

Morphological overdispersion supports the role of competition in the community assembly of dragonflies: drivers and spatio-seasonal variation

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Abstract

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. We used a unique dataset of 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), a group characterized by a pronounced competitive reproductive biology. We found that dragonfly, but not damselfly, assemblages were consistently overdispersed in the morphological traits driving inter-specific reproductive encounters, which supports the role of competition. As predicted by ecological theory, support for competition varied spatially and seasonally as a result of changes in temperature stress and niche packing. Our study provides uniquely consistent and general evidence for the role of competition in animal community assembly, and illustrates mechanistically how spatio-temporal diversity patterns arise from variation in assembly processes.

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Introduction

Understanding the processes driving community assembly is of central importance for ecological research. While dispersal and environment filter (Keddy 1992) from the regional pool of species, those able to occur in a given location, biotic interactions determine which of these species can co-occur. In particular, interspecific competition may prevent the coexistence of species using similar resources (Kaplan & Denno 2007). Our understanding of community-level assembly processes is however, and most particularly for animals, limited to local systems due to the poor availability of reliable community data across large spatial extents, hindering our ability to draw generalised inferences (Lawton 1999). The role of competition has been particularly an almost eternal (Pianka 1981) and controversial issue (Willis & Whittaker 2002; 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 necessarily coarse resolution and poorly sampling representativeness of those (e.g. 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 & Whittaker 2002). Fortunately, the recent increasing availability of high-resolution occurrence data promises an unprecedented general understanding of assembly processes across large spatial scales. That is particularly important within the current global change context. How biotic interactions will modulate the redistribution of species in the face of environment changes 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. Predominance of environmental filtering processes causes assemblages to convergence on the particularly suitable traits towards environmental conditions, resulting in lower functional diversity (FD) than expected by chance (Götzenberger *et al.* 2012). By contrast, predominance of 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). 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 support for environmental filtering processes include studies on birds (Ricklefs 2012; Montaña-Centellas *et al.* 2021), mammals (Belmaker & Jetz 2013), anurans (Schalk *et al.* 2015), fish (Fitzgerald *et al.* 2017) or arthropods (Van der Plas *et al.* 2012; Greenop *et al.* 2021; Muller *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 e.g. (Ding *et al.* 2021; Jarzyna *et al.* 2021; Montano-Centellas *et al.* 2021).

Insects are the most diverse group of animals, yet their assembly processes are comparatively understudied (Wong *et al.* 2019). Besides spatial patterns of community assembly, many insect groups show particular replacement of species over the season or phenological patterns (Wolda 1988) which are the result of complex and poorly understood mechanisms. The phenological dimension of diversity is, in fact, often neglected (Forrest & Miller-Rushing 2010; Ramirez *et al.* 2015; Ponti & Sannolo 2022) despite its importance in understanding the distribution of biological phenomena (Woods *et al.* 2022). The Odonata (with suborders dragonflies: Anisoptera, and damselflies: Zygoptera) are an insect order with rich natural history record 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 the males of many species, most particularly the larger and more active dragonflies (Crabot *et al.* 2022), allocate much of their adult time to protecting territories (Corbet 2004b). Odonata competitive reproductive encounters are targeted towards conspecifics, but also occur frequently — sometimes as intensely — interspecifically, particularly between morphologically similar species in body size, body proportions, and colour, which is likely caused by visual recognition errors (Moore 1964; Anderson & Grether 2010, 2011; Chaves Resende 2010; Worthen & Phillips 2014). Odonate interspecific encounters are known to interfere with reproductive behaviour (Rehfeldt & Hadrys 1988), and modify habitat use (Moore 1964; Worthen &

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 morphology-based functional diversity approach and an unprecedented combination of fine-scale and ecologically meaningful 5694 and 1806 assemblages of dragonflies and damselflies respectively across Great Britain (United Kingdom), Bavaria (Germany), and Catalonia (Spain) to better understand the processes driving 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 (4) assembly processes to change seasonally corresponding to seasonal changes in environmental stress. Finally, we expect (5) 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.

