30	17	5451	1662	2641	958	5.42 \pm 1.64	4.55 \pm 0.77
	Bavaria	45	21	96	80	75	64	6.91 \pm 2.87	5.65 \pm 1.77
	Catalonia	37	20	144	63	70	39	6.27 \pm 2.17	4.66 \pm 0.88
Phenological	GB	28	16	1593	435	722	272	4.36 \pm 1.53	3.53 \pm 0.79

wing length (alternative trait set 1), abdomen length and colour (alternative trait set 2), and wing length and colour (alternative trait set 3). Note that we include body size in all alternative trait sets because of the notion that it is essential to characterise species' performance and ecological niches. For the same reason, we also computed FD based on body size alone, as frequently done in animal community assembly studies (Fraser et al. 2017, Fernandez-Fournier et al. 2018, Pineda-Munoz et al. 2021).

We measured FD using the commonly used metric FDis (Laliberte and Legendre 2010), which is not strongly dependent on species richness, to quantify FD. We also used the metric RaoQ (Rao 1982), although it rendered highly correlated values to FDis ($r=0.97$), and therefore its results were not included. Trait values were standardized to mean 0 and unit variance. To measure multi-trait FD, we coded colour as three separated variables corresponding to R, G, B channels and we decreased their individual weight in the computation of FD to 1/3 relative to the other – single variable – traits (de Bello et al. 2021). Additionally, while equal weighting of traits is common practise when measuring FD (Palacio et al. 2022), the assumption that all traits are equally important is almost never justified. We alternatively measured multi-trait FD (all trait sets) by increasing the weight of body size to half of the total summed weight of traits (Supporting information) because of its possible greater importance.

FDis was not independent from species' richness (Linear model: $\beta=0.27$, $R^2=0.07$, $p < 0.05$) as expected for FD metrics (Percey and Gaston 2002). Therefore we used standard effect sizes to quantify functional over- or underdispersion relative to null expectations based on random assemblages of equal richness (de Bello et al. 2021). We first generated expectations on null community assembly (not driven by ecological processes) by randomising assemblage composition 100 times from the corresponding regional species' pools (Münkemüller et al. 2020). Subsequently, we quantified standardized effect sizes (Gotelli and McCabe 2002) of FD (FDses). FDses higher than 0 indicate functional overdispersion relative to null expectations based on random assemblages, thus supporting a prevalent effect of competition. FDses lower than 0 indicate functional underdispersion, supporting the role of environmental filtering. Additionally, we calculated the percentage of assemblages with higher observed FD than the 50th and 95th percentiles of their respective null distributions (FDp50 and FDp95, respectively). Deviations below or above $FDp50=0.50$ and $FDp95=0.05$ indicate functional underdispersion or overdispersion, respectively. For damselfly assemblages, we exclude the four *Calopteryx* species (Supporting information) from main results because they constitute a remarkably distinct morpho-ecological group. They have much larger body size ($\sim \times 3$), singular butterfly-like flight, territorial displays, and shady habitat preferences, and are thus unlikely to compete with other damselflies. Nonetheless, results including *Calopteryx* are provided as Supporting information.

Environmental drivers of functional diversity

We chose temperature to investigate whether multi-trait FDses was affected by changes in environmental stress because it is the main limiting factor driving adult Odonata abiotic suitability (May 1976). Furthermore, warm temperature intensifies the density of territorial male odonates and increases the strength of territorial competition (Corbet 2004a). We retrieved data on mean temperature of summer (Bio 10, CHELSA V1.2, Karger et al. 2017). We also considered forest cover as a covariate because it might influence community assembly by increasing water quality (Duffy et al. 2020) or by filtering shade-intolerant species (Cordero-Rivera 2006). We downloaded a landcover raster map (CorineLC2006, <https://land.copernicus.eu/pan-european/corine-land-cover>), at 100 m resolution, grouped all forest subcategories, and calculated their proportion at 1 km resolution. Then, we extracted the environmental values corresponding to assemblages' locations. To identify the drivers of FDses, we built a single linear model comprising all three study regions because they have complementary environmental ranges. We undersampled the assemblages of GB to a sample size roughly similar to the other three datasets to prevent an overrepresentation of the conditions of GB. For that, we randomly selected 100 assemblages from the highly clustered assemblages below a latitude of 55°N . We iterated this process to obtain 100 different sets of subsampled occurrence records for GB that we later used in the models. To model the drivers of multi-trait FDses, we started with all predictors: summer temperature, proportion of forest, and richness, and controlled for potential phenological effects by adding day of the year. We considered the interaction between summer temperature with study regions because we expected responses to vary across regions: if competition effects are stronger under low abiotic stress, we expected multi-trait FDses to increase with temperature in the thermally constrained regions of Bavaria and GB but not in the warm Mediterranean region of Catalonia. We carried out model selection based on AIC. The final model for dragonflies was $FDses \sim \text{Temp} \times \text{Study region} + \text{Richness} + \text{Day}$. For damselflies, the final model was $FDses \sim \text{Day} \times \text{Study region}$ as none of the other variables affected multi-trait FDses. We calculated averaged model estimates \pm standard deviation across 100 models with the sets of thinned assemblages for GB. Absence of spatial autocorrelation was validated with a semivariogram (Supporting information). Assumptions of normality of the residuals of statistical models were validated.

