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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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1 **Abstract**

- 2 1. One of the major current ecological challenges is to understand how to reconcile human
3 activities with biodiversity conservation concerns. This issue is particularly relevant in
4 freshwater ecosystems where biodiversity is globally under severe threat. Artificial
5 waterbodies, such as ditch networks, are part of the few remaining wetlands in
6 agricultural landscapes and hence play a crucial role in maintaining aquatic biodiversity
7 in these landscapes.
- 8 2. We investigated the responses of adult Odonata assemblages at different spatial scales
9 in a marshland crossed by ditches to two factors expected to be pivotal influences on
10 assemblages. At the local scale, this was mainly the water regime in ditches and, at a
11 broader scale, the composition of the landscape. Both taxonomic alpha and beta
12 diversity, and functional trait composition were considered as response variables.
- 13 3. Significant differences were found between the responses of the two Odonata suborders.
14 We showed that Zygoptera species richness decreased and species turnover increased
15 with the duration of drying episodes in ditches. Geographical distances between local
16 assemblages as well as landscape characteristics, notably woodland cover, meadow
17 cover, and ditch network length, also significantly shaped the distribution of Zygoptera.
18 For Anisoptera, species richness was not explained by environmental variables and beta
19 diversity was associated only with local conditions; it increased with increasing
20 dissimilarity in water quality and riparian vegetation. We also found evidence of
21 functional trait syndromes (combinations of correlated traits) in Odonata assemblages,
22 but without clear relationships to environmental gradients.
- 23 4. This study reveals the structuring role of water regime for Odonata in ditch networks
24 and demonstrates the need to jointly consider environmental variables at different
25 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).

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

76 Odonata are suitable model organisms to study the drivers of biodiversity structure in
77 agricultural marshland landscapes crossed by ditches for several reasons. Firstly, they have a
78 wide range of habitat requirements and a complex life cycle that makes them dependent on both
79 terrestrial and aquatic habitats (McPeck, 2008; Balzan, 2012; Barros Miguel *et al.*, 2017). Then,
80 they are sensitive to environmental changes at various spatiotemporal scales (Crowley &
81 Johnson, 1992; Nagy *et al.*, 2019) and, lastly, they are easy to monitor (Oertli, 2008; Giugliano,
82 Hardersen & Santini, 2012). Unlike other aquatic habitats such as ponds (e.g. Raebel *et al.*,
83 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

109 surrounding meadows. To this end, we studied 22 transects characterizing the range of
110 landscape and local environmental conditions recorded in the study area over a five-year period.
111 Water regime in ditches, notably very shallow waters and drying out, was expected to have
112 critical effects on Odonata assemblages (Piersanti *et al.*, 2007; Crumrine, Switzer & Crowley,
113 2008; Pires *et al.*, 2019). Drying might promote pioneer species with late emergence, known as
114 summer species, cascading into a decrease in alpha diversity and an increase in spatial beta
115 diversity. Landscape features are also expected to shape Odonata assemblages, with an expected
116 positive link between landscape openness (woodlands versus meadows and crops covers) and
117 dispersal abilities of adults (Raebel *et al.*, 2012; Nagy *et al.*, 2019). We also expected a positive
118 effect of the availability of aquatic habitats – more precisely the total length of the ditch network
119 – on species richness, and a decrease in beta diversity due to increased aquatic connectivity.
120 Drivers of Odonata assemblages are expected to vary between the two main suborders because
121 Zygoptera are mainly small-bodied, specialist species with a weaker dispersal capability than
122 Anisoptera which are typically large-bodied, rather generalist species with a stronger dispersal
123 ability (Corbet, 1999; Alves-Martins *et al.*, 2019; Nagy *et al.*, 2019). Hence, it is commonly
124 accepted that the effects of landscapes on Zygoptera are more difficult to detect than for
125 Anisoptera, and that Zygoptera should be more influenced by local environmental variables
126 (Raebel *et al.*, 2012; Nagy *et al.*, 2019). Also, we predicted the occurrence of a combination of
127 biological traits that would discriminate members of the two Odonata suborders.