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/artenschutzkartierung). For Catalonia, the database from *Institucio Catalana d'Historia Natural*. After removing records with unspecific taxonomy and larvae, we retained 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. Occurrence records in all databases were expert-validated and therefore we assume reliable species identification.

Building assemblages from occurrence records

We used each database on species-level observations to build ecologically meaningful assemblages (*sensu* Fauth *et al.* 1996) defined as a group of taxonomically related species co-occurring in space and time likely to interact (Stroud *et al.* 2015). We generated separated assemblages for dragonflies and damselflies because competition is only likely to occur within subgroups based on their markedly differentiated morphology and ecological niches. We first defined the following spatio-temporal and sampling representativeness parameters:

* *Spatial resolution (resSp)*. Maximum spatial distance among observations, which should allow observed individuals to have the potential to interact. We considered 100 m for medium to large-size flying insects.

* *Phenological resolution (resPh)*. Maximum difference in days of the year among observations. Should allow adult individuals observed in different days to have the potential to interact. We considered 14 and 30 days based on the phenological turnover of Odonata species.

* *Temporal resolution (resTem)*. Maximum difference in years among observations. It allows increasing sampling completeness. We considered strict thresholds of 0 and 3 years to avoid compositional changes over years due to for instance landcover or climate changes.

* *Sampling effort (samEf)*. Number of sampling events. We considered a minimum of 4.

* *Sampling coverage* (*samCov*). Observed richness relative to expected. We choose a conservative threshold of 80%.

* *Richness minimum* (*Smin*). Absolute minimum species richness to constitute an assemblage. We considered 3 and 4 species.

We pooled 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 (*spaccum*, R package *vegan*, Oksanen *et al.* 2019), species accumulation curves, and used those to estimate predicted richness based on Chao’s index (Chao 1987). Those record pools reaching the thresholds of *samEf*, *samCov*, and *Smin*, were kept and regarded as ecologically meaningful assemblages. Species’ presence/absence was used because abundance data was not systematically obtained in the occurrence record databases. We followed this process to build assemblages for each study region using the parameters: *resSp* = 0.1 km, *resPh* = 30, *resTem* = 3, *samEff* = 4, *SamCov* = 80, *Smin* = 4 aiming for a balance between fine spatio-temporal resolution and reliable sample size across study regions. Study system with resulting assemblages are shown in Fig. 1. Additionally, we used the occurrence dataset of GB to generate a phenologically higher resolution assemblage dataset adequate to analyse changes in assembly processes over the flight season of Odonata (May-October). For this, we used the parameters: *resPh* = 14, *resTem* = 0, and *Smin* = 3. Because we were interested in phenological changes, we focused on the 99% of assemblages below 55degN to reduce potential confounding effect of latitudinal variation. Assemblage datasets are described in Table 1. Species included are shown in Table S1. Our spatio-temporal definition of assemblages based on finer spatial resolution than the range of movement of individuals, and finer phenological resolution than species’ flight periods allows for the detection of realistic co-occurrences. We therefore overcome limitations of macroecological studies that typically use unsuitable large spatial units (Willis & Whittaker 2002), e.g 50km (Fraser *et al.* 2017), or ignore the seasonal component of species’ occurrences (Zeuss *et al.* 2014; Pinkert *et al.* 2017). In addition, we reduce the likelihood of false absences resulting from insufficiently sampled assemblages by controlling for sampling representativeness. This is rarely considered in macroecological studies (e.g. Cooper *et al.* 2008; Ovaskainen *et al.* 2016, but see Marta *et al.* 2021), despite it can mislead 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 single most important trait characterising animal’s performance and ecological niches (Schmidt-Nielsen & Knut 1984; Peters & Peters 1986; Gaston *et al.* 2009). In Odonata, wing size affects gliding and dispersal, and together with abdomen length influence flight manoeuvrability (Wootton 1991; Sacchi & Hardersen 2013). Abdomen length is also linked to thermoregulatory physiology (May 1976), and body colour contributes to Odonata thermoregulatory performance (Corbet 2004d). Besides influencing species’ ecological niches, these traits link to our hypothesised mechanism of interspecific competition (de Bello *et al.* 2021). Odonate species that are more similar in body size, morphology, and colour, are more prone to engage in interspecific competitive reproductive encounters as they are more likely to be mistaken as co-specifics (Moore 1964; Corbet 2004b; Worthen & Jones 2007; Anderson & Grether 2010, 2011; Worthen & 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 (Fig. S1), which we allowed because they contribute to colour.