Phenological variation of functional diversity

To assess how multi-trait and body size FDses change over the flight season (May–October), we used the higher phenological resolution dataset of GB. We additionally calculated community weighted means of body size and explored its variation across the days of the year to better interpret seasonal change in body size FDses. Then, we downloaded, for each day of the year between 2004 and 2014, raster maps of near-surface air temperature at 30 arcsec (~ 1 km) resolution

(Chelsa v5e5v1.0, <https://chelsa-climate.org/chelsa-w5e5-v1-0-daily-climate-data-at-1km-resolution/>; Karger et al. 2022) to identify the drivers of this phenological pattern. We calculated average temperature for each cell and day of the year across the 10 year period. We extracted values corresponding to the assemblages' locations and their central sampling day. Then, we used linear models to assess whether seasonal changes in multi-trait FDses were linked to temperature and richness. We plotted the residuals of this model against day of the year and fitted a LOESS regression to assess whether the phenological variation of FDses was removed once accounting for temperature and richness.

Results

Dragonfly and damselfly functional diversities

Dragonfly datasets contained 5451 assemblages in GB, 96 in Bavaria, and 144 in Catalonia. Mean species richness of these assemblages was 5.42 ± 1.64 , 6.91 ± 2.87 , and 6.27 ± 2.17 , respectively (Table 1). Multi-trait functional diversity (FD) of dragonfly assemblages was consistently overdispersed across regions based on either FDses (GB: 0.94 ± 0.75 , Bavaria: 0.54 ± 0.94 , Catalonia: 0.56 ± 0.81 , Fig. 2a–f, Supporting information), FDP50, or FDP95 (Supporting information), and also when measuring FD from alternative sets of traits (Supporting information). Thus, dragonfly assemblages were composed of species morphologically more different than expected by chance. Dragonfly body size FD was also consistently overdispersed across study regions based on either FDses (GB: 0.80 ± 0.82 , Bavaria: 0.92 ± 0.92 , Catalonia: 0.61 ± 0.88 , Fig. 2g–i, Supporting information), FDP50, or FDP95 (Supporting information). Damselfly datasets of 1662 assemblages in GB, 80 in Bavaria, and 63 in Catalonia had an average species richness of 4.55 ± 0.77 , 5.65 ± 1.77 , and 4.66 ± 0.88 , respectively (Table 1). Conversely to dragonflies, multi-trait FD of damselfly assemblages was mostly random or underdispersed across regions based on either FDses (GB: -0.16 ± 0.98 , Bavaria: -0.49 ± 0.82 , Catalonia: -0.24 ± 1.08 , Fig. 2a–f, Supporting information), FDP50 or FDP95 (Supporting information). Similar results arose when measuring FD from alternative trait sets 1 and 2, but set 3 rendered slight overdispersion in GB (Supporting information). Therefore, damselfly assemblages were composed of species either morphologically more similar or as similar as expected by chance. Damselfly body size FD showed stronger functional underdispersion than multi-trait FD based on either FDses (GB: -0.52 ± 0.57 , Bavaria: -0.55 ± 0.64 , Catalonia: -0.62 ± 1.01 , Fig. 2g–i, Supporting information), FDP50, or FDP95 (Supporting information). When including the morphologically distinct genus *Calopteryx* within damselflies, multi-trait FDses increased slightly, and body size FDses became bimodal (Supporting information) depending on its presence. When overweighing body size in multi-trait FD measure, previous patterns of dragonfly

overdispersion and damselfly underdispersion became slightly stronger (Supporting information).

