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# Trait clustering at low and high temperatures: Seasonal changes in functional diversity of dragonfly assemblages in temperate forest streams

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# Trait clustering at low and high temperatures: Seasonal changes in functional diversity of dragonfly assemblages in temperate forest streams

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*We extend occurrence-based evidence with local abundance data. Seasonal tracking reveals trait clustering at both thermal extremes. This adds a temporal dimension to trait-based community ecology.*

**Author Contributions:** RM conceived the study and designed the research. RM conducted the field surveys, prepared the trait data, performed the image analyses, compiled the environmental data, conducted the statistical analyses, and wrote the original draft. RM and MY developed and verified the R code. RM, ST, SM, and MY interpreted the results. ST, SM, and MY critically revised the manuscript and supervised the study. All authors read and approved the final manuscript.

Abstract

Understanding the mechanisms that drive spatiotemporal variation in community assembly is a central challenge in ecology. Among the multiple temporal and spatial filters that shape species assemblages, seasonal environmental fluctuations at fine spatial scales have received little attention. We used repeated field surveys and a functional diversity approach to examine spatiotemporal variation in adult dragonfly assemblages along temperate forest streams. We surveyed adult dragonflies along five fixed routes from April to October 2025. Species abundances were combined with traits related to body size, wing and abdomen morphology, and body coloration. We calculated standardized functional diversity (FDses) from abundance-weighted functional dispersion using a null model that preserved observed species richness and abundance structure. Across 60 route censuses, 2,687 individuals representing 26 species were recorded. Species composition differed among months from June to October, and community-weighted means of several traits were significantly associated with this seasonal compositional change. We constructed linear mixed-effects models (LMMs) with FDses as the response variable, air temperature, solar radiation, and species richness as explanatory variables. The best-supported LMM included both linear and quadratic effects of air temperature. FDses increased with temperature but declined again under high-temperature conditions. By contrast, solar radiation and species richness were not included in the best model. Our results show that the functional structure of local adult dragonfly assemblages changes along seasonal

temperature gradients. These functional diversity patterns suggest that the observed seasonal changes in community structure are driven by seasonal variation in environmental filtering.

Word count: 242/250 words

Keywords:

Community; Environmental filtering; Functional traits; Odonata; Standardized effect size

## Introduction

Understanding the processes driving species assembly is a central challenge in community ecology. Species that colonize a local site are first subject to environmental filtering (Keddy 1992), followed by interspecific interactions that further shape species composition. Environmental filters are often represented by abiotic conditions that affect species survival, growth, and establishment at a given site, such as temperature and resource availability. On the other hand, in habitats where environmental constraints are relatively moderate, interspecific competition is expected to act as a major process shaping community composition (Pianka 1981; Barnagaud et al. 2021). In natural systems, these abiotic and biotic processes often operate in concert. Resolving their relative importance along ecological gradients can be a crucial step toward the effective conservation of biological communities.

Species traits are widely used to infer the relative importance of environmental filtering and interspecific competition. When environmental filtering is strong, species with functional traits that allow them to tolerate local conditions are more likely to persist. This process can cause co-occurring species to share similar traits, resulting in lower functional diversity (FD) than expected by chance, a pattern referred to as functional clustering (Götzenberger et al. 2012). In contrast, when interspecific competition is strong, competitive exclusion and niche differentiation among functionally similar species should favor the coexistence of species with

45 distinct functional traits (Schoener 1974). Such processes can lead to trait overdispersion, where
46 co-occurring species are more dissimilar in functional traits than expected by chance
47 (Götzenberger et al. 2012; de Bello et al. 2021).
48
49 While the spatial variation in assembly processes has been well documented, their temporal
50 variation has been less studied. Insects often show phenological shifts in community structure,
51 suggesting changes in assembly processes across seasonal climatic gradients (Wolda 1988;
52 Forrest and Miller-Rushing 2010). Several studies in tropical systems have focused on wet–dry
53 seasonal contrasts in FD, including studies of bees (Ramírez et al. 2015), fishes (Fitzgerald et
54 al. 2017), and stream benthic macroinvertebrates (Wang et al. 2020). These studies have shown
55 that FD can differ between the wet and dry seasons. By contrast, seasonal changes in FD remain
56 understudied in temperate regions, where air temperature and solar radiation show pronounced
57 seasonal changes. Understanding how community FD responds to seasonal environmental
58 factors can provide important insights into community assembly under climate change
59 (Wolkovich and Donahue 2021; Woods et al. 2022).
60
61 Dragonflies are an ideal taxonomic group for examining how the relative importance of
62 environmental filtering and interspecific competition in community assembly varies along
63 environmental gradients. Adult dragonfly activity is strongly regulated by body temperature,

which is driven by abiotic conditions, such as air temperature (May 1976) and solar radiation (Corbet 2004a). Adult males of many species spend much of their time defending territories, indicating a strong investment in biotic interactions (Moore 1964; Corbet 2004b). Recent trait-based studies have shown that competition can influence the functional structure of dragonfly assemblages (Oliveira-Junior et al. 2021; Neale and Rudolf 2023). Furthermore, dragonflies often exhibit marked phenological shifts in adult community structure (May 1976; Corbet 2004a). Recently, Novella-Fernandez et al. (2024) analyzed the FD of adult dragonfly assemblages using broad-scale occurrence records and showed that seasonal variation in FD was explained by temperature and species richness. Building on this work, abundance data can provide complementary information by accounting for variation in the relative dominance of co-occurring species, which is known to vary among habitats and along environmental gradients in dragonfly assemblages (Silva et al. 2010; De Marco Júnior et al. 2015). Presence–absence and abundance-weighted FD emphasize different aspects of community structure because the former gives equal weight to all species, whereas the latter also reflects differences in their relative dominance (Mouchet et al. 2010; Silva et al. 2024). To extend this approach, we repeatedly surveyed adult dragonfly assemblages throughout the season and calculated abundance-weighted FD to examine how the relative importance of environmental filtering and interspecific interactions varies along seasonal environmental gradients.

