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1 **Landscape models can predict the distribution of**
2 **aquatic insects across agricultural areas**

3
4 Short title: aquatic insect distribution in agricultural landscape

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20 **Abstract**

21 Context.

22 Adult aquatic insects are major vectors of aquatic subsidies to terrestrial ecosystems, providing
23 substantial ecosystem services to agriculture. Distance to water is reported as the prime factor to model
24 their spatial distribution, but the role of local drivers, either terrestrial or aquatic habitat features, is not
25 well established, notably in highly heterogeneous landscapes.

26 Objectives.

27 We assess the distribution and prioritise explanatory factors of aquatic insects in agricultural
28 landscapes.

29 Methods.

30 Adult aquatic insects (Ephemeroptera, Plecoptera, Trichoptera) were caught with sticky traps on a
31 regular grid-pattern set across a heterogeneous agricultural landscape during two years. Using
32 innovative landscape variables related to water, woodland, elevation and insolation (derived from
33 drone data), classical random forest models were run to predict the distribution of insects.

34 Results.

35 Variables that significantly explained insect distribution differed between insect orders, but the
36 distance to water was consistently amongst the three most informative variables in models.
37 Ephemeroptera occurrence was influenced by woodland density, while Plecoptera and Trichoptera
38 were more influenced by potential insolation. Predictions revealed a low distribution pattern for
39 Ephemeroptera and a high probability of occurrence for Plecoptera across terrestrial ecosystems.
40 Predictions were poor for Trichoptera, perhaps reflecting various dispersal patterns among species that
41 emerged earlier or later in spring and from a wide range of aquatic habitats.

42 Conclusions.

43 This work is the first to predict the probability of occurrence of aquatic insects across a spatially
44 heterogeneous agricultural landscape. Prediction maps suggest that the aquatic footprint, defined as the
45 occurrence of aquatic insects across a terrestrial landscape, is higher than previously thought.

46 **Keywords:** stoneflies, mayflies, caddisflies, random forest, merolimnic insect

47

48 **Introduction**

49 Aquatic insects constitute major biological flows from aquatic to terrestrial ecosystems (Polis et al.
50 1997; Nakano and Murakami 2001). After their aquatic larval stage, numerous insect species emerge
51 as winged adults and disperse across the terrestrial ecosystems. Characterizing the spatial and temporal
52 magnitude of such movements is central to understand the associated ecological functions for receiving
53 ecosystems, as well as potential services to agriculture (Raitif et al. 2019). Notably, various aquatic
54 insect species can feed on pollen during their adult stage (e.g., Winterbourn 2005; Hass et al. 2018),
55 and thus have the potential to contribute to pollination while agroecosystems suffer a global decline in
56 pollinators (Potts et al. 2010). These aquatic insects also provide nutritional subsidies to terrestrial
57 consumers in the riparian zone and farther inland from banksides (Baxter et al. 2005; Uno 2016). They
58 disseminate essential polyunsaturated fatty acids from aquatic environments to terrestrial ecosystems
59 (Martin-Creuzburg et al. 2017; Mathieu-Resuge et al. 2021), and they are recognized as key elements
60 of terrestrial food web functioning (Wesner 2010; Lafage et al. 2019). Many terrestrial predators are
61 natural enemies of pest outbreaks in cropland (e.g., spiders and carabids, Riechert and Lockley 2003;
62 Paetzold et al. 2005; Symondson et al. 2006; Stenroth et al. 2015), and can benefit from aquatic prey
63 that usually emerges when terrestrial prey is scarce. Significant quantities of winged insects can emerge
64 from lakes, reaching 1,200 to 2,500 kg.ha⁻¹.yr⁻¹ (Gratton et al. 2008) and generally exceeding that of
65 rivers (Williams et al. 2004; Bartrons et al. 2013). In agricultural landscapes however, 14 to 74 kg.ha⁻¹
66 yr⁻¹ of insect dry mass can emerge from streams (Raitif et al. 2018), among which 12.5 kg.ha⁻¹.yr⁻¹,
67 on average, ultimately fell to the ground (Raitif et al. 2022). This is a substantial source of fertilization
68 for soils (Jefferies et al. 2004). Notably, stream-derived N deposition on land can exceed the current
69 amounts of atmospheric N deposition in temperate regions (Raitif et al. 2019). These study cases on
70 winged aquatic insects highlight that the mechanisms governing their dispersal and distribution must
71 be understood before appropriate prediction of their distribution across terrestrial areas, and latent
72 beneficial impacts to agriculture, can be made.