Environmental drivers of dragonfly and damselfly functional diversity

Variation in dragonfly multi-trait FDses was differently driven by summer temperature across study regions: higher summer temperature increased FDses in the cooler regions Bavaria and GB but decreased FDses in the warm region of Catalonia (Table 2, Fig. 3a). Across the cross-region temperature gradient, FDses was highest under medium summer temperature (Fig. 3a). Day of the year and richness had both positive but weak effects (Table 2). In contrast to dragonflies, multi-trait FDses of damselflies was neither affected by temperature (Fig. 3b) nor by other environmental variables. Instead, it only depended on the interaction between day of the year with study region; FDses decreased with day of the year in GB and Bavaria, but increased in Catalonia (Table 2).

Phenological changes in dragonfly and damselfly functional diversity

The phenologically higher-resolution dataset of GB included 1593 dragonfly assemblages and had an average species richness of 4.36 ± 1.53 . Dragonfly multi-trait FDses showed a seasonal pattern whereby FDses increased from the beginning of the season, peaked in mid-July and then decreased until November (Fig. 4a). The variation of multi-trait FDses over the season was almost completely explained by species richness and temperature (Fig. 4e–f, Table 2); residuals, once the effect of these two variables was removed, showed no seasonal pattern (Fig. 4b). Body size FDses had similar overall seasonal variation of increased central season overdispersion (Fig. 4c). At early season, body size FDses was underdispersed, driven by predominance of large body-sized dragonflies (Fig. 4d). From there, body size FDses increased steeply to become mostly overdispersed (FDses > 0) by mid-June, peaking in mid-July and afterwards decreasing slightly until November although remaining overdispersed (Fig. 4c). For damselfies, the phenologically higher-resolution dataset of GB consisted of 435 assemblages with 3.53 ± 0.79 species on average. Damselfly multi-trait FDses also showed seasonal variation, but was overdispersed early and underdispersed late in the flight season (Supporting information). Damselfly body size FDses had little variation over the season, showing only a slight decrease during summer (Supporting information), similarly to community weighted means of body size, which was relatively constant and lower than expected across the season (Supporting information).

Discussion

Insufficient understanding of animal community assembly processes is a key knowledge gap hindering predictions on how natural systems respond to environmental changes