128

129 **Material and Methods**

130 *Study area*

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

134 agricultural practices, notably grassland to cropland conversion, has resulted in the drastic
135 shrinking of major aquatic habitats such as marshes, salt marshes and other marine habitats
136 (Duncan *et al.*, 1999; Godet & Thomas, 2013). Currently, land uses in the Marais poitevin are
137 dominated by crops and meadows, and, to a lesser extent, by woodlands (respectively 48%,
138 42% and 10%; EPMP, 2015), with contrasted mosaics of land uses between localities. It is also
139 composed of a complex network of drainage ditches (8,200 km long) sub-divided into numerous
140 independent blocks (called hydrological units hereafter) in which the water depth is controlled
141 (see EPMP (2015) and Mauchamp *et al.* (2021) for a detailed description of the study area).
142 Recent inventories have shown that the Marais poitevin harbors 54 Odonata species (Deux-
143 Sèvres Nature Environnement *et al.*, 2018) out of 89 recorded in France (UICN France *et al.*,
144 2016). In the present work, we studied Odonata assemblages across 11 similar-sized and
145 independent hydrological units (300–365 ha; Figure 1) over a five-year period (2015–2019).
146 The hydrological units were mostly selected to represent the diversity of the environmental
147 conditions in terms of the water regime.

148

149 *Odonata assemblage monitoring*

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

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

162 *Odonata traits*

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

169 *Environmental conditions*

170 For each transect, the daily water depth of the adjacent ditch was obtained from the water level
171 measurement recorded by a limnigraph located in one representative ditch of each hydrological
172 unit, corrected according to the altitude of the ditch bottom. The monthly average water depths
173 were calculated from January to August. Ditches generally dry out from August to November
174 in the Marais poitevin; and drying duration (in days) was thus calculated for each transect over
175 the 12-month period preceding the Odonata sampling. The ditches were considered dry when
176 the daily water depth was below 5 cm, to take into account the uncertainty associated with the
177 elevation measurement from the bottom of the ditch. To assess the temporary open water
178 habitats available within the adjacent meadows, we used the number of days during spring
179 (April to June) on which 20% of the meadow area of each hydrological unit was flooded (later
180 in the season, no such flooded threshold occurred). Specifically, a pixel of one square meter on
181 a LIDAR imaging raster was considered as flooded when its altitude on the digital elevation
182 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.)

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

213

214 *Statistical analysis*

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

222 Firstly, we used generalized-linear mixed models (GLMM, with a Poisson error distribution)
223 with the hydrological unit and the year as random effects, to assess which environmental
224 variables (scaled data) explained the variation in alpha diversity (*lme4* package, Bates *et al.*,
225 2019). We produced all candidate models testing all simple and additive effects up to a
226 maximum of three variables per model to limit the complexity of the models. We then used a
227 multi-model inference approach to calculate model-averaged parameter estimates (with 95%
228 Confidence Intervals, 95% CIs) for the variables included in the selection of models (cumulated
229 weight $AICc < 0.95$, the Akaike information criterion corrected for small sample sizes,
230 Burnham & Anderson, 2002). The dredging and model averaging procedures were performed
231 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).

257 We used an RLQ analysis combined with a fourth-corner analysis to explore the trait-
258 environment relations (Dray *et al.*, 2014). RLQ is a multivariate technique consisting of a three-
259 table ordination to identify the co-structures between an environmental table (R), a presence-
260 absence species table (L) and a trait table (Q) (Dolédec *et al.*, 1996). We generated a
261 Correspondence Analysis (CA) on the species table. The table of environmental variables was
262 analysed using a Principal Component Analysis (PCA), with the CA transect scores used as the
263 row weight. The table of traits was analysed with a Hill Smith PCA, using the CA species scores
264 as the column weight. Then, the simultaneous ordination plot was computed by combining the
265 independent analyses with RLQ, using the “rlq” function of package *ade4* (Dray & Dufour,
266 2007). A global Monte-Carlo test with 10,000 random permutations was performed on the RLQ
267 values to test the relationships under two models. One tested the relationship between the
268 species composition and the environmental conditions (described as Model 2 by Dray &
269 Legendre (2008)) and the other tested the species distribution according to their traits (described
270 as Model 4 as defined in Dray & Legendre (2008)). We will refer to trait syndromes when
271 describing the combination of related traits for each axis of the co-inertia analysis (Dray *et al.*,
272 2014). To complement the RLQ results, an improved version of the fourth-corner method
273 including adjustments for multiple comparisons was used with 10,000 random permutations
274 (ter Braak, Cormont & Dray, 2012; Dray *et al.*, 2014), allowing to test for individual
275 correlations between each trait and each environmental variable, using the “fourthcorner”
276 function of package *ade4* (Dray & Dufour, 2007).