We computed multi-trait measures of 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 body size, abdomen length, wing length, and the three RGB colour channels. However, we computed alternative multi-trait FD (Supplementary Fig. S2) based on body size together with alternative traits: abdomen length and wing length (alternative trait set 1), abdomen length and colour (alternative trait set 2), and wing length and colour (alternative trait set 3). For interpretability, we also computed FD based on body size (body volume) alone because it is the single most important trait, and as it is commonly done in animal community assembly studies (e.g. Fraser *et al.* 2017; Fernandez-Fournier *et al.* 2018; Pineda-Munoz *et al.* 2021).

Functional diversity quantification

We used the common metric FDis (Laliberte & Legendre 2010), which is not strongly dependant on species richness, to quantify FD. For 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. Based on our believe that body size may be of greater importance for both characterising species ecological niches as species recognition, we alternatively measured multi-trait FD (all trait sets) by increasing the weight of body size to represent half of the total summed weigh of traits (Fig. S3).

FD typically increases with richness (Petchey & Gaston 2002), therefore inferences on assembly processes are based on functional over- or under dispersion relative to null expectations based on random assemblages of equal richness (de Bello *et al.* 2021). We generated expectations on null community assembly (not driven by ecological processes) by randomising assemblage composition 100 times from the corresponding regional species' pools (Munkemuller *et al.* 2020). Subsequently, we quantified standardized effect sizes (Gotelli & 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 bellow or above FDp50=0.50 and FDp95=0.05 indicate functional underdispersion or overdispersion respectively. For damselfly assemblages, we present our main results excluding the four *Calopteryx* species (Table S2) because they constitute a morphologically distinct group i.e. with much larger (~x3) body size, but also ecologically differentiated with butterfly-like flight, particular shady habitat, or territorial displays, and therefore are unlikely to compete with other damselflies. FDses results including *Calopteryx* are provided as Supplementary information (Fig. S4).

Environmental drivers of functional diversity

To investigate whether overdispersion in multi-trait FDses was driven by environmentally suitable conditions, we chose temperature, the main abiotic driver known to determine Odonata abiotic suitability. Temperature affects physiological rates of insects (Gillooly *et al.* 2001), and Odonata activity is particularly dependant on it (May 1976). Besides, temperature intensifies the density of territorial male odonates (Corbet 2004b). We retrieved the data on mean temperature of the warmest quarter (Bio 10, CHELSA V1.2, Karger *et al.* 2017). We considered forest cover as a covariate because it might influence community assembly for instance by increasing water quality (Duffy *et al.* 2020) or by filtering most shade-untolerant species (Cordero-Rivera 2006). We downloaded a landcover raster map (CorineLC2006, <https://land.copernicus.eu/pan-european/corine-land-cover>), at 100m resolution, grouped all forest subcategories and calculated their proportion at 1 km resolution. To identify the drivers of FDses, we built a single model comprising all three study regions because they have complementary environmental ranges. We thinned the assemblages of GB to roughly

similar sampling size to the other three datasets to prevent overrepresenting the conditions of GB. For that, we randomly selected from the highly clustered assemblages under latitude 55 Ndeg, 100 assemblages. We iterated this process to obtain 100 different sets of subsampled occurrence records for GB that we will later use in 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 phenologic 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 expect multi-trait FDses to increase with temperature in the thermally constrained Bavaria and GB but not in the warm Mediterranean system of Catalonia. We carried out model selection based on AIC. The final model for dragonflies was $FDses \sim Temp * Study\ region + Richness + Day$. For damselflies, final model was $FDses \sim Day * Study\ region$ as all other variables did not affect 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 (Fig. S6). Assumptions of normality of the residuals of statistical models were validated.