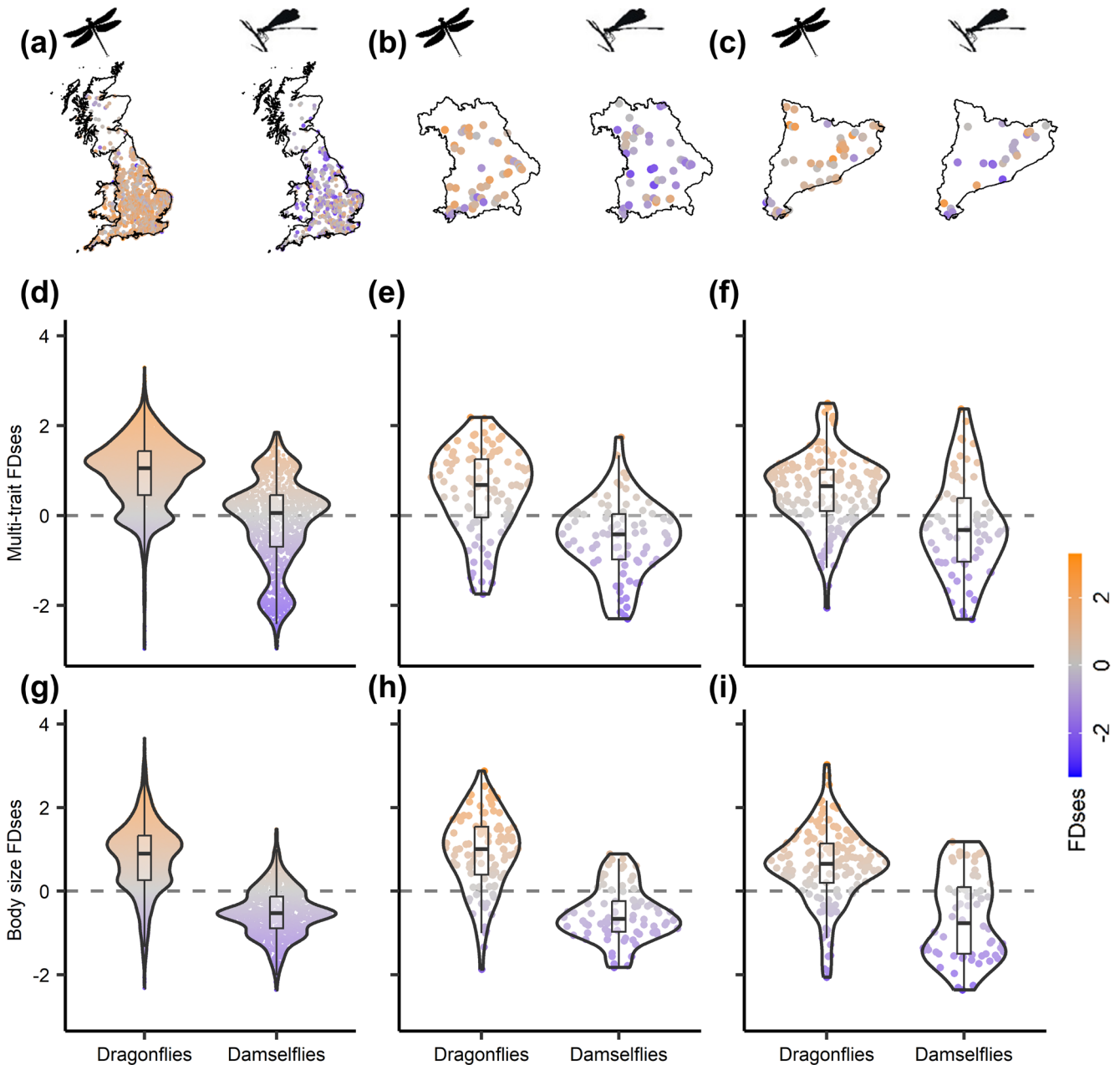


Figure 2. Functional diversity (FDses) of dragonfly and damselfly assemblages across the three European study regions of Great Britain (a, d, g), Bavaria (b, e, h), and Catalonia (c, f, i) based on multiple traits (a–f): body size, relative abdomen length, relative wing length, and colour, and based on body size alone (g–i). FDses > 0 indicates morphological overdispersion and FDses < 0 morphological underdispersion relative to random assemblages of equal richness. Boxes indicate first quartile, median, and third quartile. FDses indicates standard effect size of functional diversity based on the metric FDis.

(Tylianakis et al. 2008, García-Girón et al. 2020). Our results, based on sets of finely defined assemblages across three study regions, show that dragonfly – but not damselfly – assemblages are composed by more morphologically distinct species than expected at random, which supports the role of competition in driving their community assembly. The consistency of morphological overdispersion found across regions and with alternative trait sets, together with the number and resolution of assemblages involved, renders

this study a strong case supporting the role of competition in animal community assembly. Moreover, variation in environmental stress and richness drove changes in the support for competition across space and season, as expected from ecological theory. Competition was highest in warm locations and in species-rich assemblages, particularly during mid-summer (i.e. warm conditions). This study in Odonata therefore contributes to providing insights into the mechanisms driving spatial variation of insect community assembly

Table 2. Linear models of the drivers of multi-trait FDses for dragonfly (dr) and damselfly (da) assemblages for both analyses: across study regions (Main) and within the phenologically higher resolution dataset of Great Britain (GB) (Phenological). Coefficients are standardised. For the main analysis, the assemblages of Great Britain were undersampled (methods), and SD shows parameter variation across 100 models using different assemblage subsets. FDses indicates standard effect size of functional diversity based on the metric FDis.