In this study, we applied the FD framework to adult dragonfly communities in a temperate region of Japan to examine how community assembly processes vary along seasonal environmental gradients. Specifically, we tested the following three hypotheses: (1) Both the compositional and functional structures of adult dragonfly communities shift significantly throughout the season; (2) Seasonal changes in FD are related to environmental variables such as temperature, because adult dragonfly activity is strongly regulated by body temperature; and (3) Seasonal changes in FD are related to species richness, reflecting the potential role of interspecific competition.

## Materials and Methods

### Study site and field surveys

We conducted this study at the Ashiu Forest Research Station of Kyoto University, located in Nantan City, Kyoto Prefecture, Japan (Fig. 1). The Ashiu Forest Research Station ranges in elevation from 355 to 959 m and lies in the transition zone from evergreen broad-leaved forests to deciduous broad-leaved forests. The research forest covers approximately 4,200 ha and includes extensive natural forests. The forest also encompasses most of the upper basin of the Yura River, and its headwater area includes raised bogs and other aquatic habitats that can serve as breeding sites for dragonflies.

Abundance surveys of adult dragonflies were conducted using the route census method. Five survey routes were established in the middle and headwater reaches of the Yura River basin. The five survey routes were 600, 860, 590, 710, and 790 m long. Because movement ability varies greatly among dragonfly species, it is difficult to define distances between sites or time intervals that completely eliminate the possibility of duplicate counts (Aromaa et al. 2019). To reduce this possibility as much as possible, adjacent survey routes were separated by at least 200 m. In addition, surveys at each pair of adjacent sites (a–b, c–d, and d–e; Fig. 1) were conducted consecutively, with no more than 15 min between surveys.

In this study, we focused on adult dragonflies. Dragonflies have an aquatic larval stage and a terrestrial and aerial adult stage, and therefore the habitats they use and the major ecological constraints they experience differ greatly between life stages (Crowley and Johnson 1982; Corbet 2004c). Adult habitat selection can strongly influence larval dragonfly assemblages; for example, French and McCauley (2018) found that adult habitat selection played a dominant role in structuring larval assemblages across a canopy-cover gradient, whereas canopy cover had no detectable effect on larval growth or survival. Therefore, this study did not address community assembly processes in the larval stage, but instead focused on seasonal community structure and functional diversity in the adult stage.

Surveys were carried out from 21 Apr 2025 to 14 Oct 2025, on sunny or slightly cloudy days with no wind or only light wind (Table 1). Censuses were conducted at least twice in each month from April to September at sites a and b, and from April to October at sites c, d, and e (Fig. 1; Table 1). During each census, observers walked along each survey route at a constant speed and recorded the species identity and number of individuals observed within 5 m on either side of the route. Dragonfly species were identified primarily from individuals observed in flight or at rest, based on external morphological features such as wing markings and patterns on the thorax and abdomen. Species with similar external morphology were captured with an insect net and identified based on wing venation and abdominal appendages. Species identification and taxonomy followed Ozono et al. (2022). When dense aggregations made precise counting difficult, individual counts were estimated to the nearest 10 individuals. Because route length differed among sites, these counts were standardized to the number of individuals $km^{-1}$ of route and used as abundance in subsequent analyses. Each community unit was defined as the species composition and abundance recorded during a single route census at a given site on a given survey date. A total of 60 route censuses were conducted during the survey period (Table 1). Three censuses conducted in April and May were excluded from community-level analyses because fewer than two species were recorded. The remaining 57 censuses, conducted from June to October, were treated as community units and used in the subsequent analyses of community composition and FD.

140

141 Functional trait data

142 To infer community assembly processes based on FD, it is necessary to select functional traits
143 that are ecologically relevant to species' niches (de Bello et al. 2021). We focused on four
144 traits—body volume as a proxy for body size, hindwing length, abdomen length, and body
145 coloration—as functional traits based on recent work on odonate functional ecology (Novella-
146 Fernandez et al. 2024). Body size is generally regarded as one of the most important traits
147 associated with physiological performance and ecological niches in animals (Schmidt-Nielsen
148 1984; Peters 1986). Hindwing length of dragonflies is related to gliding and dispersal ability,
149 and, together with abdomen length, may also influence flight maneuverability (Wootton 1991;
150 Sacchi and Hardersen 2013). Body coloration is known to be important for thermoregulation
151 (May 1976; Corbet 2004a).

152

153 The four traits were measured for all species observed during the survey period. For each
154 species, image-based measurements were obtained from a mature male, using one dorsal image
155 for body volume and one lateral image for body coloration. Body volume was estimated from
156 dorsal images obtained from Odonata of KOBE (https://www.odonata.jp/; last accessed 30 July
157 2026) using ImageJ 1.54g (Abramoff et al. 2004) and a custom macro based on a solid-of-
158 revolution approximation. After extracting the body outline by thresholding, a longitudinal