277 **Results**

278 *Description of assemblages*

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

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

291 *Environmental variables associated with taxonomic alpha diversity*

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

303 *Environmental variables associated with taxonomic beta diversity*

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

306 distance between pairs of transects, drying duration and the hedge index were significant
307 predictors of beta diversity when considering all species together and Zygoptera alone (Table
308 2, Figure 2a, b). More specifically, beta diversity kept increasing with increasing geographic
309 distances and drying duration and it increased with the hedge index above a threshold. For
310 Anisoptera, beta diversity increased with increasing geographic distance up to 20 km before
311 reaching a plateau. It also increased with nitrite concentration in ditch water and herbaceous
312 vegetation density on the upper banks (Figure 2c). Considering abundance data for beta
313 diversity calculation led to a higher explained deviance than with the presence-absence data. It
314 particularly highlighted an effect of vegetation density on lower banks on Zygoptera beta
315 diversity and a strong effect of water depth on Anisoptera beta diversity (Table S4).

316 *Functional trait patterns along environmental gradients*

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

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

331 first axis of the co-inertia analysis (Figure 3d). In the fourth-corner analysis, the environmental
332 gradients of the first RLQ axis were negatively correlated with late flight start, univoltinism
333 and dispersal ability (Figure 4a). The combination of traits correlated with the first RLQ axis
334 (first trait syndrome) was negatively correlated with the landscape openness gradient and the
335 cover of aquatic vegetation within the ditches, and positively correlated with the ditch network
336 length and vegetation density on the lower banks (Figure 4b). The second axis of the ordination
337 was mostly structured by water quality and the vegetation density on the upper banks (Figure
338 3c). The main traits structuring the second axis were larval strategy, oviposition mode, body
339 size and dispersal ability. These traits formed a second trait syndrome (Figure 3d) which
340 primarily differentiated Anisoptera from Zygoptera (Figure 3b). In the fourth-corner analysis,
341 dispersal ability was positively correlated with the water quality gradient (Figure 4a), and there
342 was no environmental variable significantly correlated with the trait syndrome of the second
343 axis (Figure 4b).

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

350

351 **Discussion**

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

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

366 *Predominant role of the temporary nature of ditch waters*

367 We found that the alpha diversity of Odonata assemblages greatly decreased when the duration
368 of drying increased in ditches. This agrees with Piersanti *et al.* (2007) and Pires, Stenert &
369 Maltchik (2017) who found that drying events in ponds eliminate the larvae of most Odonata
370 species, and therefore have an impact on local populations of adults (McPeck, 2008). Drying
371 duration was also the environmental predictor that best explained the dissimilarities in Odonata
372 assemblage composition between sites. Conversely to Bogan *et al.* (2020) who found that short
373 drying events (i.e. a couple of days) did not impact Odonata assemblages, beta diversity for all
374 species combined increased linearly with drying duration in the present study. To be precise,
375 drying duration varied strongly among sites in the Marais poitevin (on average 23 ± 47 days,
376 range: 1-194 days), representing severe conditions. The patterns of variation in alpha and beta
377 diversity as a function of drying duration we found were however similar to what has been
378 documented for other aquatic macroinvertebrates elsewhere, notably in intermittent streams
379 (e.g. Ephemeroptera, Plecoptera, Trichoptera; Bonada, Rieradevall & Prat, 2007; Datry *et al.*,
380 2014; Crabot *et al.*, 2020). Odonata are often presented as the most resilient macroinvertebrates