Phenological variation of functional diversity

To assess whether assembly processes change over the flight season of Odonata (May-October), we represented, using the higher phenological resolution dataset of GB, multi-trait and body size FDses across day of the year. 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. To identify the drivers of this phenological pattern, we downloaded, for each day of the year between 2004 and 2014, raster maps of near-surface air temperature at 30arcsec (~ 1 km) resolution (Chelsa w5e5v1.0, Karger *et al.* 2022) <https://chelsa-climate.org/chelsa-w5e5-v1-0-daily-climate-data-at-1km-resolution/>. 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 identify whether multi-trait FDses was driven by 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 by temperature and richness.

Results

Dragonfly and damselfly functional diversity

Dragonfly datasets contained 5454 assemblages in GB, 96 in Bavaria, and 144 in Catalonia. Species richness of these assemblages was 5.42 ± 1.64 , 6.91 ± 2.87 , and 6.27 ± 2.17 , respectively (Table 1). Multi-trait 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, Table S2), FDP50, or FDP95 (Table S2), and also when measuring FD from alternative sets of traits (Fig. S2). Therefore, 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, Table S2), FDP50, or FDP95 (Table S2). Damselfly datasets of 1662 assemblages in GB, 80 in Bavaria, and 64 in Catalonia had 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, Table S2), FDP50 or FDP95 (Table S2). Similar results arose when measuring FD from alternative trait sets 1 and 2 but set 3 rendered slight overdispersion in GB (Fig. S2). Therefore, damselfly assemblages were composed of species either morphologically more similar or 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, Table S2), FDP50, or FDP95 (Table S2). When including the morphologically distinct genus *Calopteryx* within damselflies, multi-trait FDses increased slightly, and body size FDses became bimodal (Fig. S4) depending

on its presence. When overweighing body size in multi-trait FD measure, previous patterns of dragonfly overdispersion and damselfly underdispersion became slightly stronger (Fig. S3).

Environmental drivers of dragonfly and damselfly functional diversity

Variation in dragonfly multi-trait FDses was driven by summer temperature differently across study regions; Higher summer temperature increased FDses in the cooler regions Bavaria and GB but decreased FDses in the warm region, 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 not 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 1600 dragonfly assemblages and had 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 change of multi-trait FDses over the season was explained by seasonal variation in species richness and temperature (Fig. 4b insert, Table 2). Once the effect of richness and temperature was removed, residuals 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). Damselfly's phenologically higher-resolution dataset consisted of 439 assemblages in 272 locations with average of 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 (Fig. S5a). Damselfly body size FDses had little variation over the season, showing only a slight decrease during summer (Fig. S5b), similarly to community weighted means of body size which was rather constant and lower than expected across the season (Fig. S5c).

Discussion

Insufficient understanding on animal community assembly processes is a key knowledge gap hindering predictions on how natural systems respond to environmental changes (Willis & Whittaker 2002; Wiens 2011; Fraterrigo *et al.* 2014). Our results based on unique sets of finely defined assemblages across study systems show that dragonfly –but not damselfly– assemblages are composed by more morphologically distinct species than expected at random, which supports a primary role of competition in driving their community assembly. The consistency of morphological overdispersion found across regions together with the number and resolution of assemblages involved, renders this study a uniquely strong case supporting the role of competition in animal community assembly. Variation in environmental stress and richness drove changes in the support for competition across space and season as expected from theoretical expectations. Competition was highest in warm locations and in species-rich assemblages, particularly during mid-summer –warm– conditions. This study therefore provides mechanistic insights into the spatial and also the poorly addressed phenological variation of insect community assembly.

Our consistent support for competition in dragonflies contrasts with the general absence of support for competition in animal community assembly (e.g. Kaplan & Denno 2007; Nakadai *et al.* 2018; Bird *et al.* 2019). Only 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 & 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- suborders 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 which was moreover robust to similar alternative trait combinations. Based on our results, the particular striking and continuous territorial disputes of dragonflies over reproductive habitats would shape community assembly by limiting the similarity of coexistent species. Other competition mechanisms are compatible with morphological overdispersion, although less likely in Odonata. Trophic exploitation -requiring limiting prey- is generally suggested unlikely for generalist predators feeding on abundant small flying insects (Kaunisto *et al.* 2017, e.g. in aerial-foraging bats: Arlettaz 1999; Kruger *et al.* 2014). Resource limitation is particularly unlikely in Odonata because both Odonata and their prey are active under the same thermal conditions. Moreover, trophic competition mediated by interference is only anecdotally reported in Odonata (Corbet 2004c).