73 To date, the most studied factor to explain the distribution of winged aquatic insects is the
74 distance to water, their abundance decreasing rapidly farther inland from aquatic edges after a few
75 meters (Svensson 1974; Miller et al. 2002; Carlson et al. 2016). Dispersal distances likely vary between
76 species (Muehlbauer et al. 2014; Peredo Arce et al. 2021), but also depend on the aquatic habitat
77 considered (Gratton and Vander Zanden 2009; Schindler and Smits 2017). To date, a majority of
78 studies have focused on a single habitat type, mostly permanent streams or lakes (Gratton and Vander
79 Zanden 2009; Carlson et al. 2016; Mathieu-Resuge et al. 2021). Yet many invertebrate species live in
80 other temporary or permanent environments such as ponds, ditches or irrigation canals (Williams 1997;
81 Labat et al. 2022). These habitats may represent a substantial proportion of surface water in these
82 landscapes (Davies et al. 2010), more particularly in agricultural areas (Williams et al. 2004). In a
83 recent study, Gerber et al. (2022a) raised the issue of defining aquatic habitats that serve as potential
84 sources of emerging insects, highlighting the need for fine and thorough hydrographic mapping for
85 studying aquatic insects' dispersal and distribution at the landscape scale. Additionally, several
86 landscape features likely modulate the distribution of winged aquatic insects dispersing across
87 terrestrial ecosystems, but again, underlying mechanisms are poorly characterised. It has been
88 reported that riparian woodland density can hamper the dispersal of emerging chironomids and
89 caddisflies (Delettre and Morvan 2000; Greenwood 2014). Temperature, woodland edges and
90 topography are other variables that control the flight and movements of terrestrial insects across the
91 landscape (Mattila 2015; Tonkin et al. 2018; Sweaney et al. 2022); however, they have been rarely
92 investigated for winged aquatic insects. Some studies have shown the importance of temperature for
93 aquatic insects. In the case of specific Diptera such as the crane fly, *Tipula maxima* (Jourdan et al.
94 2019), dispersal-related traits vary depending on ambient environmental conditions (temperature
95 regimes, discharge patterns and biotic interactions during individual development). For adult
96 Plecoptera, air temperature acts as a factor that potentially influences longevity (Collier and Smith

97 2010). This result suggests that maintenance of appropriate microclimatic conditions should be a
98 consideration in riparian management (Petersen et al. 2004). Consequently, the biophysical
99 characteristics of riparian zones and, more broadly, terrestrial areas adjacent to aquatic environments,
100 are an important factor to consider when studying the distribution of aquatic insects. Accordingly,
101 much research attention has focused on how terrestrial environmental features regulate subsidy
102 dispersal and the responses of terrestrial consumers (e.g., forest cover, complexity of ground habitats,
103 availability of terrestrial resources), and on how human activities alter these linkages (Petersen et al.
104 2004). For example, small aquatic insects (Nematocera) were most abundant under agricultural land
105 use, whereas larger bodied aquatic insects (Plecoptera and Trichoptera) were more associated with
106 forest land use (Stenroth et al. 2015).

107 In this work, we aim at (1) identifying landscapes features, defined hereafter as explanatory
108 factors, that explain the occurrence of some aquatic insects (i.e., Ephemeroptera, Plecoptera and
109 Trichoptera, namely EPTs) and (2) developing a spatially explicit statistical model to predict their
110 potential distribution across an agricultural landscape. Investigations were performed in a 140ha
111 agricultural area including meadows, crops, woodlands and a variety of aquatic ecosystems (stream,
112 ponds and ditches). Winged EPTs were collected during their aerial dispersal across the area in spring
113 and summer for two consecutive years. Random forest models were run on high-resolution landscape
114 variables (e.g., distance to water, potential insolation, elevation and woodland density) extracted from
115 drone data to predict the distribution of EPTs across the experimental area. Notably, we hypothesized
116 that distance from water edge negatively correlates with the probability of occurrence of aquatic
117 insects, while high densities of riparian trees along streams could hamper inland distribution. We also
118 investigated differences among species owing to their ecological preference for woody and shaded or
119 open and insolated habitats.