159 body axis was manually defined from the head to the abdominal tip. At 1-pixel intervals along
160 this axis, body width perpendicular to the axis was measured and treated as the diameter of a
161 circular cross-section. Body volume was estimated by summing these cross-sectional volumes
162 along the body axis. Pixel dimensions were converted to metric units using a species-specific
163 scale factor calculated from the ratio of species mean body length measured from specimens to
164 body-axis length in pixels, and body volume was expressed in $mm^3$. This calculation assumes
165 that the body is approximately rotationally symmetric around its longitudinal axis. Body
166 coloration was quantified from lateral images of mature males obtained from Odonata of KOBE.
167 Before analysis, the wings and legs were removed from each image. The body area was
168 identified by converting a copy of each image to 8-bit grayscale and applying a threshold. The
169 original image was then separated into red, green, and blue (RGB) channels, and the mean
170 intensity of each channel was measured within the body area. These RGB values were used as
171 measures of body coloration following previous image-based approaches (Zeuss et al. 2014;
172 Pinkert et al. 2017). Hindwing length, abdomen length, and body length were measured from
173 3–5 mature male specimens collected in the Ashiu Forest Research Station and averaged for
174 each species, except for *Tanypteryx pryeri* and *Sarasaeschna pryeri*, for which only one mature
175 male specimen could be obtained. To reduce collinearity among traits caused by body size,
176 hindwing length and abdomen length were expressed relative to body length. These ratios are
177 hereafter referred to as relative hindwing length and relative abdomen length, respectively.

178 Pairwise correlations among traits were generally low ($r < 0.7$), except between the blue and
179 green color components (Online Resource 1: Fig. S1).
180
181 Because estimates of functional diversity can depend on the choice and weighting of traits, we
182 evaluated the robustness of our results using alternative trait sets (de Bello et al. 2021). For the
183 primary analysis, we calculated FD using four equally weighted trait categories: body size,
184 relative abdomen length, relative hindwing length, and body coloration (Set 1). Body coloration
185 was represented by three variables (R, G, and B), each assigned one-third of the weight of the
186 other single-variable traits so that coloration as a whole had the same total weight as each of
187 the other trait categories (de Bello et al. 2021). Equal weighting of trait categories is commonly
188 used in functional diversity analyses (Palacio et al. 2022). We then conducted two sensitivity
189 analyses. First, we calculated FD using body size alone (Set 2), because body size is widely
190 regarded as a key trait related to animal performance and ecological niches (Fraser et al. 2017;
191 Fernandez-Fournier et al. 2018; Pineda-Munoz et al. 2021). Second, following Novella-
192 Fernandez et al. (2024), we used an alternative weighting scheme in which body size accounted
193 for half of the total trait weight (Set 3). This analysis was used to assess the sensitivity of our
194 conclusions to trait weighting by placing greater emphasis on body size.
195
196 Environmental data

197 Air temperature and solar radiation were used as environmental predictors of variation in FD.
198 Because adult dragonfly activity is strongly constrained by body temperature (May 1976), air
199 temperature (May 1976) and solar radiation (Corbet 2004a) were included as key variables
200 related to thermoregulation. Air temperature and solar radiation were continuously recorded at
201 10-min intervals by meteorological stations located near sites a and c (Fig. 1). Survey data from
202 sites a and b were matched with meteorological data from the station near site a, whereas survey
203 data from sites c, d, and e were matched with data from the station near site c. For each route
204 census, we used the mean values recorded from the start to the end of the census for each
205 environmental variable. Species richness was also included as an explanatory variable to
206 evaluate the prediction that competitive effects are stronger in species-rich communities under
207 low abiotic stress (Pianka 1966).
208
209 Calculation of standardized functional diversity (FDses)
210 As an index of FD, we calculated functional dispersion (FDis) using the R package FD (Version
211 1.0-12.3; Laliberté and Legendre 2010). FDis quantifies the mean distance of species to the
212 centroid of multidimensional trait space and therefore reflects multidimensional variation in
213 functional traits. FDis is also relatively robust to changes in species richness and can incorporate
214 abundance-based weighting (Laliberté and Legendre 2010). Based on these properties, we
215 considered FDis an appropriate index for this study of dragonfly communities characterized by

marked seasonal variation in species richness and abundance. Rao's quadratic entropy (RaoQ; Rao 1982) was also calculated, but it was not included in subsequent analyses because it was strongly correlated with FDis across all trait sets ($r > 0.94$, $P < 0.001$). Functional trait values were standardized to zero mean and unit variance before the FD and CWM analyses. A functional distance matrix among species was then constructed using Gower distance. Abundance-weighted FDis was calculated for each community unit.

Although FDis is relatively robust to variation in species richness, observed FDis values can still be influenced by the number of species in a community, making it difficult to separate variation in trait structure from variation in species richness based on observed values alone (Petchey and Gaston 2002). Therefore, following Kraft et al. (2011), we performed randomization-based standardization. Specifically, species richness and the abundance of each species within each community were kept fixed, while the complete trait vector of each species was randomly reassigned among species. All traits of a species were shuffled together, thereby preserving correlations among traits while randomizing only the correspondence between species identity and trait values. This randomization was repeated 999 times to generate a null distribution of FDis for each community. In other words, this method allowed us to evaluate whether observed trait clustering or overdispersion exceeded the expectation based on species richness and abundance structure alone. FDis was calculated for each randomized community

(FDis_null), and the observed FDis was standardized as a Z-score using the mean and standard deviation of the null distribution. This Z-score was defined as standardized FD (FDses; Gotelli and McCabe 2002) and was calculated using the following equation:

$$FDses = (FDis_{observed} - mean(FDis_{null})) / SD(FDis_{null})$$

FDses was interpreted relative to 0. Positive values indicate that traits within a community are more overdispersed than expected under the null model. By contrast, negative values indicate stronger trait clustering than expected under the null model.

## Statistical analyses

### Community–trait structure

For the analysis of community structure, each combination of day of year (DOY) and survey site was defined as a community unit, and a community unit × species matrix was constructed, with species abundance entered in each cell. To visualize similarities in species composition among communities, we used non-metric multidimensional scaling (NMDS). Bray–Curtis distance was used as the dissimilarity measure among communities. A two-dimensional NMDS solution was adopted, and the solution with the lowest stress value was selected from multiple random starts to reduce the influence of initial configurations. Each point in the resulting

NMDS space represented a community unit.