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 Bavaria and GB but decreased in Catalonia, where summer temperature is not limiting. 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; Montano-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 (Suarez-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; Boye *et al.* 2019; Montano-Centellas *et al.* 2021), and calls for future research.

Phenological turnover in assemblage composition is among the least understood components of diversity variation. The observed seasonal patterns in FDses in the phenologically higher resolution dataset of GB suggests that dragonfly assembly processes change over the season, as has been reported in assemblages of fishes (Fitzgerald *et al.* 2017), carabid beetles (Marrec *et al.* 2021), and benthic macroinvertebrates (Wang *et al.* 2020). Variation in the support for competition over the season was explained by seasonal changes in temperature and richness, the same factors driving variation of assembly processes across space. Underdispersed FDses of early -cold- season assemblages became overdispersed following seasonal increases in temperature and richness until peaking in mid-summer, and then decreased. This pattern provides unique support for theoretical expectations on the drivers of competition, which would drive not only spatial, also phenological patterns of community assembly. Dragonfly early-season body size underdispersion was, moreover, driven by a high prevalence of large body-sized species, likely because large -endotherm- dragonflies are able to thermoregulate in colder, early-season conditions (May 1976). A similar pattern was found in Catalonia (Spain) where early and late season bee species had large body sizes, which was suggested to allow them to deal with cold temperatures (Osorio-Canadas *et al.* 2016). These results provide mechanistic understanding on the processes shaping the phenological variation of insect diversity and highlight that phenological patterns cannot be neglected if we aim for a comprehensive understanding of natural systems (Ramirez *et al.* 2015; Ponti & Sannolo 2022).

Damselfly community assembly

The lack of support for the role of competition on 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. Aromaa *et al.* 2019: $8.6 \pm 27.0\text{m}^2$ vs $99.1 \pm 323.6\text{m}^2$ respectively). 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 neither driven by the environmental factors considered nor by species richness, stressing previously supported differences in ecological drivers between dragonflies and damselflies (Carvalho *et al.* 2013; Oliveira-Junior & Juen 2019; Crabot *et al.* 2022). Despite being closely related, both suborders differ markedly regarding their morphology, mobility, habitat use and thermoregulatory physiology (Corbet 2004a). 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 microhabitat characteristics (Crabot *et al.* 2022) that were not assessed in this study.

Additional considerations

This study focuses on the adult stage of Odonata. While a complete understanding on Odonata community assembly would require the integration of both development stages (Grether *et al.* 2023), larval life may likely offer less opportunities for competitive exclusion because aquatic habitats provide a wider range of microhabitats (water column, sediments, vegetation), towards which specific lifestyle specialisation has evolved (borrower, deep borrower, clasper, hider, sprawler), allowing coexistence (Crowley & Johnson 1982). Larval interspecific predation from large to small individuals (Benke 1978) can occur between either morphologically dissimilar species or between morphologically similar species at different developmental stages (Grether *et al.* 2023), and therefore it is unlikely to result in the morphological overdispersion patterns reported in this study.

Conclusion and implications for climate change impacts

By combining mechanistic-driven functional approaches with sets of ecologically-sensible defined assemblages, our study develops generalised understanding on the ecological processes driving spatial and phenological patterns of insect community assembly. More complete understanding of assembly processes is essential for addressing the challenges arising from biodiversity changes caused by climate change. Odonata are well known to respond to present climate change with strong latitudinal (Hickling *et al.* 2005; Hassall *et al.* 2007; Grewe *et al.* 2013; Termaat *et al.* 2019) and phenological shifts (Scranton & Amarasekare 2017; De Lisle *et al.* 2022). Our support for the role of competition in dragonflies supports previous speculations (Ott 2001) suggesting that competition may play a relevant role in mediating future climate change effects in this taxa. Hence, colonising dragonflies to 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 uniquely useful study system to understand how climate change and biotic effects interact (Poloczanska *et al.* 2008; Tylianakis *et al.* 2008; Urban *et al.* 2013). For this, Mediterranean range-expanding species in central and north 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

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

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 +/- sd.