Analysis		Model	Predictor	Coef ± SD	t ± SD	p
Main	dr	Multi-trait FDses ~ Temp × Study-region+ Richness + Day $F_{7,388} = 14.54 \pm 1.67, R^2 = 0.19 \pm 0.02$ $p < 0.001$	Richness	0.14 ± 0.01	3.46 ± 0.36	< 0.05*
			Day	0.12 ± 0.01	3.04 ± 0.37	< 0.05*
			Temp	1.50 ± 0.01	6.17 ± 0.11	< 0.05*
			DatasetCat	-0.14 ± 0.01	-0.55 ± 0.05	> 0.05
			DatasetGB	0.67 ± 0.13	3.36 ± 0.68	< 0.05*
			Temp × DatasetCat	-1.75 ± 0.01	-5.90 ± 0.11	< 0.05*
			Temp × DatasetGB	-0.50 ± 0.10	-1.65 ± 0.34	> 0.05
			Day	-0.35 ± 0.01	-3.67 ± 0.11	< 0.05*
			DatasetCat	0.28 ± 0.02	1.94 ± 0.14	< 0.05*
			DatasetGB	0.34 ± 0.07	2.84 ± 0.62	< 0.05*
Main	da	Multi-trait Fdses ~ Day × Study-region $F_{5,264} = 13.61 \pm 2.42, R^2 = 0.19 \pm 0.03, p < 0.001$	Day	0.70 ± 0.01	5.55 ± 0.16	< 0.05*
			Day × DatasetCat	-0.14 ± 0.09	-1.03 ± 0.68	> 0.05
			Day × DatasetGB	-0.14 ± 0.09	-1.03 ± 0.68	> 0.05
			Richness	0.23 ± 0.02	12.60	< 0.05*
			Temp	0.11 ± 0.02	5.88	< 0.05*
			Temp	0.11 ± 0.02	5.88	< 0.05*
Phenological	dr	Multi-trait FDses ~ Temp + Richness $F_{2,1553} = 116.47, R^2 = 0.13, p < 0.001$	Richness	0.23 ± 0.02	12.60	< 0.05*
			Temp	0.11 ± 0.02	5.88	< 0.05*

and also across the poorly addressed phenological variation of insect community assembly.

These consistent patterns of overdispersed dragonfly assemblages contrasts with the general absence of support for competition in animal community assembly (Kaplan and Denno 2007, Nakadai et al. 2018, Bird et al. 2019). The few exceptions based on functional overdispersion include studies based on 142 mammal assemblages worldwide (Cooper et al. 2008), 53 spider assemblages across America (Fernandez-Fournier et al. 2018), or 45 ant assemblages in a national park in Australia (Nipperess and Beattie 2004). In Odonata, previous local studies carried out in Brazil detected

phylogenetic underdispersion (Saito et al. 2016), or morphologic overdispersion in damselflies, but not in dragonflies (Oliveira-Junior et al. 2021). Such incongruence may be driven by considering both – functionally different – sub-orders together, or because species' morphology links better to ecological niches than species' phylogeny (Cadotte et al. 2017). While the main limitation of functional diversity inferences in community assembly is the uncertainty of the link between the traits chosen and the subjacent ecological mechanisms driving assembly, our trait choice was empirically informed based on the hypothesised mechanism of competition and was robust to similar alternative trait combinations.

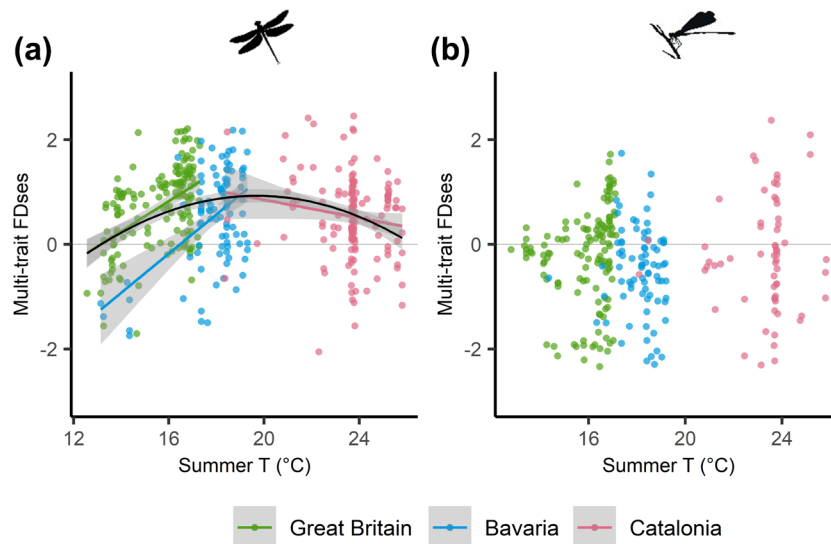


Figure 3. Multi-trait FDses of (a) dragonfly and (b) damselfly assemblages depending on summer temperature across the study regions of Great Britain, Bavaria and Catalonia. Solid coloured lines represent linear model including study region as interaction effect (multi-trait FDses ~ Temp × Study-region). The black curved line indicates a linear model with a quadratic term without considering study region (multi-trait FDses ~ Temp + Temp²). No significant relationship was found in (b). Assemblages of Great Britain were undersampled (methods). FDses > 0 indicates morphological overdispersion and FDses < 0 morphological underdispersion relative to random assemblages of equal richness. FDses indicates standard effect size of functional diversity based on the metric FDis.