120

121 **Methods**

122 ***Study area***

123 The study site was located at the northeast of Brittany (48°36' N, 1° 32' W, France), is part of the
124 European LTSER (Long-Term Socio-Ecological Research) network and occurs within the “Zone
125 Atelier Armorique” (ZAAR). The ZAAR is a temperate region with no dry season and warm summers.
126 The area is representative of an intensive agricultural area dominated by dairy production, composed
127 of small fields separated by a hedgerow network called “bocage” (Baudry et al. 2000). Annual crops
128 in this area are winter cereals and maize (Fig. 1A). The study area was selected based on the
129 representativeness of the different landscape elements within it, based on the Shannon Diversity Index
130 (SHDI) using Chloé software (Boussard and Baudry 2017). The average SHDI index for the ZAAR is
131 0.29 ± 0.10 (calculated at a resolution of 1 km by 1 km) and that for the study area is 0.39 ± 0.12 . The
132 140ha study area consisted of a patchwork landscape of woodland, hedgerows, pastures, croplands,
133 and agricultural areas (Fig. 1B), and is crossed by a 33.2 km long first-order (Strahler 1952) stream
134 named Le Guyoult.

135 ***Sampling***

136 Emerging EPTs were caught using interception traps called sticky traps (Raitif et al. 2022).
137 Sticky traps consisted of a transparent A3 plastic cover (42 x 29.7 cm, 2 mm thick) on which was
138 spread a thin layer of non-drying glue (Tanglefoot®, Tangle-Trap® Sticky Coatings). The plastic cover
139 sprayed with glue was fixed cylindrically around a stake at 1 m height to catch insects coming from all
140 possible directions (Wesner 2010). Hoops placed inside the cylinder reinforced the structure (Fig. 1C).
141 The sticky traps were set in a grid pattern spaced out by at least 50 m to cover the entire study site
142 homogeneously.

143 Two sampling campaigns were carried out, in spring and summer in 2020 and 2021, from April
144 to June, which is the period of emergence of most aquatic insects in Brittany (Raitif et al. 2018). In

145 2020, 56 sticky traps were placed. In 2021, 64 sticky traps were placed, among which 20 were co-
146 localized with those in 2020 (Fig. 1B). The plastic covers spread with glue remained in place for 15
147 consecutive days for each sampling session before being retrieved and frozen in the laboratory.
148 Monitoring of the traps throughout the emergence period has made it possible to visualize the
149 emergence peaks of the insects, which are dependent on the weather. Therefore, two sampling sessions
150 were conducted in 2020, from May 18th to June 2nd and from June 2nd to June 16th. In 2021, three
151 sampling sessions were conducted, from April 1st to April 15th, from April 26th to May 10th, and from
152 May 20th to June 3rd. For each sampling session, only the plastic covers were replaced.

153 In the laboratory, EPTs were extracted from the glue using D-limonene terpene and stored in
154 96°C alcohol. All specimens were identified using a stereomicroscope (Leica M205 C) equipped with
155 a binocular camera (Leica DMC4500) at the species or genus level using several identification keys
156 (Ephemeroptera: Elliott 1983; Bauernfeind and Soldán 2013, Plecoptera: Despax 1951; Lubini et al.
157 2012, Trichoptera: Malicky 2010; Barnard and Ross 2012).

158 *Selected landscape features as explanatory factors*

159 *Water maps.* We characterized the full hydrographic networks including all water bodies (i.e., the
160 mainstream, the tributaries, the ditches, and the water-full ponds at the time of the survey). For 2020,
161 the hydrographic networks used were directly extracted from Gerber et al. (2022a). For 2021,
162 hydrographic networks were characterized at four successive dates (April 12th, May 5th, May 27th, and
163 June 29th). We divided the water bodies into five aquatic habitats: the mainstream, the tributaries,
164 ditches with running water, ditches with standing water, and ponds. From the aquatic habitats and the
165 four dates of mapping, we defined 14 hydrographic networks. For each year and each order, we defined
166 the hydrographic network that best explains the distribution of the aquatic insects following Gerber et
167 al. (2022a). All the details are provided in the Supplementary information (S1).