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

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

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

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

419 *Influence of landscape characteristics*

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

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

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

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

455 Anisoptera started to respond to landscape variables from a 1600-m buffer radius. Similarly,
456 Nagy *et al.* (2019) detected responses of Anisoptera but only at large buffer size (i.e. 5000m).
457 Furthermore, beta diversity of Odonata overall increased with geographic distance between
458 sites, which is generally interpreted as an increasing role of dispersal limitation (Heino *et al.*,
459 2015). More precisely, beta diversity kept increasing for Zygoptera with geographic distance
460 but quickly reached a plateau for Anisoptera. In addition, the fact that the GDM analysis
461 performed on Anisoptera was less predictive than for Zygoptera might reflect a more random
462 spatial distribution of Anisoptera. This is another sign, along with the broad distribution of these
463 species in the co-inertia analysis, of both the stronger dispersal ability of Anisoptera and their
464 higher tolerance of diverse environmental conditions compared to Zygoptera (Alves-Martins *et*
465 *al.*, 2019). Future investigations are needed to progress in the understanding of the effect of
466 large-scale variables on Odonata assemblage composition, notably consideration of the
467 configuration of landscapes.

468 *Minor influence of other local environmental variables*

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

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

480 and perchers, which are thermal conformers and need to relocate to maintain their body
481 temperature, for both Zygoptera and Anisoptera (Corbet & May, 2008). In addition, some
482 Odonata avoid overgrown riparian vegetation that shades the water surface, probably because
483 it makes it more difficult to recognize a habitat (Painter, 1998; Remsburg, Olson & Samways,
484 2008; Harabiš, 2016). Aquatic vegetation cover within ditches was linked to the functional
485 structure of Odonata assemblages, but surprisingly not to endophytic egg-laying species, (but
486 see Buchwald, 1992). Perhaps the limited range of aquatic vegetation cover within ditches made
487 it impossible to detect such an effect. In any case, maintaining microhabitat heterogeneity and
488 vegetation at different stages of succession likely promotes Odonata biodiversity (Harabiš,
489 2016; Simaika *et al.*, 2016; Johansson *et al.*, 2019). Lastly, crayfish abundances and algae cover
490 did not influence Odonata assemblages in this study, something that is congruent with results
491 found elsewhere for crayfish (e.g. Siesa *et al.*, 2014) but not for algae (e.g. Johansson *et al.*,
492 2019).

493 *Conclusion*

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

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

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

514

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529 **Author contribution statement**

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

532 **Data availability statement**

533 The traits database and datasets are available on a public data repository at
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541 **Conflict of interest statement**

542 Authors have no conflict of interest to declare.

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838 **Tables**

839

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

845

	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		

846

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

854

	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

855

856

Figure captions

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

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

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

873 **Figure 4.** Combination of the fourth-corner and RLQ results: relationships between the
874 environmental descriptors and functional traits. (a) Fourth-corner tests between the first two
875 RLQ axes for the environmental gradients (AxcR1 and AxcR2) and traits. (b) Fourth-corner
876 tests between the first two RLQ axes for the trait syndromes (AxcQ1 and AxcQ2) and
877 environmental variables. Positive significant relationships are represented by red cells, and
878 negative significant associations by blue cells. Variables with no significant associations are
879 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

