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How hydrology and landscape shape Odonata assemblages in marshlands crossed by ditches

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Running head: Odonata assemblages in marshlands crossed by temporary ditches

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Abstract

1. One of the major current ecological challenges is to understand how to reconcile human activities with biodiversity conservation concerns. This issue is particularly relevant in freshwater ecosystems where biodiversity is globally under severe threat. Artificial waterbodies, such as ditch networks, are part of the few remaining wetlands in agricultural landscapes and hence play a crucial role in maintaining aquatic biodiversity in these landscapes.
2. We investigated the responses of adult Odonata assemblages at different spatial scales in a marshland crossed by ditches to two factors expected to be pivotal influences on assemblages. At the local scale, this was mainly the water regime in ditches and, at a broader scale, the composition of the landscape. Both taxonomic alpha and beta diversity, and functional trait composition were considered as response variables.
3. Significant differences were found between the responses of the two Odonata suborders. We showed that Zygoptera species richness decreased and species turnover increased with the duration of drying episodes in ditches. Geographical distances between local assemblages as well as landscape characteristics, notably woodland cover, meadow cover, and ditch network length, also significantly shaped the distribution of Zygoptera. For Anisoptera, species richness was not explained by environmental variables and beta diversity was associated only with local conditions; it increased with increasing dissimilarity in water quality and riparian vegetation. We also found evidence of functional trait syndromes (combinations of correlated traits) in Odonata assemblages, but without clear relationships to environmental gradients.
4. This study reveals the structuring role of water regime for Odonata in ditch networks and demonstrates the need to jointly consider environmental variables at different spatial scales to properly understand the distribution of Odonata.

26 5. Our findings have important conservation implications as the water regime is heavily
27 managed in such ecosystems. Even though the relationship between functional
28 composition and environmental gradients was found to be of limited extent in this study,
29 we discuss how it might provide new insights for Odonata assemblage structure and be
30 useful, locally, for stakeholders and managers. Lastly, we call for further multiscale
31 investigations considering both the taxonomic and functional responses of Odonata
32 assemblages (functional analyses with multiple traits and several species being scarce
33 in this taxonomic group) in other anthropogenic freshwater ecosystems to gather more
34 lessons for their conservation.

35 **Introduction**

36 The current erosion of biodiversity is a major threat to the ecological integrity of ecosystems
37 (Groom, Meffe & Carroll, 2006; He *et al.*, 2019). This is particularly true for freshwater
38 ecosystems that have to face multiple threats such as agricultural land use, deterioration of water
39 quality or modification of the flow regime, which result in habitat alteration and loss (Dudgeon
40 *et al.*, 2007; Reid *et al.*, 2019). Furthermore, artificial waterbodies such as ditches and ponds
41 are among the few remaining aquatic habitats in many agricultural landscapes (Biggs, von
42 Fumetti & Kelly-Quinn, 2017; Favre-Bac *et al.*, 2017; Zamora-Marín *et al.*, 2021). These
43 waterbodies may increase the diversity of aquatic habitats (Verdonschot, Keizer-vlek &
44 Verdonschot, 2011; Deacon, Samways & Pryke, 2018) and thus play a significant role for
45 biodiversity even if they are generally characterized by lower taxonomic richness than rivers or
46 lakes (Painter, 1999; Bubíková & Hrivnák, 2018). They may indeed support rare species, and
47 thereby increase regional biodiversity, particularly in an agricultural context (Chester &
48 Robson, 2013). Among artificial waterbodies, drainage ditches can sometimes represent
49 densely interconnected aquatic habitats (Herzon & Helenius, 2008; Favre-Bac *et al.*, 2017). In
50 many wetlands where agricultural lands required low water level for sowing in spring, the water
51 regime in ditches is heavily managed with, generally, three main periods: high water levels
52 during the rainy season (in winter for temperate wetlands), and, conversely, decreasing water
53 levels in spring to evacuate the water out, sometimes even going so far as to total drying out of
54 ditches in summer (Duncan *et al.*, 1999; Williams, 2006). Beyond agricultural purposes, the
55 water regime may impact a variety of taxa depending on the water in ditches and the associated
56 environmental conditions, for part or all their life cycle. There is thus a need to address
57 biodiversity consequences of water regime and to assess its importance compared to other
58 environmental variables (Williams, 2006).

To meet biodiversity conservation purposes, sufficient knowledge on the effect of water regime on biological communities, amongst other environmental features, is unquestionably required. Additionally, such issues need to be investigated at different spatial scales (Vellend, 2010). A body of literature supports the importance of local environmental conditions, including water regime, on alpha diversity in agricultural ditch networks. For instance, high water depth (Mauchamp *et al.* 2021) but also temporary drying out promotes local plant species richness (Bonis, Lepart & Grillas, 1995), whereas shade (Shaw *et al.*, 2015; Mauchamp *et al.*, 2021) and nutrient input (Herzon & Helenius, 2008) have a negative impact. At a larger scale, environmental contrasts between localities can result in a high regional (i.e. gamma) diversity, as demonstrated for a large variety of taxa including plants (Armitage *et al.*, 2003), birds (Herzon & Helenius, 2008) and invertebrates (Verdonschot *et al.*, 2011). In addition, connectivity between habitat patches may promote the spread of species and, ultimately, influence community structure in ditch networks at different scales (e.g. Favre-Bac *et al.*, 2017 for plants). This means that identifying the drivers of beta diversity (defined as the extent of change in species composition between localities; Anderson, 2001), is crucial to better understand the relations between local and regional biodiversity patterns in ditches, as well as the underlying processes and drivers.

Odonata are suitable model organisms to study the drivers of biodiversity structure in agricultural marshland landscapes crossed by ditches for several reasons. Firstly, they have a wide range of habitat requirements and a complex life cycle that makes them dependent on both terrestrial and aquatic habitats (McPeck, 2008; Balzan, 2012; Barros Miguel *et al.*, 2017). Then, they are sensitive to environmental changes at various spatiotemporal scales (Crowley & Johnson, 1992; Nagy *et al.*, 2019) and, lastly, they are easy to monitor (Oertli, 2008; Giugliano, Hardersen & Santini, 2012). Unlike other aquatic habitats such as ponds (e.g. Raebel *et al.*, 2012; Simaika, Samways & Frenzel, 2016; Briggs *et al.*, 2019), the drivers of Odonata

84 assemblage structure remain poorly known in ditch networks (Harabiš & Dolný, 2015; Giuliano
85 & Bogliani, 2019). The high dispersal ability of adult Odonata, together with their dependency
86 on local resources, also make them ideal organisms to study variation in assemblages as a
87 function of both the local and landscape environment (i.e. multiscale; Raebel *et al.*, 2012;
88 Briggs *et al.*, 2019). Up to now, most studies of Odonata in ditch networks were conducted at
89 small spatial scale (e.g. (Painter, 1999; Tichanek & Tropek, 2015) and focused mainly on
90 specific species (e.g. (Rouquette & Thompson, 2005; Harabiš & Dolný, 2015; Kastner,
91 Buchwald & Biedermann, 2018). Very few multiscale studies have been conducted on Odonata,
92 and the importance of landscape on Odonata biodiversity in ditch systems remains an open
93 question (Kadoya *et al.*, 2008; Balzan, 2012; Raebel *et al.*, 2012; Nagy *et al.*, 2019).