To test whether community composition differed among months, we conducted permutational multivariate analysis of variance (PERMANOVA) based on Bray–Curtis dissimilarities. Month was treated as a categorical factor. Because the same five survey sites were repeatedly surveyed throughout the season, statistical significance was assessed using 999 permutations restricted within each survey site. Homogeneity of multivariate dispersion among months was evaluated using betadisper, with significance likewise assessed using 999 permutations restricted within each survey site.

To quantify the functional characteristics of each community unit, we calculated community-weighted means (CWMs) for each trait. For each community unit, the relative abundance of each species was calculated as its abundance divided by the total abundance of all species in that unit. CWM was then calculated as the weighted mean of species trait values using these relative abundances as weights.

To evaluate associations between community compositional variation and functional traits, community-weighted mean (CWM) values were fitted onto the NMDS ordination using envfit. The envfit fits each trait gradient as a vector onto the ordination space, indicating the direction

and strength of its association with community composition. The significance of each trait vector was assessed using the same set of 999 permutations restricted within each survey site. All community-structure analyses were performed using the R package vegan (Version 2.7-2; Oksanen et al. 2025).

Seasonal changes in functional diversity

To examine how FD in local dragonfly communities varied with seasonal changes in environmental conditions and species richness, we used linear mixed-effects models (LMMs). FDses was used as the response variable.

Solar radiation (Solar), air temperature (Temp), and species richness (Species) were included as candidate fixed effects that may explain variation in FDses. Although species richness was held constant in the null model used to calculate FDses, we included it in the LMM to test whether the degree of functional clustering or overdispersion changed with the number of species in a community. This also allowed us to evaluate the prediction that competitive effects would be more evident in species-rich communities (Pianka 1966). In addition, recent studies of animal communities along spatial temperature gradients have suggested that FD may plateau and subsequently decline with increasing temperature (Lazarina et al. 2023; Novella-Fernandez et al. 2024). To test whether a similar pattern occurred along seasonal temperature gradients, a

quadratic term for air temperature was included as a fixed effect. Survey site was included as a random intercept to account for differences among sites. Linear mixed-effects models were fitted using the R package lme4 (Version 1.1-37; Bates et al. 2015).

For model selection, we fitted all possible subsets of the candidate fixed effects, with the constraint that the quadratic temperature term was included only together with the linear term, and compared them using AICc (Akaike's information criterion corrected for small sample size). AICc values and all-subset model comparisons were obtained using the R package MuMIn (Version 1.48.11; Bartoń 2025). To allow likelihood-based comparisons among models with different fixed effects, candidate models were fitted using maximum likelihood. The model with the lowest AICc was defined as the best-supported model, and models with $\Delta AICc < 2$ were considered competitive models. After model selection, competitive models were refitted using restricted maximum likelihood. Fixed-effect estimates, degrees of freedom, and P-values were obtained from the REML-refitted models using the R package lmerTest (Version 3.2-1; Kuznetsova et al. 2017). Marginal and conditional $R^2$ values were calculated for the REML-refitted models using the R package performance (Lüdecke et al. 2021), following Nakagawa et al. (2017). Model assumptions for the best-supported REML-refitted models were evaluated using plots of standardized residuals against fitted values and normal Q–Q plots (Online Resource 1: Fig. S2). We also examined the variance of the random intercept for survey site

and checked model singularity using isSingular in the R package lme4 (Online Resource 1: Table S4). Because the number of survey sites was limited to five, we additionally repeated the all-subset AICc model selection with survey site treated as a fixed effect rather than a random intercept. The same candidate environmental variables and the same hierarchy constraint for the quadratic temperature term were used in this sensitivity analysis (Online Resource 1: Table S5). All analyses were conducted in R version 4.5.1 (R Core Team 2025).

## Results

During the survey period, we conducted a total of 60 route censuses across five sites and recorded 2,687 adult dragonfly individuals representing 26 species. *Sympetrum frequens* was the dominant species, accounting for 41.3% of the total abundance. This was followed by *Calopteryx cornelia* (13.7%) and *Sympetrum darwinianum* (12.2%), and these three species together accounted for 67.2% of the total. In contrast, *Lanthus fujiacus*, *Lestes temporalis*, and *Sympetrum risi* were each represented by only a single individual (Online Resource 1: Table S1).

### Community composition and trait structure

The NMDS ordination represented variation in species composition among dragonfly communities, defined by each combination of survey date and survey site, in a two-dimensional

space. The final stress value of the NMDS based on Bray–Curtis dissimilarity was 0.176. The ordination showed a seasonal shift in community composition, primarily along NMDS1 (Fig. 2). PERMANOVA showed a significant effect of Month on community composition (Table 2). The betadisper test showed no significant difference in multivariate dispersion among months (Table 2).

Fitting CWMs onto the NMDS ordination using envfit showed significant associations between community composition and body size, relative hindwing length, relative abdomen length, and red coloration (Fig. 2; Table 3). Among these traits, red coloration showed the strongest association with the ordination, followed by relative hindwing length, relative abdomen length, and body size. In contrast, neither blue nor green coloration was significantly associated with the ordination (Table 3).

Seasonal changes in functional diversity

Across the three trait sets, the lowest-AICc model consistently included the linear and quadratic terms of air temperature. In all three best-supported models, Temp had a positive coefficient, whereas $Temp^2$ had a negative coefficient, indicating that FDses increased with air temperature but declined again under high-temperature conditions (Fig. 3; Table 4; Online Resource 1: Tables S2, S3). By contrast, Solar and Species were not included in the lowest-AICc model for

any trait set (Table 4; Online Resource 1: Table S2).