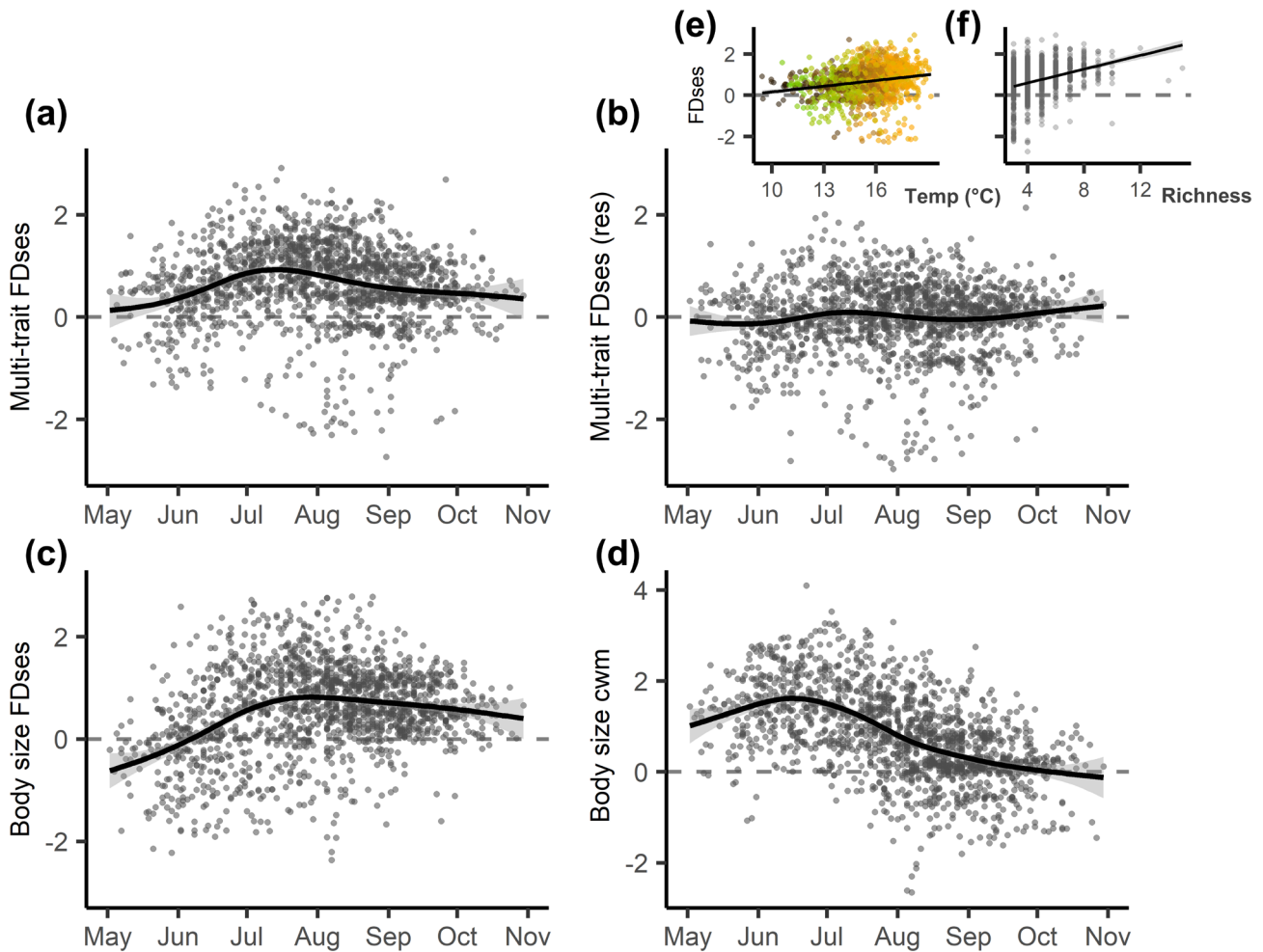


Figure 4. Phenological variation of functional diversity (FDses) of dragonfly assemblages in Great Britain over the flight season of the group. (a) Variation of multi-trait FDses over the season. (b) Variation of residual multi-trait FDses over the season after removing the effects of temperature and richness. (c) Variation of body size FDses over the season. (d) Variation of community weighted means of body size over the season. Black lines represent LOESS models. (e and f): components of the LM: $FDses \sim temperature + richness$. Colour indicates day of the year from May (green) to October (dark brown). $FDses > 0$ indicates morphological overdispersion and $FDses < 0$ morphological underdispersion relative to random assemblages of equal richness. $FDses$ indicates standard effect size of functional diversity based on the metric $FDIs$.

Our results therefore support our initial expectation that the striking and continuous territorial disputes of dragonflies over reproductive habitats would shape community assembly by limiting the similarity of coexistent species. This is in line with a previous study indicating that body size may drive dragonfly microhabitat partitioning (Worthen and Jones 2007). Our interpretation, however, cannot exclude the possible contribution of other, but potentially less likely, competitive mechanisms. Trophic exploitation, which requires prey limitation, is generally suggested unlikely for generalist predators feeding on abundant small prey such as flying insects, e.g. in aerial-foraging bats (Arlettaz 1999). Moreover, resource limitation is particularly unlikely in Odonata as their prey is active under the same thermal conditions. Alternatively, trophic competition mediated by interference is only anecdotally reported in Odonata (Corbet 2004c). While our study focuses on adult-level assembly processes,

the complete Odonata assemblage of a location results from assembly processes occurring at both the adult and the larval level. Therefore, the pattern observed may also be influenced by larval-level processes. While a more comprehensive understanding of Odonata community assembly would require the integration of both development stages (Grether et al. 2023), this is challenging due to the scarcity of observational data of larvae at the scale of this study. For larvae, however, aquatic habitats are known to provide a wide range of microhabitats (water column, sediments, vegetation), towards which specific lifestyle specialisation has evolved (burrower, deep burrower, clasper, hider, sprawler), facilitating coexistence (Crowley and Johnson 1982). Note that even in the case of a strong phylogenetic influence on species' morphologies, i.e. of closely related species being more similar than expected by chance, this would imply that morphologically overdispersed assemblages would also be phylogenetically overdispersed,

which deviates from niche conservatism expectations and is another commonly used inference for competition.