94 Additionally to the study of the drivers of taxonomic diversity, a trait-based approach has been
95 shown to be a promising way to investigate how communities face environmental conditions
96 (Violle *et al.*, 2011; Powney *et al.*, 2014). Functional analyses rely on the assumption that
97 similar environmental conditions induce a convergence in the functional (trait-based)
98 composition of communities. Some of these traits (i.e. morphological, behavioural or
99 phenological features) are expected to highlight the mechanistic processes structuring
100 communities and how they face ecological challenges. Despite the relatively good knowledge
101 of the biology of Odonata in Europe, functional studies considering multiple traits and multiple
102 taxa are still very scarce (but see recent works, for instance Pires, Stenert & Maltchik, 2019;
103 Dalzochio *et al.*, 2020), and to our knowledge, no such study has yet been conducted in
104 agricultural marshlands.

105 The aim of this study was to identify key environmental factors for Odonata assemblages in
106 marshlands crossed by ditches, focusing, in particular, on hydrology and landscape
107 characteristics. More particularly, we examined variation in taxonomic (alpha and beta)
108 diversity and functional composition of adult Odonata assemblages in ditches and the

surrounding meadows. To this end, we studied 22 transects characterizing the range of landscape and local environmental conditions recorded in the study area over a five-year period. Water regime in ditches, notably very shallow waters and drying out, was expected to have critical effects on Odonata assemblages (Piersanti *et al.*, 2007; Crumrine, Switzer & Crowley, 2008; Pires *et al.*, 2019). Drying might promote pioneer species with late emergence, known as summer species, cascading into a decrease in alpha diversity and an increase in spatial beta diversity. Landscape features are also expected to shape Odonata assemblages, with an expected positive link between landscape openness (woodlands versus meadows and crops covers) and dispersal abilities of adults (Raebel *et al.*, 2012; Nagy *et al.*, 2019). We also expected a positive effect of the availability of aquatic habitats – more precisely the total length of the ditch network – on species richness, and a decrease in beta diversity due to increased aquatic connectivity. Drivers of Odonata assemblages are expected to vary between the two main suborders because Zygoptera are mainly small-bodied, specialist species with a weaker dispersal capability than Anisoptera which are typically large-bodied, rather generalist species with a stronger dispersal ability (Corbet, 1999; Alves-Martins *et al.*, 2019; Nagy *et al.*, 2019). Hence, it is commonly accepted that the effects of landscapes on Zygoptera are more difficult to detect than for Anisoptera, and that Zygoptera should be more influenced by local environmental variables (Raebel *et al.*, 2012; Nagy *et al.*, 2019). Also, we predicted the occurrence of a combination of biological traits that would discriminate members of the two Odonata suborders.

Material and Methods

Study area

The Marais poitevin is the second largest marshland in France (>1000 km²) located along the Atlantic coast (46°30'–46°15'N and 1°30'–0°35'W, Figure 1). It is known to be of international importance for wildlife (Duncan *et al.*, 1999). During the 20th century, the intensification of

agricultural practices, notably grassland to cropland conversion, has resulted in the drastic shrinking of major aquatic habitats such as marshes, salt marshes and other marine habitats (Duncan *et al.*, 1999; Godet & Thomas, 2013). Currently, land uses in the Marais poitevin are dominated by crops and meadows, and, to a lesser extent, by woodlands (respectively 48%, 42% and 10%; EPMP, 2015), with contrasted mosaics of land uses between localities. It is also composed of a complex network of drainage ditches (8,200 km long) sub-divided into numerous independent blocks (called hydrological units hereafter) in which the water depth is controlled (see EPMP (2015) and Mauchamp *et al.* (2021) for a detailed description of the study area). Recent inventories have shown that the Marais poitevin harbors 54 Odonata species (Deux-Sèvres Nature Environnement *et al.*, 2018) out of 89 recorded in France (UICN France *et al.*, 2016). In the present work, we studied Odonata assemblages across 11 similar-sized and independent hydrological units (300–365 ha; Figure 1) over a five-year period (2015–2019). The hydrological units were mostly selected to represent the diversity of the environmental conditions in terms of the water regime.

Odonata assemblage monitoring

Twenty-two standardized 500 m-long transects (350 m along a ditch and 150 m within its adjacent meadow) were selected among the hydrological units with two transects per unit (Figure 1). On average, the distance to the closest transect was 900 ± 580 m (mean \pm standard deviation; Euclidean distance between the barycentre of transects). Transects were surveyed each year once a month from May to August, in order to detect all Odonata species due to differences in phenology (Balzan, 2012; Simaika *et al.*, 2016; Giuliano & Bogliani, 2019). Individuals were recorded and identified at the species level while walking the transects at a slow pace for a duration of 60 minutes, via a visual census within a 5-meter width, using binoculars combined with occasional captures of individuals using a hand net. Sampling took

place during clement weather conditions (temperature > 20°C, sunny and windless days) between 10am and 6pm as recommend by Brooks (1993). The abundances of each species for the four annual visits were pooled into a single record prior to analysis.

Odonata traits

We compiled 15 biological and behavioural traits for all of the sampled Odonata species using existing trait databases (mainly Harabiš & Hronková (2020) and Powney *et al.* (2014)) together with additional literature for the few missing data (see Table S1). The traits considered were: abdomen size, adult body size, voltinism, flight period (start, end and duration), flight mode, oviposition mode, overwintering stage, territorial behaviour, courtship behaviour, dispersal ability, migratory behaviour, larval body size and larval behaviour.

Environmental conditions

For each transect, the daily water depth of the adjacent ditch was obtained from the water level measurement recorded by a limnigraph located in one representative ditch of each hydrological unit, corrected according to the altitude of the ditch bottom. The monthly average water depths were calculated from January to August. Ditches generally dry out from August to November in the Marais poitevin; and drying duration (in days) was thus calculated for each transect over the 12-month period preceding the Odonata sampling. The ditches were considered dry when the daily water depth was below 5 cm, to take into account the uncertainty associated with the elevation measurement from the bottom of the ditch. To assess the temporary open water habitats available within the adjacent meadows, we used the number of days during spring (April to June) on which 20% of the meadow area of each hydrological unit was flooded (later in the season, no such flooded threshold occurred). Specifically, a pixel of one square meter on a LIDAR imaging raster was considered as flooded when its altitude on the digital elevation model was lower than the water depth recorded using limnigraphs (Rapinel *et al.*, 2018). Other

183 flood duration quantiles (e.g. 5% or 10%) were considered initially but they were found to be
184 highly correlated with the water depths in ditches so they were not retained.