For Sets 1 and 3, the model including Temp and Temp² was the only competitive model (ΔAICc < 2), and both temperature terms were statistically significant in the REML-refitted best-supported models. For Set 2, the same model had the lowest AICc, but three models were within ΔAICc < 2 and neither temperature term was statistically significant (Table 4; Online Resource 1: Tables S2, S3).

Residual diagnostic plots showed no substantial heteroscedasticity or other systematic residual patterns, although slight departures from normality were apparent in the upper tails for Sets 2 and 3 (Online Resource 1: Fig. S2). None of the best-supported models showed a singular fit, and the random intercept variance for survey site was estimated above zero for all three trait sets (Online Resource 1: Table S4). Treating survey site as a fixed effect produced the same best-supported model structure with respect to temperature for all three trait sets, with temperature coefficients similar to those obtained from the random-intercept models (Online Resource 1: Table S5).

## Discussion

This study examined phenological changes in community structure and assembly processes in

368 adult dragonfly communities using cross-seasonal field surveys. The results of NMDS and
369 PERMANOVA support our first hypothesis that both compositional and functional structures
370 of adult dragonfly communities change with season. The associations between CWM values
371 and the NMDS ordination further indicated that these compositional changes were accompanied
372 by shifts in multiple functional traits (Fig. 2; Tables 2, 3). Our second hypothesis was also
373 broadly supported. Specifically, air temperature was–associated with the FD of dragonfly
374 communities; FDses increased under favorable temperature conditions but declined again under
375 high-temperature conditions (Fig. 3; Table 4; Online Resource 1: Tables S2, S3). The similar
376 temperature responses obtained when survey site was treated as either a random or fixed effect
377 further indicate that this pattern was not sensitive to how the five survey sites were represented
378 in the models (Online Resource 1: Table S5). Our third hypothesis, which predicted stronger
379 competitive effects in species-rich communities, was not supported. Species richness was not
380 included in the lowest-AICc model, and variation in FDses was better explained by air
381 temperature than by species richness (Fig. 3; Table 4; Online Resource 1: Table S2).
382 Furthermore, FDses values at moderate temperatures were close to 0 (Fig. 3). Thus, no clear
383 functional overdispersion was observed throughout the season. Novella-Fernandez et al. (2024)
384 previously showed consistent functional overdispersion in adult dragonfly assemblages and
385 demonstrated that seasonal variation in FD was associated with temperature and species
386 richness using presence–absence data. Our abundance-weighted analysis extends this

perspective by incorporating seasonal changes in the relative dominance of species. Presence–absence and abundance-weighted FD emphasize different aspects of community structure because the former gives equal weight to all species, whereas the latter also reflects their relative dominance (Mouchet et al. 2010; Silva et al. 2024). Because the relative dominance of dragonfly species is known to vary among habitats and along environmental gradients (Silva et al. 2010; De Marco Júnior et al. 2015), repeated abundance data allowed us to evaluate seasonal temperature responses in functional structure.

We observed low FDses in low-temperature seasons, indicating environmental filtering (Fig. 3). Because dragonflies are ectotherms and their adult activity is constrained by body temperature (May 1976; Corbet 2004a), species capable of flight activity, foraging, and reproductive behavior are likely to be restricted under low-temperature conditions. Previous studies have shown that thermal performance differs among dragonflies according to functional traits. Larger species can maintain thoracic temperature more effectively, whereas some small species remain active under cool conditions because they have lower minimum flight temperatures (Sformo and Doak 2006). Body coloration is also associated with thermal conditions, with darker dragonfly assemblages occurring during cooler parts of the flight season, consistent with improved heat absorption under low solar radiation (Novella-Fernandez et al. 2023). These trait-dependent thermal strategies suggest that low-temperature conditions may selectively

406 favor species with combinations of functional traits, resulting in the reduced FDses observed in
407 our study.
408
409 FDses showed a hump-shaped response to temperature, with functional clustering observed
410 under both low- and high-temperature conditions (Fig. 3; Table 4; Online Resource 1: Tables
411 S2, S3). This pattern suggests that increasing air temperature does not simply relax activity
412 constraints on adult dragonflies. Rather, during warmer seasons, species with particular traits
413 became dominant, leading to renewed convergence in community trait composition.
414 Specifically, traits related to thermoregulation and flight activity are closely associated with the
415 ability to remain active under high-temperature conditions (May 1976; Schmidt-Nielsen 1984;
416 Peters 1986). The decline in FDses may therefore reflect the relative dominance of species with
417 traits suited to high-temperature conditions.
418
419 Furthermore, the decline in FDses observed under high-temperature conditions suggests that
420 increasing temperature does not necessarily lead to greater functional diversification in
421 dragonfly communities. This has important implications for understanding the responses of
422 dragonflies to warming. Rising air temperatures may relax activity constraints imposed by low
423 temperatures, but above a certain temperature threshold they may also favor species with traits
424 suited to high-temperature conditions. In this case, warming may lead not only to changes in

425 species richness and abundance, but also to the homogenization of the functional structure of
426 local communities by promoting trait convergence. Nevertheless, this study was based on
427 observational data on within-season variation and did not directly test community responses to
428 long-term climate change. Therefore, the results should be interpreted not as a direct prediction
429 of warming effects, but rather as mechanistic evidence suggesting that increasing temperature
430 can alter the functional structure of adult dragonfly communities.
431
432 This study shows that the functional structure of adult dragonfly communities changes along
433 short-term seasonal environmental gradients. Previous studies of FD have often focused on
434 broad-scale environmental gradients, such as latitudinal and elevational gradients (Van der Plas
435 et al. 2012; Fernandez-Fournier et al. 2018; Müller et al. 2022). Such studies are valuable for
436 clarifying relationships between broad-scale climatic conditions and FD. By contrast, focusing
437 on seasonal environmental gradients is important for understanding how the trait composition
438 of local communities changes over time (Wolda 1988; Forrest and Miller-Rushing 2010;
439 Tatsumi et al. 2019). In insects, where the timing of adult emergence differs markedly among
440 species, seasonal changes in community structure may provide important information for
441 understanding community assembly processes (Forrest and Miller-Rushing 2010; Ponti and
442 Sannolo 2023; Shinohara et al. 2023). Our study therefore highlights the value of integrating
443 seasonal dynamics with FD to improve our understanding of how community assembly

processes change throughout the season.