Drivers of dragonfly community assembly across space and season

The observed positive effects of temperature and richness on morphological overdispersion of dragonflies across the three study regions validates theoretical expectations that competition is greatest under low abiotic stress and in assemblages with increasingly filled ecological niches (Pianka 1966). Warm conditions are essential for Odonata activity (May 1976). Accordingly, morphological overdispersion increased with temperature in the colder regions of Bavaria and GB but decreased in Catalonia, where summer temperature is not limiting and where highest temperature is likely associated with drought. These results echo previous findings of varying support for competition along environmental stress driven by altitudinal gradients in bird (Ding et al. 2021, Jarzyna et al. 2021, Montaña-Centellas et al. 2021) and ant assemblages (Fontanilla et al. 2019). Increase of absolute functional diversity with richness is often used to assess functional redundancy (Suárez-Castro et al. 2022), but the relation between functional overdispersion and richness is not well understood. The positive effect found in this study adds a case to previous mixed results (Almeida et al. 2016, Boyé et al. 2019, Montaña-Centellas et al. 2021), and calls for future research.

Seasonal variation in FD has been recently described for a few taxa, which was suggested to inform changes in the contribution of assembly processes along changing seasonal conditions (Shinohara et al. 2023), e.g. in tropical freshwater benthic macroinvertebrates (Wang et al. 2020) or fishes, which became more strongly underdispersed during the wet season (Fitzgerald et al. 2017). However, for taxa whose seasonal changes in assemblages are caused by phenological structure, seasonal variation of FD has, to our knowledge, remained unexplored so far. Our study shows that the phenological structure of adult dragonfly and damselfly assemblages translates into seasonal variation in FD. The interpretation of such variation may, nevertheless, not be straightforward because phenological turnover of species is complexly determined (Wolkovich and Donahue 2021). Remarkably, seasonal variation of dragonfly FD, which consisted of a humped pattern of highest overdispersion during the central season, was entirely explained by seasonal changes in temperature and richness, the same two factors that drove spatial variation of FD. Moreover, early-season dragonfly body size underdispersion was driven by species with large body sizes, as similarly found for wild bees in Catalonia, suggesting that this allows them to deal with cold temperatures (Osorio-Canadas et al. 2016). While further research on the interpretation of seasonal changes in FD is needed, altogether, our results are compatible with the expectation that the relative contribution of competition and environmental stress may drive not only spatial patterns but also influence the phenological variation of community assembly. Thereby, stronger early-season environmental filtering may have