185 A series of landscape characteristics were measured in a 500-m buffer radius around each
186 transect. This buffer size is in the range of distances proved to be important for adult Odonata
187 (100 m to 1600 m in Raebel *et al.* (2012), but larger distances were used in Nagy *et al.* (2019):
188 1.25 to 5 km) and it represents a compromise to examine the distribution of Odonata at a
189 landscape scale without significant overlapping between transects. Meadow cover and crop
190 cover (%) were measured using land-use maps (EPMP (2015) based on IGN (2016)) and
191 woodland cover (%) using remote sensing data (Rapinel *et al.*, 2015). The length of the ditch
192 network (i.e. a proxy for the amount of aquatic habitats) was also measured. All of the landscape
193 variables were measured using QGIS 3.2 (QGIS Development Team, 2018).

194 We did not expect Odonata to exhibit a strong response to water quality conditions as the overall
195 eutrophication of the Marais poitevin has likely filtered out eutrophication-intolerant species
196 (Mauchamp *et al.*, 2021). However, eutrophication can be a relevant proxy of other
197 environmental variables such as farming intensification and we therefore used ten water quality
198 variables in the subsequent analysis: water conductivity, pH, saturation in oxygen and the
199 concentrations of ammonium, nitrite, nitrate, total nitrogen (Kjeldahl), orthophosphate,
200 dissolved organic carbon and chlorophyll a (more details on sampling are provided in Table
201 S2A). For each ditch belonging to a surveyed transect, we also included six additional habitat
202 variables of interest for adult Odonata. (1) We considered a possible shade effect using an index
203 representing hedge cover. Two indices characterizing the herbaceous vegetation density (2-3)
204 were considered on the lower banks (helophyte species) and upper banks (other herbaceous
205 species) close to each transect. We differentiated helophyte species from other herbaceous
206 species as they might play different ecological functions during the life cycle of Odonata (Lenz,
207 1991; Rouquette & Thompson, 2005). (4) Algae cover (mainly *Enteromorpha* and *Ulva* spp.)

and (5) aquatic vegetation (macrophyte) cover were assessed in the ditches occurring along the transects as described in Mauchamp *et al.* (2021). (6) As invasive crayfish may have a deleterious effect on Odonata (Mccarthy *et al.*, 2006; Siesa *et al.*, 2014), we assessed the abundance of the red swamp crayfish (*Procambarus clarkii*) which is widely distributed in the study area. Complementary information on these six habitat indices is given in Table S2A.

Statistical analysis

All of the data analyses were performed with R software (R Core Team, 2021). After a standard data exploration, we retained 20 variables with limited collinearity from the initial set of 33 environmental variables (with the “vifcor” function in the *usdm* package, Naimi, 2017) using a correlation threshold of 0.7 as recommended in Dormann *et al.* (2013) (range of values in Table S2B; correlations between variables in Table S2C). Three water quality variables (chlorophyll a content, total nitrogen and dissolved organic carbon), and all of the water depth variables except water depth in July were excluded from the subsequent analyses.

Firstly, we used generalized-linear mixed models (GLMM, with a Poisson error distribution) with the hydrological unit and the year as random effects, to assess which environmental variables (scaled data) explained the variation in alpha diversity (*lme4* package, Bates *et al.*, 2019). We produced all candidate models testing all simple and additive effects up to a maximum of three variables per model to limit the complexity of the models. We then used a multi-model inference approach to calculate model-averaged parameter estimates (with 95% Confidence Intervals, 95% CIs) for the variables included in the selection of models (cumulated weight $AICc < 0.95$, the Akaike information criterion corrected for small sample sizes, Burnham & Anderson, 2002). The dredging and model averaging procedures were performed using the *MuMin* package (Bartoń, 2016). The effect of an explanatory variable was considered

232 significant when its estimate (the slope of the relation) was different from zero (when its 95%
233 CI excluded zero). The quality of the models was evaluated using the r^2 values calculated for
234 the fixed effects for the global model (marginal r^2 using the “r.squaredGLMM” function in the
235 *MuMin* package; Bartoń, 2016). Analyses were performed on all species combined, and then
236 on Zygoptera and Anisoptera separately.

237 To investigate variables associated with beta diversity, we calculated the Bray-Curtis
238 dissimilarity matrix on the presence-absence data and used Generalized Dissimilarity
239 Modelling (GDM; Ferrier *et al.*, 2007). GDM is a matrix regression-based method
240 accommodating two typical non-linearities in ecological datasets: (1) variation in the rate of
241 compositional turnover at different positions along environmental gradients, and (2) the
242 curvilinear relation between the observed compositional dissimilarity, and increasing
243 ecological and geographic distances between transects. We assessed the significance of each
244 predictor using the default number of permutations (50) and plotted the I-splines only for the
245 significant predictors. To measure the relative importance of each significant predictor in
246 driving species turnover, we summed the three coefficients of the I-splines (see Ferrier *et al.*
247 (2007) for more details). We ran the GDM models, plotted the I-splines for each predictor and
248 assessed the importance of predictors on the response variables using the “gdm” and
249 “gdm.varImp” functions available in the R package *gdm* (Fitzpatrick *et al.*, 2020). We did not
250 standardize the environmental variables in GDM in order to make it easier to interpret variation
251 in beta diversity along the ecological gradients (Fitzpatrick *et al.*, 2013). As for alpha diversity,
252 analyses were performed on all species combined, and then on Zygoptera and Anisoptera
253 separately. Given the highly uneven local assemblages (see below), we also modelled beta
254 diversity using abundances. We presented only the results from presence-absence data, except
255 when complementary insightful patterns occurred (see the results of GDM models using
256 abundance data in Table S4).

We used an RLQ analysis combined with a fourth-corner analysis to explore the trait-environment relations (Dray *et al.*, 2014). RLQ is a multivariate technique consisting of a three-table ordination to identify the co-structures between an environmental table (R), a presence-absence species table (L) and a trait table (Q) (Dolédéc *et al.*, 1996). We generated a Correspondence Analysis (CA) on the species table. The table of environmental variables was analysed using a Principal Component Analysis (PCA), with the CA transect scores used as the row weight. The table of traits was analysed with a Hill Smith PCA, using the CA species scores as the column weight. Then, the simultaneous ordination plot was computed by combining the independent analyses with RLQ, using the “rlq” function of package *ade4* (Dray & Dufour, 2007). A global Monte-Carlo test with 10,000 random permutations was performed on the RLQ values to test the relationships under two models. One tested the relationship between the species composition and the environmental conditions (described as Model 2 by Dray & Legendre (2008)) and the other tested the species distribution according to their traits (described as Model 4 as defined in Dray & Legendre (2008)). We will refer to trait syndromes when describing the combination of related traits for each axis of the co-inertia analysis (Dray *et al.*, 2014). To complement the RLQ results, an improved version of the fourth-corner method including adjustments for multiple comparisons was used with 10,000 random permutations (ter Braak, Cormont & Dray, 2012; Dray *et al.*, 2014), allowing to test for individual correlations between each trait and each environmental variable, using the “fourthcorner” function of package *ade4* (Dray & Dufour, 2007).