It should be noted that further verification is needed to interpret the FDses patterns. In the present study, trait clustering and overdispersion were interpreted as reflecting environmental filtering and competitive exclusion or niche differentiation, respectively (Götzenberger et al. 2012; de Bello et al. 2021). However, when trait structure and phylogenetic structure are concordant (i.e., phylogenetic niche conservatism), even if the observed communities are functionally biased, it is not possible to distinguish whether this is the result of filtering by the local environment or interspecific competition, or whether the pool of species capable of occurring during a given period is itself phylogenetically biased (de Bello et al. 2012; Kraft et al. 2015). Recent studies of dragonfly communities have reported both phylogenetic clustering and trait overdispersion, but these patterns are not consistent across studies (Saito et al. 2016; Novella-Fernandez et al. 2024). Future studies that integrate trait and phylogenetic structure may help disentangle the effects of phylogenetic constraints from environmental filtering and thereby improve interpretations of community assembly processes.

In conclusion, our results demonstrate that the FD of local adult dragonfly communities shifts along seasonal environmental gradients, with trait clustering occurring under both low- and high-temperature conditions. These findings suggest that seasonal variation represents an

important gradient shaping community assembly. The nonlinear response of FDses to the temperature gradient reflects seasonally fluctuating assembly processes that cannot be captured by snapshot approaches, highlighting the importance of repeated temporal surveys. Future studies integrating multi-year data, diverse aquatic habitats, and larval-stage community data will enable direct tests of how rising air temperatures affect the functional structure of dragonfly communities.

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**Declarations**

**Funding**

No funds, grants, or other support was received.

**Competing interests**

The authors have no competing interests to declare that are relevant to the content of this article.

**Ethics approval**

This study did not involve human participants, human data, laboratory animals, or animal experiments requiring approval by an institutional ethics committee. Field surveys and specimen sampling at Ashiu Forest Research Station were conducted with permission from the Field Science Education and Research Center, Kyoto University (permit no. Ashiu-2025-106) and in accordance with all applicable institutional, local, and national regulations.

**Consent to participate**

Not applicable.

## Consent for publication

Not applicable.

## Availability of data and material

The data supporting the findings of this study, including species identities, site identities, survey dates, and environmental data, are openly available in the Zenodo repository at https://doi.org/10.5281/zenodo.23153353

## Code availability

The R code used in this study is openly available in the Zenodo repository at https://doi.org/10.5281/zenodo.23153353

## Authors' contributions

*We extend occurrence-based evidence with local abundance data. Seasonal tracking reveals trait clustering at both thermal extremes. This adds a temporal dimension to trait-based community ecology.*

RM conceived the study and designed the research. RM conducted the field surveys, prepared the trait data, performed the image analyses, compiled the environmental data, performed the statistical analyses, and wrote the original draft of the manuscript. RM and MY developed and verified the R code. RM, ST, SM, and MY interpreted the results. ST, SM, and MY critically revised the manuscript and supervised the study. All authors read and approved the final manuscript.

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## Tables

Table 1. Summary of the five study sites used in the dragonfly community survey. Route length indicates the length of the census route, and survey period indicates the first and last survey dates. Number of censuses indicates the number of sampling events, and species richness indicates the total number of dragonfly species recorded during the study period.

| Sites | Route length (m) | Survey period | Number of censuses | Species richness |
|---|---|---|---|---|
| a | 600 | 21 Apr 2025 – 19 Sep 2025 | 11 | 12 |
| b | 860 | 21 Apr 2025 – 19 Sep 2025 | 11 | 11 |
| c | 590 | 22 Apr 2025 – 14 Oct 2025 | 13 | 15 |
| d | 710 | 22 Apr 2025 – 14 Oct 2025 | 12 | 19 |
| e | 790 | 22 Apr 2025 – 14 Oct 2025 | 13 | 19 |

Table 2. Results of PERMANOVA and betadisper analyses based on Bray–Curtis dissimilarities among dragonfly communities. PERMANOVA tested whether community composition differed among calendar months from June to October, and betadisper tested the homogeneity of multivariate dispersion among months. Statistical significance was assessed using 999 permutations restricted within survey sites. $R^2$ indicates the proportion of variation in community composition explained by Month in the PERMANOVA.

| Analysis | Factor | df | Sum of squares | $R^2$ | F value | p value |
|---|---|---|---|---|---|---|
| PERMANOVA | Month | 4 | 4.524 | 0.282 | 5.103 | 0.001 |
| betadisper | Month | 4 | 0.089 | — | 1.294 | 0.251 |

Table 3. Results of envfit analyses testing associations between community-weighted mean trait values and the NMDS ordination of dragonfly communities. NMDS1 and NMDS2 indicate the directions of fitted trait vectors in the ordination space, and $r^2$ indicates the strength of the association between each trait and the NMDS configuration. Statistical significance was assessed using 999 permutations restricted within survey sites.