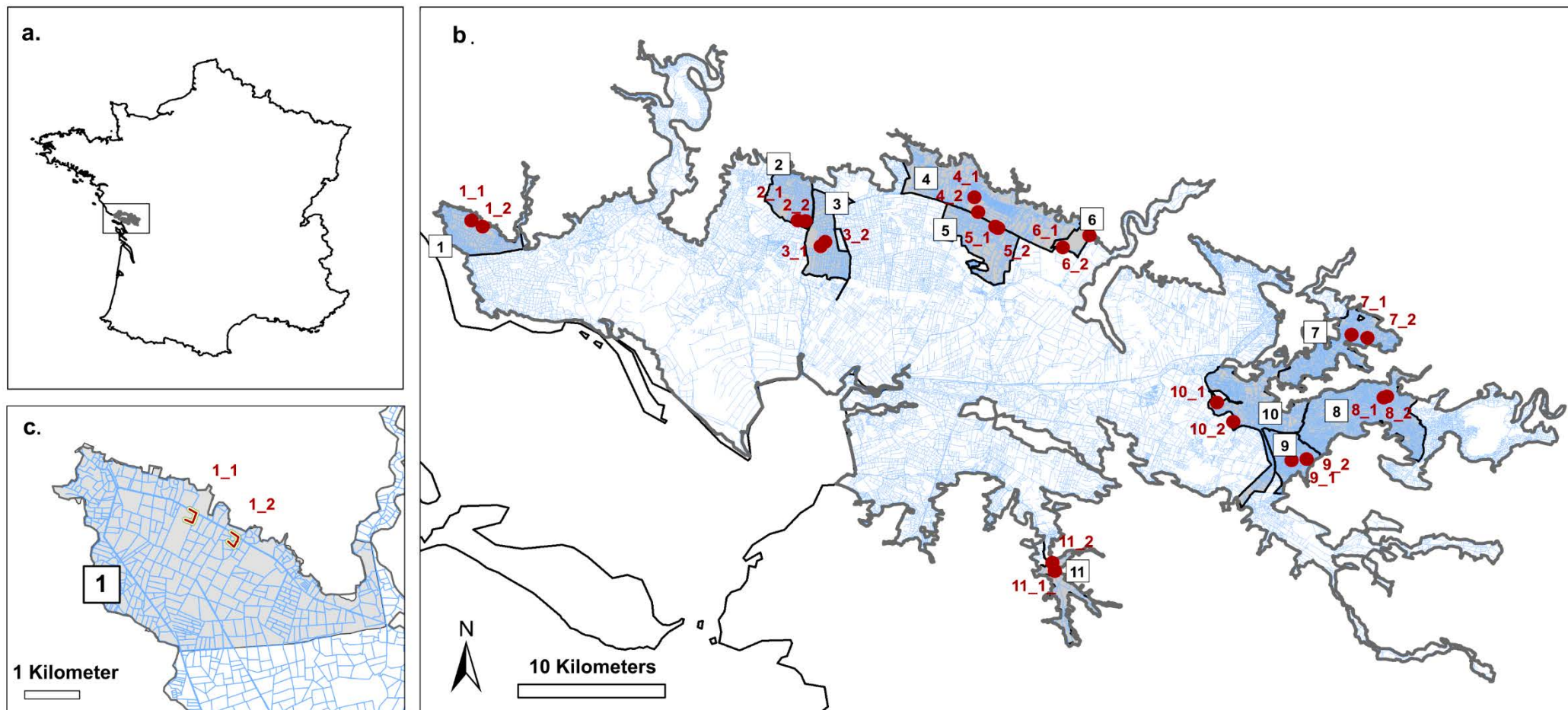


Figure 1. Location of (a) the Marais poitevin in France, showing (b) all transects (red points with numerical labels) within the 11 hydrological units studied (grey zones), and (c) a zoom on the two transects in hydrological unit 1. All of the ditches are indicated with blue lines