Results

Description of assemblages

A total of 13,124 individuals belonging to 39 Odonata species (20 Zygoptera and 19 Anisoptera species) were recorded across the 22 transects over the five-year period (Table S3). The most frequent species were respectively *Ischnura elegans* (observed on 85% of the 110 annual

censuses), *Platycnemis pennipes* (70%), *Orthetrum cancellatum* (54%) and *Platycnemis acutipennis* (54%). Additionally, the most abundant species were respectively *I. elegans*, *Erythromma viridulum*, *P. pennipes* and *P. acutipennis* (Table S3). These four species represented 91% of all Zygoptera and 82% of all Odonata individuals. *Orthetrum cancellatum*, the most abundant species among Anisoptera, was approximately ten times less abundant than the most common Zygoptera (Table S3). Conversely, three species were only recorded on one transect (*Libellula quadrimaculata*, *Aeshna cyanea* and *Somatochlora flavomaculata*; Table S3). The annual species richness per transect ranged from 2 to 20, with an average of seven species (three for Zygoptera, five for Anisoptera) per transect.

Environmental variables associated with taxonomic alpha diversity

Four environmental variables significantly influenced the total along-transect Odonata species richness, all with a negative effect (Table 1). The greatest effect size was related to the drying duration (-0.25), while the three other significant variables were all related to landscape characteristics (-0.15 to -0.20 for ditch network length, meadow cover and woodland cover; Table 1). The same explanatory variables were found for Zygoptera species richness, except the ditch network, while two additional variables were found significant: crop cover (negative relation) and the water depth of the adjacent ditch (positive relationship; Table 1). Variation in Anisoptera species richness was not significantly related to any of the environmental descriptors considered. We found a moderate effect of both random effects (years and hydrological units) on variation in the species richness when considering all species but none on Zygoptera species richness (see marginal and conditional r^2 values in Table 1).

Environmental variables associated with taxonomic beta diversity

Full GDM models accounted for 22%, 19% and 10% of the total deviance for taxonomic beta diversity considering respectively all species, Zygoptera only and Anisoptera only. Geographic

distance between pairs of transects, drying duration and the hedge index were significant predictors of beta diversity when considering all species together and Zygoptera alone (Table 2, Figure 2a, b). More specifically, beta diversity kept increasing with increasing geographic distances and drying duration and it increased with the hedge index above a threshold. For Anisoptera, beta diversity increased with increasing geographic distance up to 20 km before reaching a plateau. It also increased with nitrite concentration in ditch water and herbaceous vegetation density on the upper banks (Figure 2c). Considering abundance data for beta diversity calculation led to a higher explained deviance than with the presence-absence data. It particularly highlighted an effect of vegetation density on lower banks on Zygoptera beta diversity and a strong effect of water depth on Anisoptera beta diversity (Table S4).

Functional trait patterns along environmental gradients

The first two axes of the RLQ analysis accounted for 71% of the total co-inertia, meaning that a clear relationship occurred between the environmental conditions and the functional structure of Odonata assemblages (Figure 3). The variance was well preserved on the first two axes of the RLQ (respectively 75 and 71% for the environmental scores and 45% and 67% for the traits). The contingency structure of the co-inertia analysis was partially correlated with the ordination plot obtained with the species table alone (correlation of 0.28 for the first axis, 0.18 for the second), indicating a moderate relationship between the species distribution and the final co-structure.

The first axis of the co-inertia analysis corresponds to a landscape openness gradient. Transects on the left side of the ordination plot were characterized by the highest meadow cover while transects on the right side were characterized by the highest wooded cover values; crop cover also contributed to this axis but to a lesser extent (Figure 3a,c, correlation values in Table S5). The first axis was also highly correlated with hedge cover (Figure 3c). Overwintering stage, date of flight start and migration mainly contributed to the trait syndrome recorded along the

first axis of the co-inertia analysis (Figure 3d). In the fourth-corner analysis, the environmental gradients of the first RLQ axis were negatively correlated with late flight start, univoltinism and dispersal ability (Figure 4a). The combination of traits correlated with the first RLQ axis (first trait syndrome) was negatively correlated with the landscape openness gradient and the cover of aquatic vegetation within the ditches, and positively correlated with the ditch network length and vegetation density on the lower banks (Figure 4b). The second axis of the ordination was mostly structured by water quality and the vegetation density on the upper banks (Figure 3c). The main traits structuring the second axis were larval strategy, oviposition mode, body size and dispersal ability. These traits formed a second trait syndrome (Figure 3d) which primarily differentiated Anisoptera from Zygoptera (Figure 3b). In the fourth-corner analysis, dispersal ability was positively correlated with the water quality gradient (Figure 4a), and there was no environmental variable significantly correlated with the trait syndrome of the second axis (Figure 4b).

The species composition of assemblages was significantly related to the environmental conditions ("Model 2", p -value < 0.001) but not to traits ("Model 4", p -value = 0.126). Similar to the bivariate statistics between traits and environmental variables, the fourth-corner analysis did not show a significant relationship. All this means that the functional analyses indicated some links between the environment and the functional structure of assemblages without identifying clear bivariate relationships between species traits and environmental variables.

Discussion

In this study, we sought to examine whether the structure of Odonata assemblages in marshlands crossed by ditches is mainly controlled by hydrology and landscape among a panel of environmental variables considered. According to our expectations, we demonstrated that water regime (duration of drying events and water depth), and a set of landscape variables (land

uses and ditch network length) are the main variables associated with Odonata assemblages in the marshlands we studied. The globally eutrophic character of waters in the Marais poitevin likely filtered out species intolerant to eutrophication, explaining why these variables were poorly associated with Odonata assemblage composition among localities. The studied ditches hosted 77% of the regional diversity (Fouillet & Maillard, 1995; Deux-Sèvres Nature Environnement *et al.*, 2018), and the missing species are either very rare in the region (e.g. *Lestes macrostigma* or *Sympetrum vulgatum*) or restricted to habitats not recorded here (e.g. *Onychogomphus* spp. preferring fast-flowing waters). The influence of water regime, landscape metrics and, lastly, the other local variables are hereafter discussed considering both the taxonomic and functional descriptors of Odonata assemblages.