| Trait | NMDS1 | NMDS2 | $r^2$ | p value |
|---|---|---|---|---|
| Body size | 0.991 | 0.130 | 0.201 | 0.001 |
| Relative hindwing length | 0.874 | −0.485 | 0.583 | 0.001 |
| Relative abdomen length | −0.800 | 0.601 | 0.426 | 0.001 |
| Red component | 0.782 | −0.623 | 0.681 | 0.001 |
| Green component | −0.564 | −0.826 | 0.017 | 0.868 |
| Blue component | −0.986 | 0.167 | 0.115 | 0.068 |

Table 4. Summary of the best-supported linear mixed-effects models explaining seasonal variation in standardized functional diversity (FDses) across three trait sets. FDses was used as the response variable, while temperature (Temp), the quadratic term of temperature (Temp²), species richness, and solar radiation were considered as candidate fixed effects. Survey site was included as a random intercept. Competitive models were defined as models with $\Delta AICc < 2$. Asterisks indicate significance levels of fixed effects in the REML-refitted best models: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, and † $p < 0.10$. Marginal $R^2$ indicates the variance explained by fixed effects, whereas conditional $R^2$ indicates the variance explained by both fixed and random effects.

| Trait set | Best model | Competitive models | Temp estimate | Temp² estimate | Marginal R² | Conditional R² |
|---|---|---|---|---|---|---|
| Set 1 | Temp + Temp² | 1 | 1.747*** | −0.032*** | 0.227 | 0.418 |
| Set 2 | Temp + Temp² | 3 | 0.740† | −0.013† | 0.089 | 0.223 |
| Set 3 | Temp + Temp² | 1 | 1.460** | −0.027** | 0.186 | 0.334 |

## Figure legends

**Fig. 1** Study sites in the Ashiu Forest Research Station, Kyoto, Japan.

The map shows the location of the Ashiu Forest Research Station within Japan and the positions of the five survey sites a–e within the Research Station. Blue lines indicate streams, and grey lines indicate contour lines. Photographs show representative habitats at sites (a)–(e), corresponding to the sites shown on the map. Map data were provided by the Ashiu Forest Research Station, Kyoto University.

**Fig. 2** NMDS ordination of dragonfly communities.

Non-metric multidimensional scaling (NMDS) ordination of dragonfly communities based on Bray–Curtis dissimilarities. Each point represents a community unit defined by a combination of survey date and site, and points are colored by month. Arrows indicate community-weighted mean trait vectors fitted onto the NMDS ordination using envfit with 999 permutations. The fitted trait vectors represent body size, wing length (relative hindwing length), abdomen length (relative abdomen length), and the red, green, and blue components of body coloration. NMDS stress = 0.176.

**Fig. 3** Relationships between environmental variables, species richness, and standardized functional diversity (FDses) of dragonfly communities.

FDses denotes standardized functional diversity and was calculated using Set 1, the primary trait set. Each point represents one community unit defined by a combination of survey date and site. (a) Relationship between air temperature and FDses. The solid line represents the fixed-effect prediction from the best-supported linear mixed-effects model including the linear and quadratic terms of air temperature, and the shaded area indicates the 95% confidence interval. (b) Relationship between solar radiation and FDses, and (c) relationship between species richness and FDses. For solar radiation and species richness, only observed values are shown without fitted regression lines.

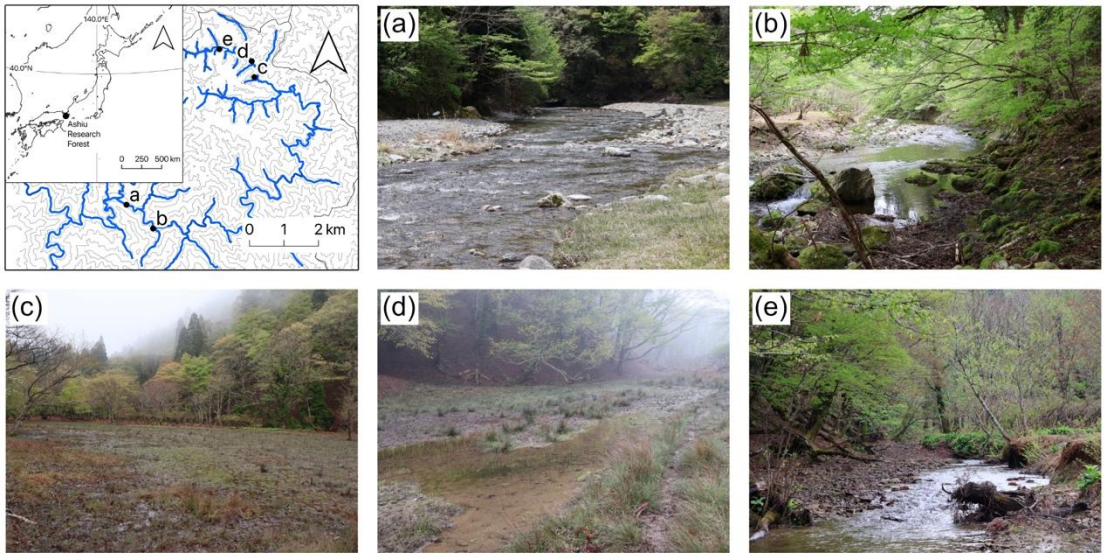

140.0°E
40.0°N
Ashiu Research Forest
0 250 500 km
e
d
c
a
b
0 1 2 km
(a)
(b)
(c)
(d)
(e)