influenced adult early-season flight periods to be restricted to a few large – endotherm – species able to thermoregulate in colder conditions (May 1976), leading to underdispersed adult assemblages. Conversely, less thermally restrictive mid-season conditions may have influenced most species to central season flight periods, leading to stronger competition in those assemblages. Our study emphasizes that if we aim for a comprehensive understanding of natural systems, carefully considering phenological variation is essential (Ramírez et al. 2015, Ponti and Sannolo 2022).

Damselfly community assembly

The lack of support for the role of competition in damselflies compared to dragonflies may be driven by their lower body size and mobility, lower degree of territoriality (Crabot et al. 2022), and much smaller territory size (e.g. 8.6 ± 27.0 versus 99.1 ± 323.6 m², respectively: Aromaa et al. 2019). Species mobility likely determines the scale at which animal diversity patterns emerge (Reiss 1988, Ofstad et al. 2016). The observed pattern of functional underdispersion in damselfly assemblages was driven neither by the environmental factors considered nor by species richness, stressing previously supported differences in ecological drivers between dragonflies and damselflies (Carvalho et al. 2013, Crabot et al. 2022). Despite being closely related, both suborders differ markedly regarding their morphology, mobility, habitat use, and thermoregulatory physiology (Corbet 2004d). Smaller bodied insects like damselflies have lower thermal requirements which may render their diversity patterns less dependent on thermoregulatory constraints. Additionally, their lower mobility may make them more dependent on fine-scale microhabitat characteristics (Crabot et al. 2022) that were not assessed in this study.

Conclusion and implications for climate change impacts

By combining functional approaches with sets of sensibly defined assemblages, our study develops understanding of the ecological processes driving spatial and phenological patterns of insect community assembly. Community assembly is fundamental for the stability and resilience of ecosystems (Lehmann-Ziebarth and Ives 2006) and can mediate biodiversity changes caused by climate change. From the relationship between temperature and competition found in this study it can be predicted that increasing temperatures will affect dragonfly assembly processes. In cold regions such as Great Britain and Bavaria, reduced environmental stress may promote stronger competition, while in already warm regions such as Catalonia, increased thermal stress may impose more severe environmental filtering. Odonata are well known to respond to present climate change with strong latitudinal and phenological shifts (Hassall 2015). Our support for the role of competition in dragonflies supports previous speculations (Ott 2001) suggesting that, in this taxon, competition

may play a relevant role in mediating future climate change effects. Hence, dragonflies colonising newly environmentally suitable areas may impact local species through competition; or, conversely, local competitors may prevent the establishment of newly colonising species (Lancaster et al. 2017). Dragonflies may therefore constitute a useful study system to understand how climate change and biotic effects interact (Tylianakis et al. 2008, Urban et al. 2013). For this, Mediterranean range-expanding species in central and northern Europe such as *Crocothemis erythraea*, *Sympetrum fonscolombii*, *Thritemis annulata* or *T. kyrbii* may be particularly relevant study cases (Ott 2001).

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Author contributions

Roberto Novella-Fernandez: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (lead); Methodology (lead); Resources (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Loïc Chalmandrier:** Formal analysis (supporting); Methodology (supporting); Supervision (supporting); Writing – review and editing (equal). **Roland Brandl:** Methodology (supporting); Supervision (supporting); Writing – review and editing (equal). **Stefan Pinkert:** Methodology (supporting); Resources (equal); Supervision (supporting); Writing – review and editing (equal). **Dirk Zeuss:** Methodology (supporting); Resources (equal); Supervision (supporting); Writing – review and editing (equal). **Christian Hof:** Funding acquisition (lead); Project administration (lead); Methodology (supporting); Resources (equal); Supervision (lead); Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.7h44j101f> (Novella-Fernandez et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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