Analysis	Study region	S	n	Locations	Richness
		dr	da	dr	da
Main	GB	30	17	5454	1662
	Bavaria	45	21	96	80
	Catalonia	37	20	144	64
Phenological	Great Britain	28	16	1593	439

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 (Phenological). Coefficients are standardised. Assemblages of Great Britain within the main analysis were undersampled (see methods). sd shows, for the main analysis, parameter variation across 100 models using different assemblages subset.

Analysis	Model
Main	dr Multi-trait FDses ~ Temp*Study-region+ Richness +Day $F_{7,388}=14.54 \pm 1.67, R^2=0.19 \pm 0.02, p<0.001$
	Day
	Temp
	DatasetCat
	DatasetGB
	Temp*DatasetCat
	Temp*DatasetGB
Main	da Multi-trait Fdses ~Day*Study-region $F_{5,264}=13.61 \pm 2.42, R^2=0.19 \pm 0.03, p<0.001$
	DatasetCat
	DatasetGB
	Day*DatasetCat
Phenological	dr Multi-trait FDses ~Temp +Richness $F_{2,1553}=116.47, R^2=0.13, p<0.001$

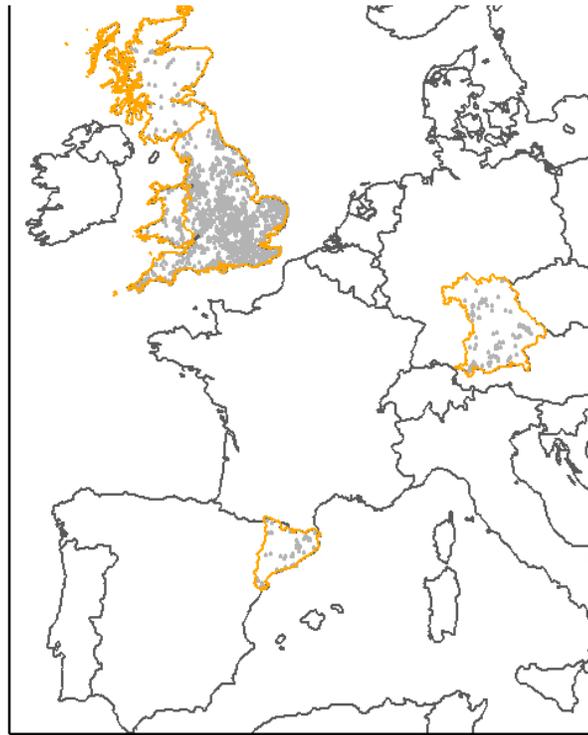


Figure 1: **Location of dragonfly and damselfly assemblages within the three complementary study regions of Great Britain (United Kingdom), Bavaria (SE Germany), and Catalonia (NE Spain).** F