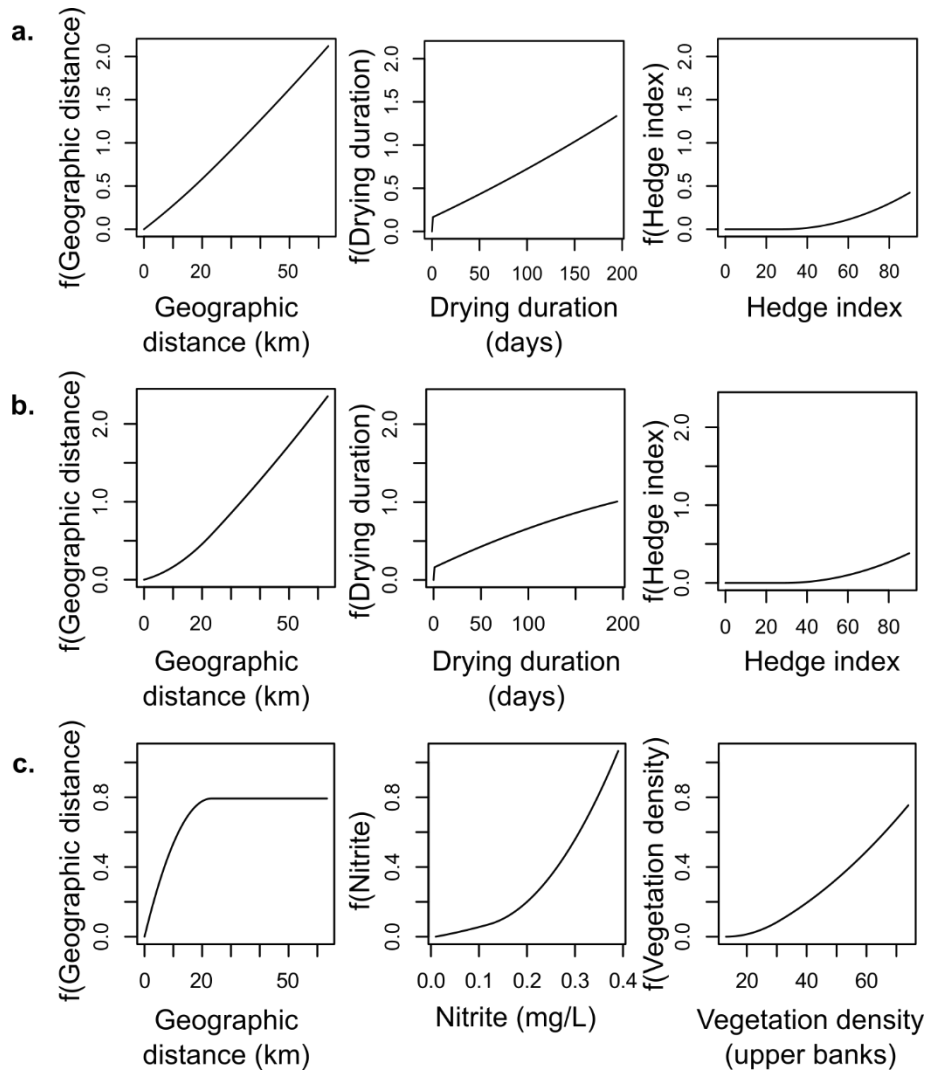


Figure 2. Generalized dissimilarity model-fitted I-splines for variables significantly associated with beta diversity for (a) all species, (b) Zygoptera and (c) Anisoptera (presence-absence data). Panels show the fitted functions (partial ecological distance between transect pairs) for each environmental 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.