Predominant role of the temporary nature of ditch waters

We found that the alpha diversity of Odonata assemblages greatly decreased when the duration of drying increased in ditches. This agrees with Piersanti *et al.* (2007) and Pires, Stenert & Maltchik (2017) who found that drying events in ponds eliminate the larvae of most Odonata species, and therefore have an impact on local populations of adults (McPeck, 2008). Drying duration was also the environmental predictor that best explained the dissimilarities in Odonata assemblage composition between sites. Conversely to Bogan *et al.* (2020) who found that short drying events (i.e. a couple of days) did not impact Odonata assemblages, beta diversity for all species combined increased linearly with drying duration in the present study. To be precise, drying duration varied strongly among sites in the Marais poitevin (on average 23 ± 47 days, range: 1-194 days), representing severe conditions. The patterns of variation in alpha and beta diversity as a function of drying duration we found were however similar to what has been documented for other aquatic macroinvertebrates elsewhere, notably in intermittent streams (e.g. Ephemeroptera, Plecoptera, Trichoptera; Bonada, Rieradevall & Prat, 2007; Datry *et al.*, 2014; Crabot *et al.*, 2020). Odonata are often presented as the most resilient macroinvertebrates

to flow intermittence since a quick recolonization from perennial refuges is frequently observed due to their strong dispersal abilities (Bogan *et al.*, 2017). Similarly, we found that drying duration did not influence alpha and beta diversity of Anisoptera, which are pioneers species and excellent colonizers of temporary habitats (Barros Miguel *et al.*, 2017). The strong dispersal abilities of these species could result in homogenization of the species composition among local assemblages irrespective of disturbance patterns (Barros Miguel *et al.*, 2017). We showed, however, that increased drying duration strongly reduced Zygoptera alpha diversity and led to an increase in spatial beta diversity. This demonstrates that managing water levels to avoid long drying events could promote local diversity of Zygoptera in ditch networks.

Traits positively correlated with each other are typical features of summer species, able to cope with temporary aquatic habitats (Corbet, 1999; Corbet, Suhling & Soendgerath, 2006; Crumrine *et al.*, 2008). For instance, late-season phenology and univoltinism characterize summer species such as certain *Aeshna* and *Sympetrum* species, which are common in temporary habitats (McCauley *et al.*, 2008). In addition, migration and strong dispersal ability are two other relevant traits for Odonata colonizing temporary aquatic habitats (Corbet, 1999). All four traits were positively associated and constituted a trait syndrome. In the co-inertia analysis, the overwintering stage also isolated species such as certain *Lestes* and *Sympetrum* species. Eggs of these species overwinter in mud and vegetation (instead of laying eggs in water) and hatch quickly. Nevertheless, no significant correlation was found between this trait syndrome and the duration of drying. One possible explanation could be that the traits of “summer species” may be selected as soon as an aquatic habitat dries out, regardless of the length of drying events. Although few relationships between functional composition and environmental gradients were found in this study, their coupled analysis can provide insightful information for management initiatives. For instance, identifying sites where species show a later phenology could determine

the timing of some conservation strategies in the marshland such as the dredging of ditches (Twisk, Noordervliet & ter Keurs, 2000).

The significant effect of the summer water depth in the ditches on the structure of the Odonata assemblages has also been reported elsewhere (Kietzka, Pryke & Samways, 2015; Simaika *et al.*, 2016). When considering the two suborders separately, only Zygoptera local species richness was higher around ditches exhibiting a high water depth, while water depth was a predictor of beta diversity for neither Anisoptera nor Zygoptera. However, when analyses were performed using abundance data, Anisoptera species turnover increased when water depth in July was low (< 0.30 m), and a significant albeit weaker effect was found for Zygoptera as well. The 0.30-m water depth threshold we found indicates that variations in the water depth have strong ecological implications in shallow waters, which are often characterized by extreme conditions (notably very high temperature and low oxygen concentrations, Williams, 2006). This again emphasizes the pivotal role of anthropic management of water regime in such systems.

Influence of landscape characteristics

Woodland cover, meadow cover and ditch network length were the main landscape characteristics shaping Odonata assemblages, with species richness negatively associated with all three. We were expecting a negative effect of woodlands on Zygoptera species richness, because woodlands likely decrease the dispersal distance of the poorly dispersing members of this group (Keller, Strien & Holderegger, 2012; Raebel *et al.*, 2012; Nagy *et al.*, 2019). However, we would have expected a positive effect of meadow cover because an open terrestrial matrix facilitates dragonfly movements (Pither & Taylor, 1998; Keller *et al.*, 2012; French & McCauley, 2019), additionally, meadows are more suitable for feeding and resting than crops (Goertzen & Suhling, 2019; Nagy *et al.*, 2019). As the percentages of all land-uses balance, the negative association between the three land-use covers and Zygoptera species

richness are, at first sight, surprising. However, it cannot be excluded that non-linear relationships between land-uses and species richness occur, which would be the case if a specific mosaic of habitats was the most beneficial to Zygoptera, something that cannot be really examined due to a limited range of land-use covers in the study area (see Table S2B). Apart from the importance of the composition of the landscape for Odonata assemblages, it would be interesting to explore in future work the possible influence of the arrangement of the different landscape elements.

Contrary to our expectation, ditch network length was negatively associated with local species richness and was not associated with beta diversity. It may be possible that many ditches in the hydrological units we studied dry out early in summer, leading to a low connectivity and poor quality habitats for Odonata. In such a case, Odonata would concentrate on the only available aquatic habitat. One possible additional explanation could be that ditch network length did not fairly represent the amount of aquatic habitat but paralleled woodland cover, which had a negative effect on Zygoptera species richness. Indeed, the high correlation between both variables ($r = 0.7$) prevents a clear understanding of their relative contribution in structuring Odonata assemblages.

We expected that landscape effects would not be detectable on Zygoptera (i.e. less mobile Odonata; Corbet, 1999) contrary to Anisoptera which display better flying abilities (Raebel *et al.*, 2012; Nagy *et al.*, 2019). Results were not in line with this prediction since the species richness of Zygoptera, and not Anisoptera, varied with some landscape characteristics, and differences in beta diversity of both groups were linked to local variables only. Within our 500-m buffers, Zygoptera could be instead very sensitive to landscape configuration precisely because they have poorer dispersal abilities and difficulties dispersing to another suitable patch when local environmental conditions deteriorate (e.g. drying of ditches). Raebel *et al.* (2012) also showed that Zygoptera responded to landscape variables within 400-m buffers, while

Anisoptera started to respond to landscape variables from a 1600-m buffer radius. Similarly, Nagy *et al.* (2019) detected responses of Anisoptera but only at large buffer size (i.e. 5000m). Furthermore, beta diversity of Odonata overall increased with geographic distance between sites, which is generally interpreted as an increasing role of dispersal limitation (Heino *et al.*, 2015). More precisely, beta diversity kept increasing for Zygoptera with geographic distance but quickly reached a plateau for Anisoptera. In addition, the fact that the GDM analysis performed on Anisoptera was less predictive than for Zygoptera might reflect a more random spatial distribution of Anisoptera. This is another sign, along with the broad distribution of these species in the co-inertia analysis, of both the stronger dispersal ability of Anisoptera and their higher tolerance of diverse environmental conditions compared to Zygoptera (Alves-Martins *et al.*, 2019). Future investigations are needed to progress in the understanding of the effect of large-scale variables on Odonata assemblage composition, notably consideration of the configuration of landscapes.

Minor influence of other local environmental variables

Our results revealed that water eutrophication influenced Anisoptera beta diversity, despite their generally greater tolerance of degraded environments (Corbet, 1999; Oliveira-Junior & Juen, 2019). This may be because ecological disparities exist within members of the Anisoptera. For instance, Libellulidae are highly environment-tolerant, whereas certain Gomphidae are sensitive to water quality (Villalobos-Jimenez, Dunn & Hassall, 2016) and, in the present study, *Gomphus pulchellus* was indeed found in the best water quality conditions.