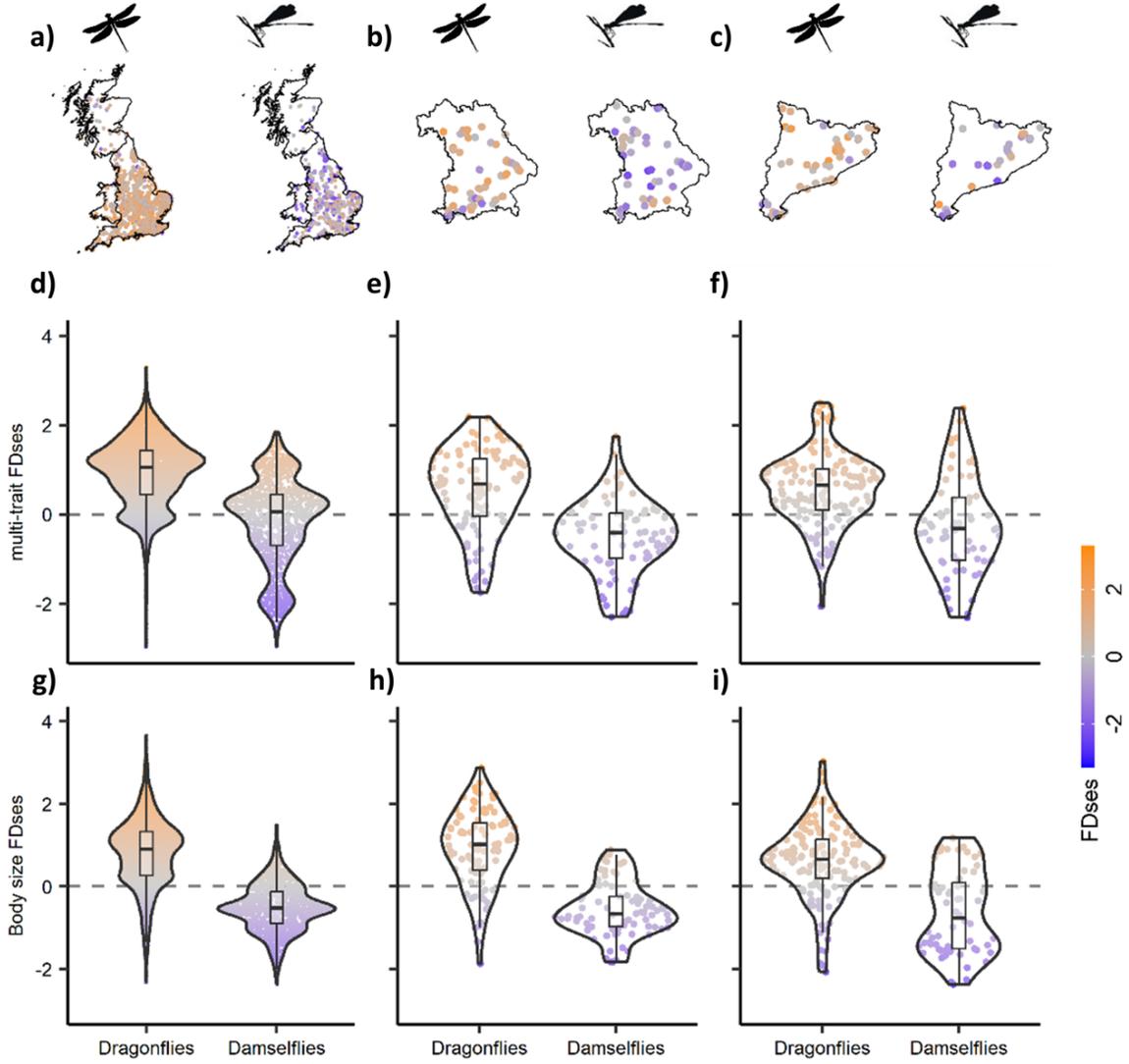


Figure 2: Functional diversity (FDses) of dragonfly and damselfly assemblages across the three European study regions of Great Britain (a, d, g), Bavaria (d, e, h), and Catalonia (c, f, i) based on multiple traits (a, b, c, d, e, f): body size, relative abdomen length, relative wing length, and colour, and based on body size alone (g, h, 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.