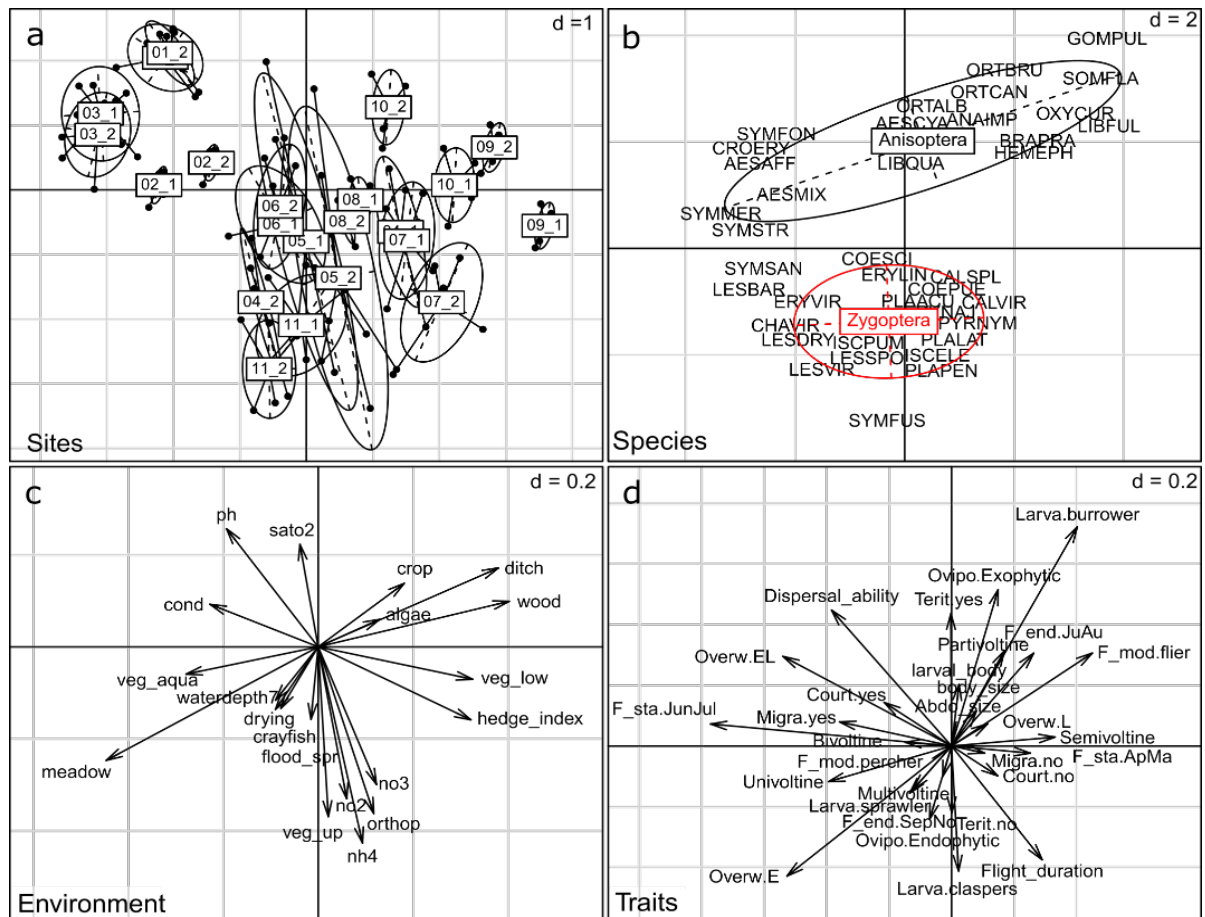


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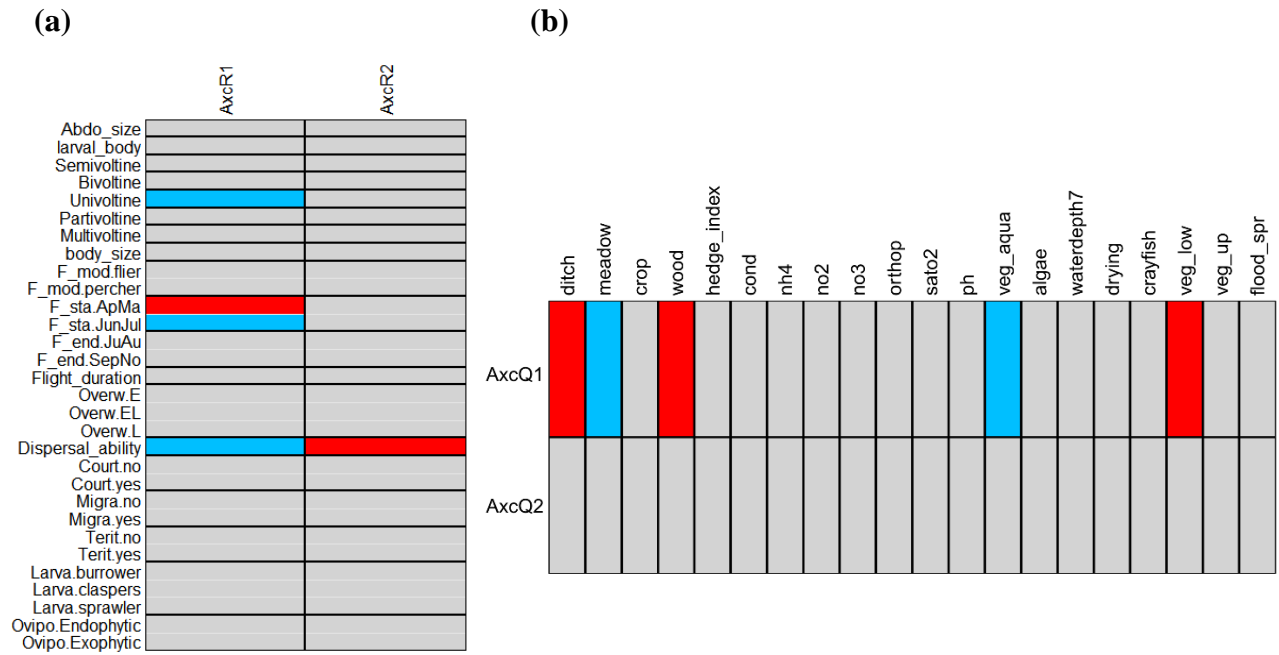


Figure 4. Combination of the fourth-corner and RLQ results: relationships between the environmental descriptors and functional traits. (a) Fourth-corner tests between the first two RLQ axes for the environmental gradients (AxcR1 and AxcR2) and traits. (b) Fourth-corner tests between the first two RLQ 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 modalities for the categorical variables. The complete names of the traits and environmental variables are available in Table S1 and S2.