Among all local variables, the vegetation both along and within ditches was also found to influence Odonata assemblage structure. Increased heterogeneity in hedge cover and vegetation density on the upper banks was associated, respectively, with an increase in Zygoptera and Anisoptera beta diversity. Although riparian vegetation can be beneficial for all species (Osborn & Samways, 1996; Schindler, Fesl & Chovanec, 2003), it mainly favors small-sized species

and perchers, which are thermal conformers and need to relocate to maintain their body temperature, for both Zygoptera and Anisoptera (Corbet & May, 2008). In addition, some Odonata avoid overgrown riparian vegetation that shades the water surface, probably because it makes it more difficult to recognize a habitat (Painter, 1998; Remsburg, Olson & Samways, 2008; Harabiš, 2016). Aquatic vegetation cover within ditches was linked to the functional structure of Odonata assemblages, but surprisingly not to endophytic egg-laying species, (but see Buchwald, 1992). Perhaps the limited range of aquatic vegetation cover within ditches made it impossible to detect such an effect. In any case, maintaining microhabitat heterogeneity and vegetation at different stages of succession likely promotes Odonata biodiversity (Harabiš, 2016; Simaika *et al.*, 2016; Johansson *et al.*, 2019). Lastly, crayfish abundances and algae cover did not influence Odonata assemblages in this study, something that is congruent with results found elsewhere for crayfish (e.g. Siesa *et al.*, 2014) but not for algae (e.g. Johansson *et al.*, 2019).

Conclusion

Our results highlighted the critical influence of hydrology (water depth and duration of the drying events) on Odonata assemblages in agricultural marshland landscapes crossed by ditches. This suggests that ditch water management offers clear possibilities to maintain and possibly promote Odonata diversity (see also Herzon & Helenius, 2008; Stratford *et al.*, 2015). For example, water management can be better designed to prevent drying episodes and hence to meet conservation purposes in anthropogenic aquatic systems (Twisk *et al.*, 2000; Bogan *et al.*, 2020; Mauchamp *et al.*, 2021). Indeed, we highlighted that maintaining a water depth of several tens of centimetres throughout the summer might play an essential role for Odonata assemblages. Moreover, the heterogeneity of local water depth conditions is essential for a high turnover of Odonata species and possibly to increase regional diversity. Furthermore, our findings support the idea that conducting multiscale studies is crucial to progress the

understanding of community assembly mechanisms; research has so far mainly focused on the effect of local processes on Odonata assemblages in agricultural landscapes. Lastly, even if we did not succeed in showing clear relationships between trait syndromes and environmental gradients, the use of a trait-based approach could contribute to better understanding of Odonata assemblage structure.

Hence, we call for further multiscale investigations considering both taxonomic and functional diversity of Odonata in other agricultural landscape contexts to provide valuable guidelines for their conservation *per se* and more broadly to preserve the ecological integrity of the anthropic freshwater ecosystems that host them.

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Author contribution statement

AB and JMP designed the research, JC, AM, OG and NR carried out the data analyses, and all authors co-wrote the manuscript.

Data availability statement

The traits database and datasets are available on a public data repository at

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Conflict of interest statement

Authors have no conflict of interest to declare.

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Tables

Table 1: GLMM results explaining variation in alpha diversity. Only significant variables from the model selections are provided (mean and 95% confidence interval for each estimate). The marginal r^2 (fixed effects) and the conditional r^2 (fixed effects and random effects) of the global model are given for each group of Odonata considered. Variation in Anisoptera species richness was not explained by the environmental descriptors considered.

| | Predictors | Estimate | | | Marginal r ² | Conditiona l r ² |
|-------------|---------------------|----------|-------------------------------|-------|----------------------------|--------------------------------|
| | | Mean | 95% confidence interval | | | |
| All species | Drying duration | -0.25 | -0.38 | -0.13 | 0.46 | 0.58 |
| | Woodland cover | -0.20 | -0.32 | -0.08 | | |
| | Meadow cover | -0.19 | -0.33 | -0.05 | | |
| | Ditch network | -0.15 | -0.25 | -0.06 | | |
| Zygoptera | Meadow cover | -0.57 | -1.02 | -0.11 | 0.40 | 0.40 |
| | Woodland cover | -0.56 | -1.01 | -0.10 | | |
| | Crop cover | -0.44 | -0.66 | -0.22 | | |
| | Drying duration | -0.21 | -0.37 | -0.05 | | |
| | Water depth in July | 0.18 | 0.06 | 0.30 | | |

Table2: Results of the GDM analysis on the relation between beta diversity (presence-absence data), geographic distance and environmental variables. The proportion of explained deviance is calculated as the change in explained deviance between a model fit with and without that variable while holding all other variables constant. The relative importance is obtained by summing the I-spline coefficients for each variable. All of the predictors in the table were significantly correlated with beta diversity and they are ranked according to their relative importance.

| | Predictor | Explained deviance (%) | Relative importance |
|--------------------|----------------------------------|------------------------|---------------------|
| All species | Geographic distance | 45 | 2.133 |
| | Drying duration | 24 | 1.342 |
| | Hedge index | 5 | 0.430 |
| Zygoptera | Geographic distance | 50 | 2.371 |
| | Drying duration | 20 | 1.001 |
| | Hedge index | 4 | 0.387 |
| Anisoptera | Nitrite | 18 | 1.078 |
| | Geographic distance | 45 | 0.793 |
| | Vegetation density (upper banks) | 24 | 0.761 |

Figure captions

Figure 1. Location of (a) the Marais poitevin in France, showing (b) all transects (red points with labels) within the 11 hydrological units studied (gray zones), and (c) a zoom on the two transects in hydrological unit 1. All of the ditches are indicated with blue lines

Figure 2. Generalized dissimilarity model-fitted I-splines for variables significantly associated with beta diversity for (a) all species, (b) Zygoptera and (c) Anisoptera (presence-absence data). Panels show the fitted functions (partial ecological distance between transect pairs) for each environmental variable significantly associated with compositional turnover. The maximum height reached by each I-spline indicates the total amount of species turnover associated with that variable, holding all other variables constant. The slope of the curve indicates the rate of species turnover and how this rate varies along the gradient of a given variable, holding all other variables constant.

Figure 3. First two axes of the ordination plot resulting from the RLQ analysis with: (a) the transect scores for each year (the labels are the transect names), (b) the species scores, and the projection of the coefficients of the environmental variables (c) and the traits (d). The values of d give the grid size (0.2, 1 or 2). The complete names of the species, traits and environmental variables are available in Table S1, S2 and S3

Figure 4. Combination of the fourth-corner and RLQ results: relationships between the environmental descriptors and functional traits. (a) Fourth-corner tests between the first two RLQ axes for the environmental gradients (AxcR1 and AxcR2) and traits. (b) Fourth-corner tests between the first two RLQ axes for the trait syndromes (AxcQ1 and AxcQ2) and environmental variables. Positive significant relationships are represented by red cells, and negative significant associations by blue cells. Variables with no significant associations are shown in gray. Black lines separate the various variables; white lines separate the different

880 modalities for the categorical variables. The complete names of the traits and environmental
881 variables are available in Table S1 and S2.