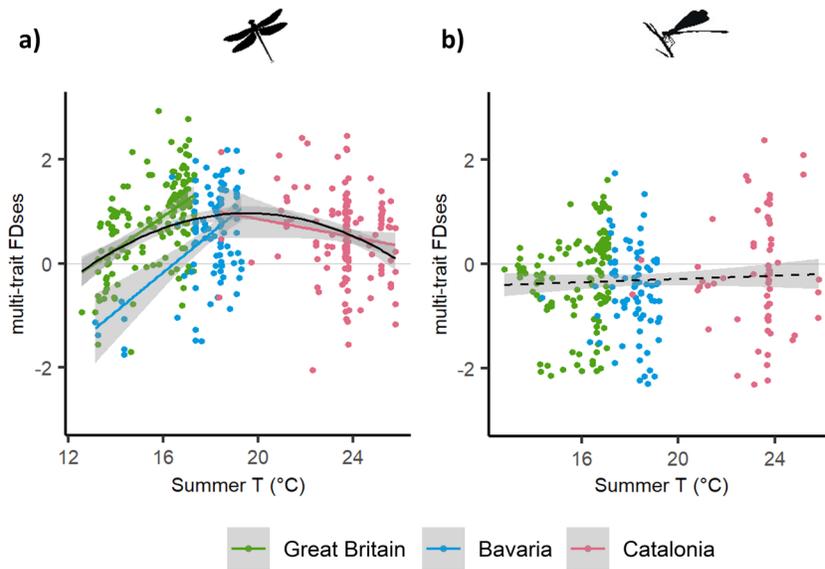


Figure 3: **Multi-trait FDses of (a) dragonfly and (b) damselfly assemblages depending on summer temperature across the study regions of Great Britain, Bavaria and Catalonia.** Solid coloured lines represent linear model including study region as interaction effect ($\text{Multi-trait FDses} \sim \text{Temp} * \text{Study-region}$). Black curved line indicates a linear model with a quadratic term without considering study region ($\text{Multi-trait FDses} \sim \text{Temp} + \text{Temp}^2$). Dashed line represents non significant model. Assemblages of Great Britain were undersampled (see methods). $\text{FDses} > 0$ indicates morphological overdispersion and $\text{FDses} < 0$ morphological underdispersion relative to random assemblages of equal richness.

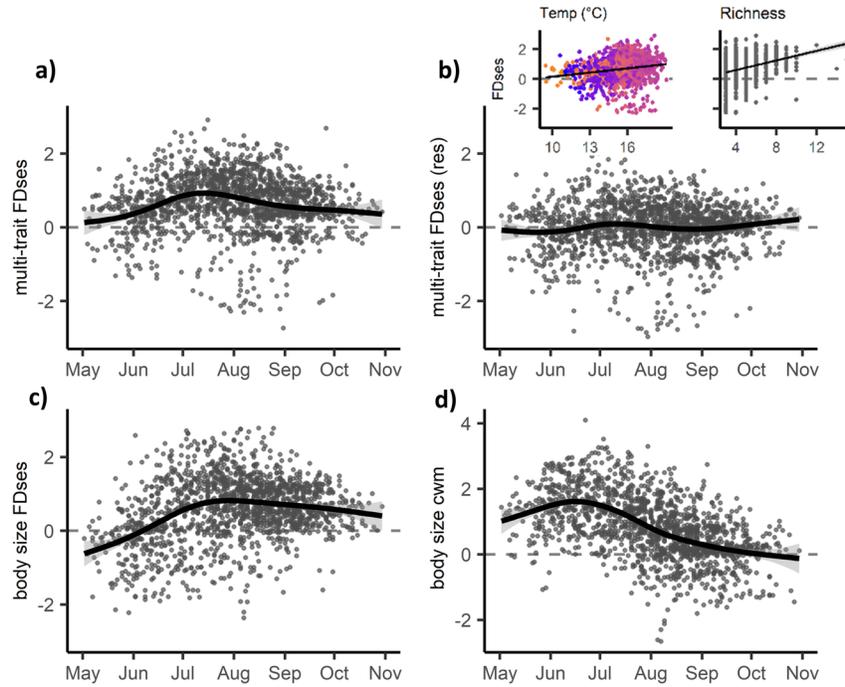


Figure 4: Phenological variation of functional diversity (FDses) of dragonfly assemblages in Great Britain over the flight season of the group (a) Variation of multi-trait FDses over the season. (b) Variation of residual multi-trait FDses over the season after removing the effects of temperature and richness (Insert: LM: $FDses \sim richness + temperature$. Colour indicates day of the year). (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. $FDses > 0$ indicates morphological overdispersion and $FDses < 0$ morphological underdispersion relative to random assemblages of equal richness.

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