Fig. 1

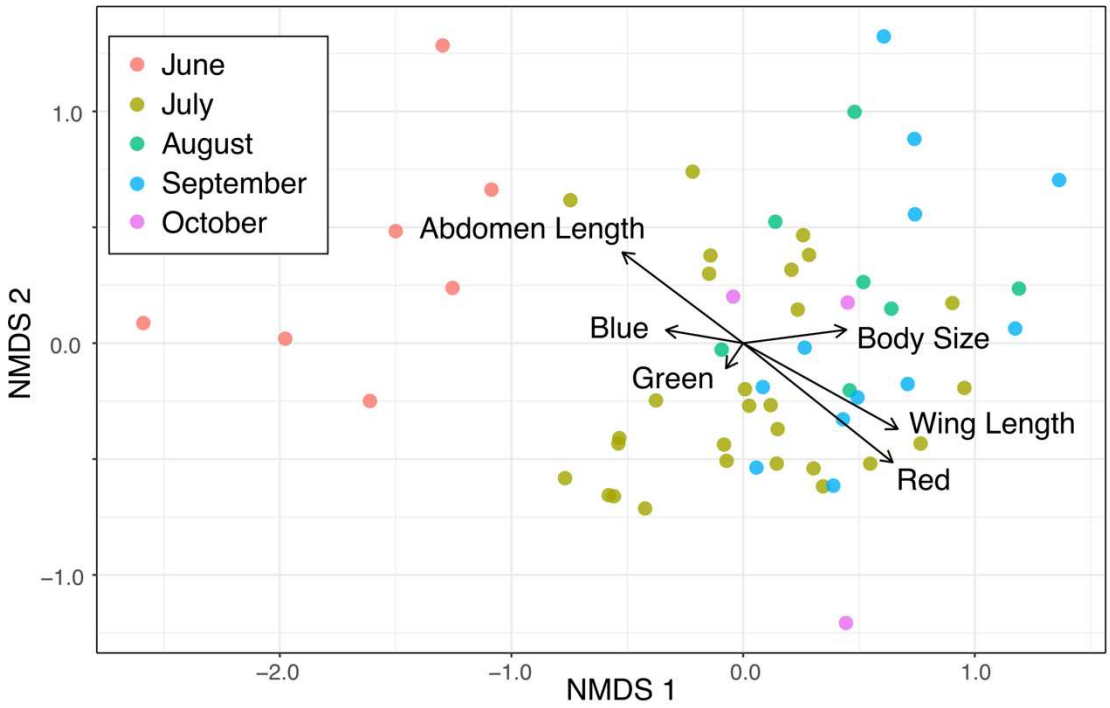

June
July
August
September
October
Abdomen Length
Blue
Body Size
Green
Wing Length
Red
NMDS 1
NMDS 2
1.0
0.0
−1.0
−2.0
−1.0
0.0
1.0

Fig. 2

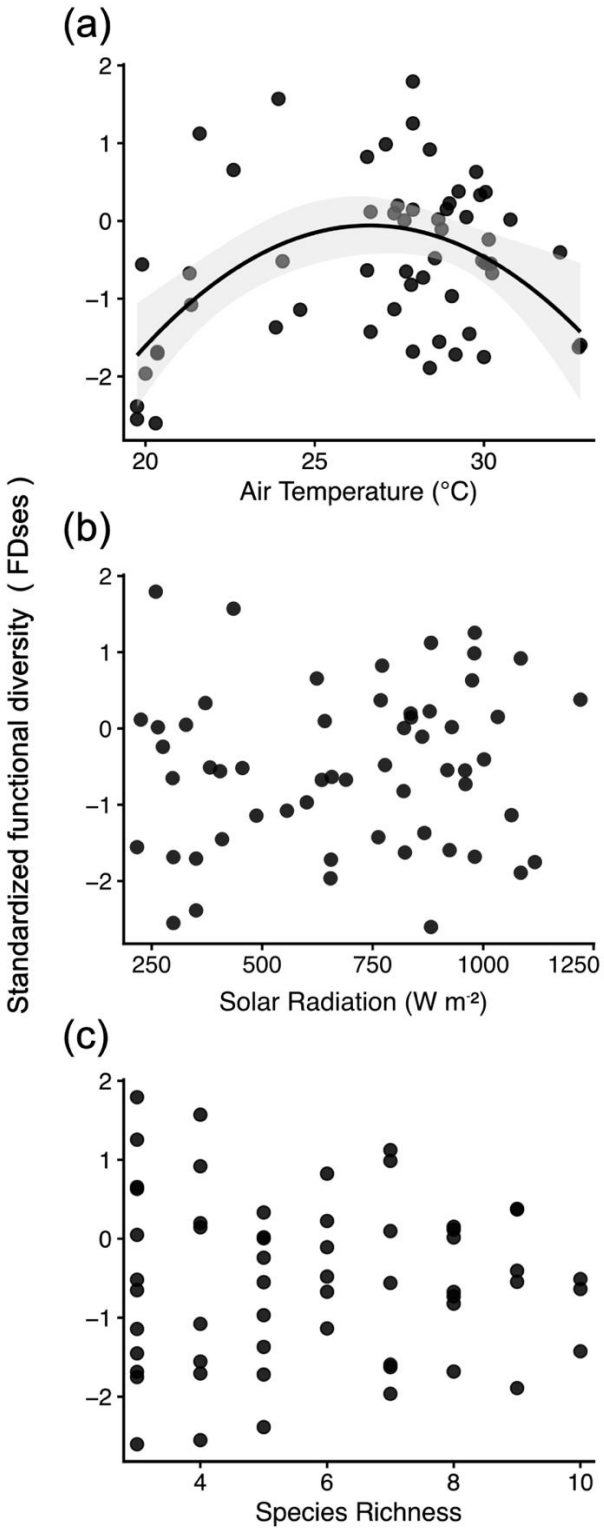

(a)
(b)
(c)
Standardized functional diversity ( FDses )
Air Temperature (°C)
Solar Radiation (W m-2)
Species Richness

Fig. 3

## Supplementary Files

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