882

883 **Table S1.** Traits database

884 **Table S2.** Summary of environmental conditions

885 **Table S3.** Details on Odonata data along the 22 transects from 2015 to 2019

886 **Table S4.** GDM analysis using Odonata abundance data

887 **Table S5.** RLQ tables

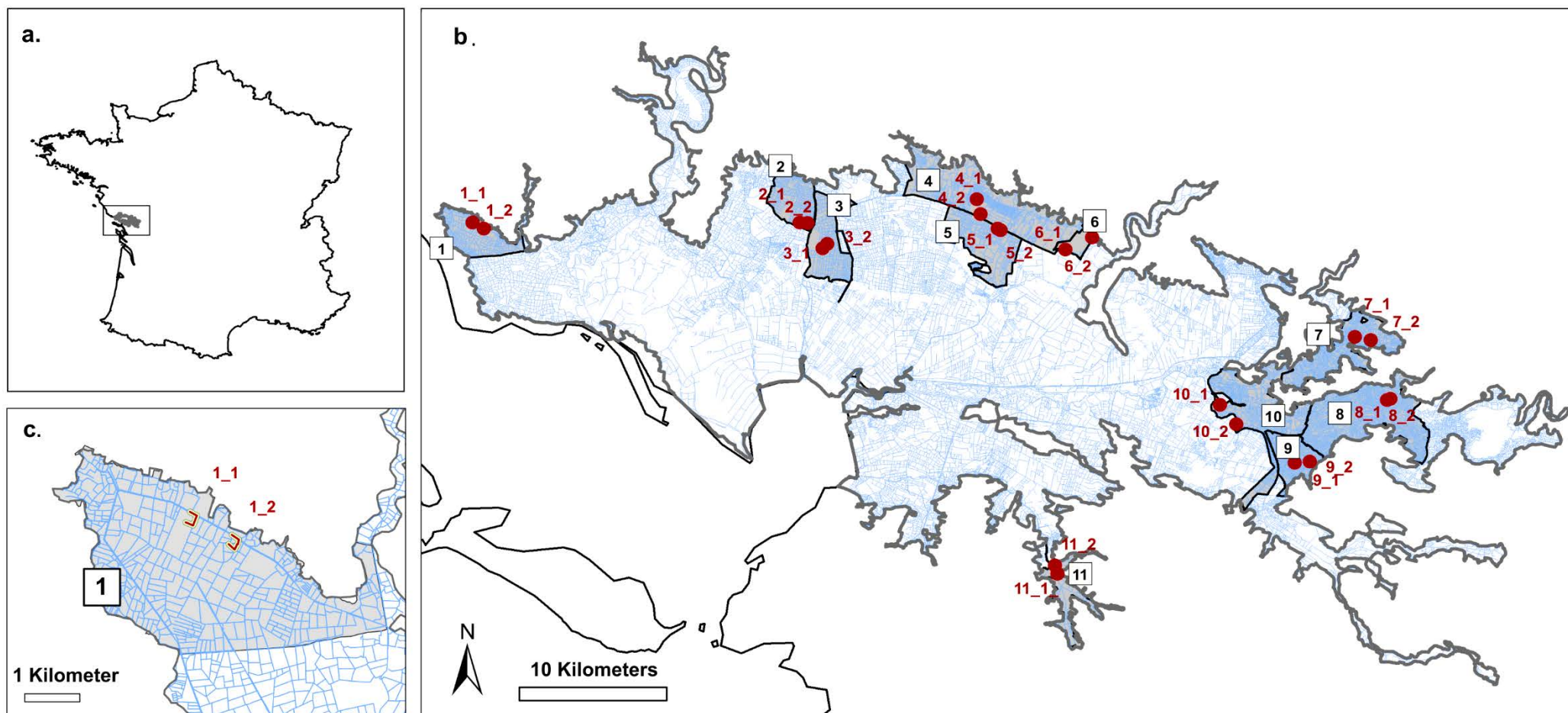


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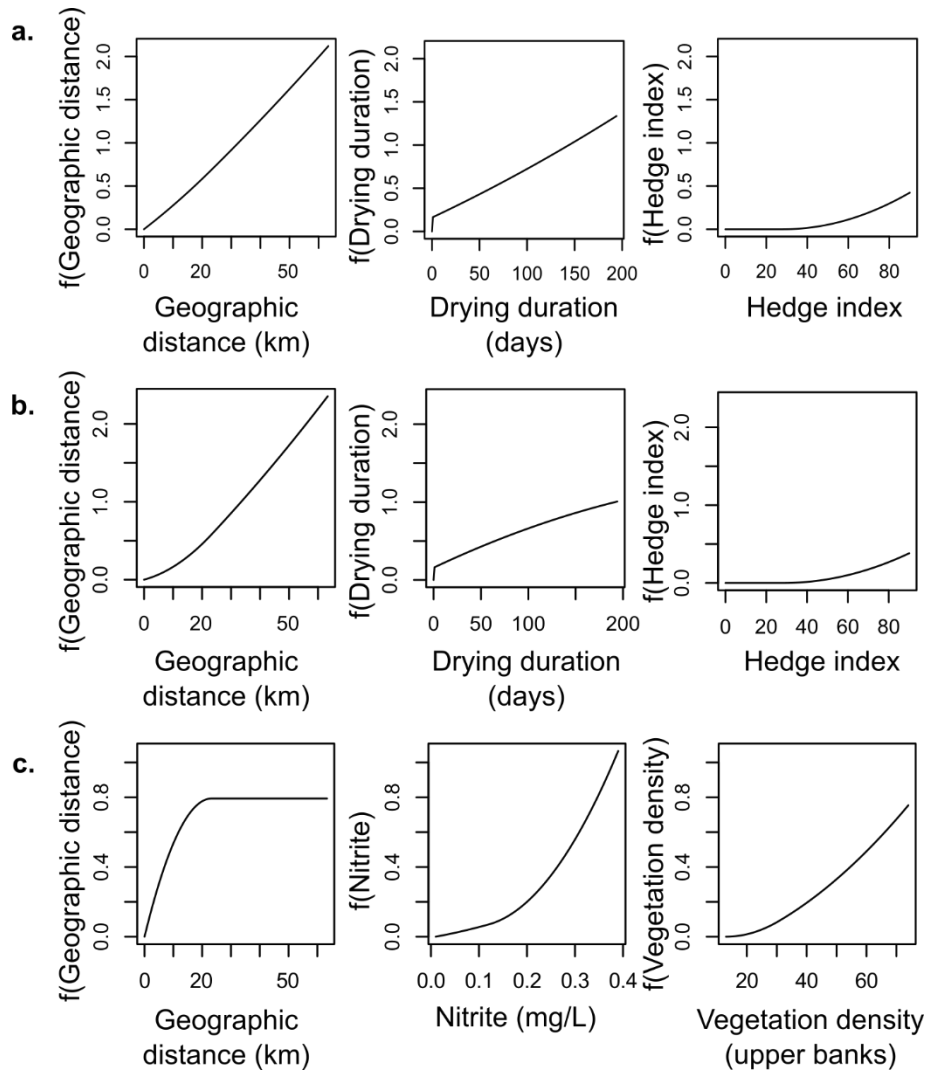


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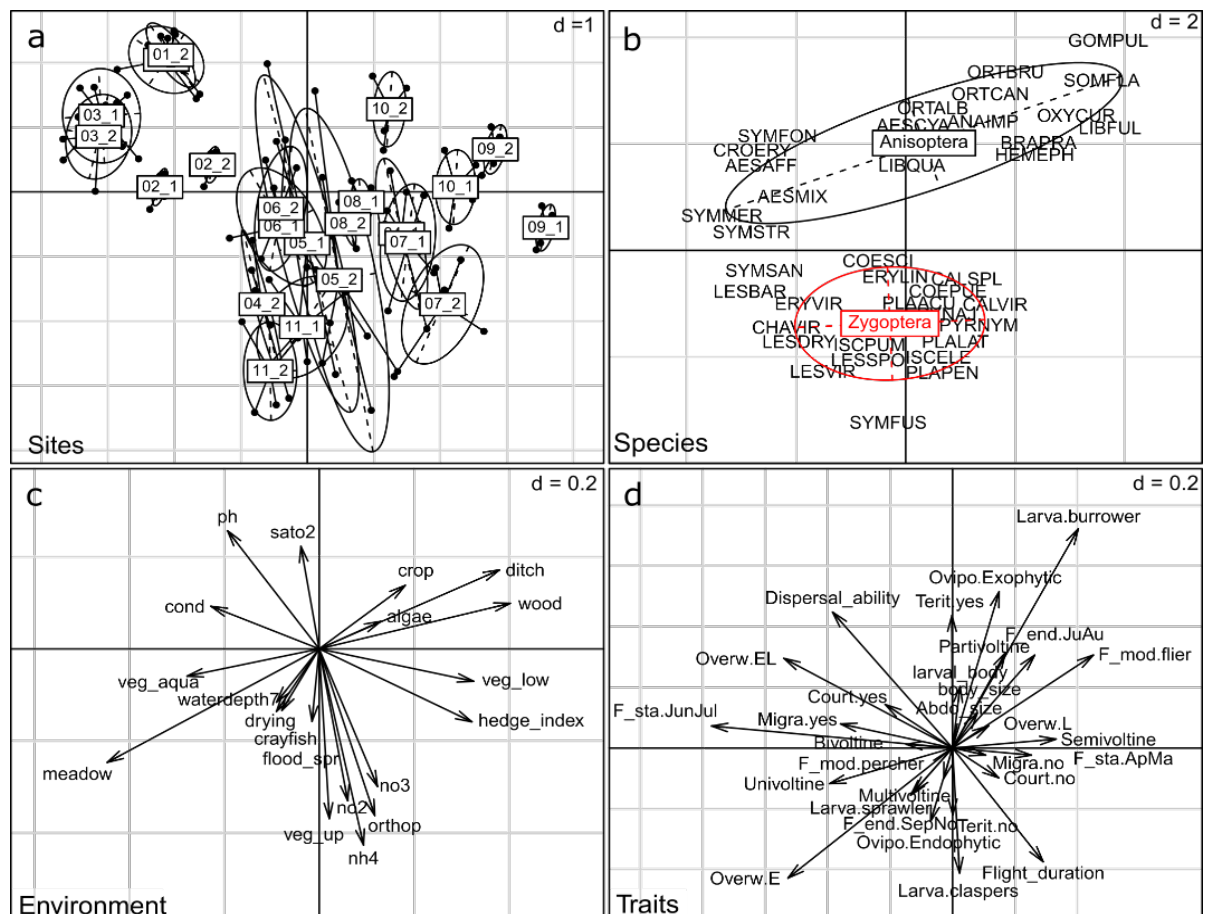


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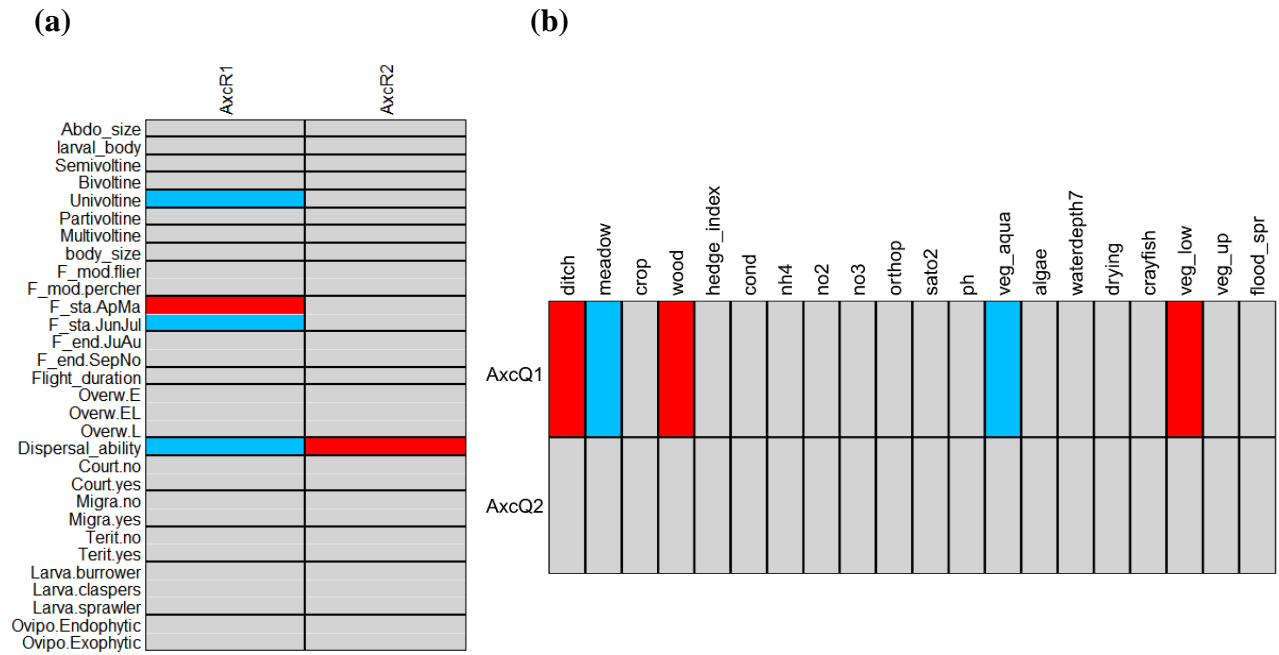


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