168 *Woodland maps.* On May 25th in 2020, a drone survey was performed to characterize the landscape
169 features of the study site. A fixed-wing (sensefly eBee X) was used to survey the whole area at once.
170 The flight altitude was 120 m above ground level. Using a RGB camera (sensefly soda 3D, 20M pixels)
171 and a photogrammetric approach, a RGB orthorectified map and a digital surface model (DSM) of 0.04
172 m and a mean XYZ geometrical horizontal and vertical accuracy of 0.016 m were obtained (Houet
173 2022). Using eCognition software, homogenous polygons according to their color and height were
174 segmented. All woodland polygons were then manually classified from RGB visual interpretation and
175 rasterized at 0.05 m. Resolution was checked using a trimble geo7x Dgps, which recorded the absolute
176 position of 10 targets covered by the drone's flight.

177 *Elevation maps.* We used a digital elevation model (DEM) with 1 m resolution obtained from the
178 French National Institute of Geographic and Forest Information (“Institut national de l'information
179 géographique et forestière”, <https://ign.fr/>)

180 *Potential insolation maps.* The potential insolation mapping (Potential Incoming Solar Radiation
181 kWh.m⁻², PISR) was calculated using the SAGA software v.7.9 (Conrad et al. 2015) for each sampling
182 session. PISR represents the sum of the solar energy per square meter and is calculated every hour
183 based on the position of the sun and the DSM. Shadowed areas near woodlands will exhibit a lower
184 PISR value than an area in the middle of a field. The PISR values are calculated for all the points of
185 the DSM, thus on the canopy. The sticky traps are sometimes located under trees, and therefore receive
186 much lower insolation than that received by the canopy. To take this into account, we removed the
187 wooded areas from the PISR. Then the missing values were interpolated from edges using the GDAL
188 translator library v. 3.5, *fillnodata* function.

189 *Explanatory factors.* We derived 19 biophysical factors from the environmental maps described
190 (Supplementary information, Table S2). Movement distances may vary according to the insect orders,
191 land uses, and models used to estimate the abundance decrease with distance from water. For example,

192 previous studies differed in the distance over which Chironomidae abundance decreased by 50%, from
193 13 m to 25 m, and of Trichoptera from 1.3 m to 5 m (Muehlbauer et al. 2014; Raitif et al. 2022). This
194 potentially modifies the extent of the variables effect. Hence, we used three buffer sizes because the
195 scale at which environmental factors may influence aquatic insect distribution is not well known. The
196 woodland density (the number of wooded pixels divided by the area) and the mean and variance of the
197 elevation and potential insolation were calculated for each sticky trap within three scale buffers: a 5 m
198 radius buffer, a 5 m to 25 m radius ring buffer (a 25 m buffer without the 5 m radius buffer) and a 25
199 m to 50 m radius ring buffer (a 50 buffer without the 25 m radius buffer) using *zonal statistics* function
200 GIS software v.3.22 (QGIS Association 2022). Then, for each sticky trap, the distance from the nearest
201 wooded area was calculated using the *st_distance* function from the *sf* package (Pebesma 2018). The
202 nearest aquatic habitat (i.e., mainstream, tributary, ditch with running water, ditch with standing water,
203 or pond) was determined using the *st_join* function from the *sf* package.

204 To help with the interpretation of the models, we explored the relationships between the factors
205 with Pearson coefficients (correlation matrix available in the Supplementary information, Fig. S3)
206 because we suspect some factors to be correlated (e.g., insolation and woodland).

207

208

209 ***Statistical analyses***

210 To identify explanatory factors for predictive models, we calibrated the models by insect order
211 (i.e., Ephemeroptera, Trichoptera and Plecoptera) with the random forest algorithm using the
212 *randomForest* package (Liaw and Wiener 2002). Random forest, based on recursive partitioning, does
213 not rely on assumptions about relationship between the explanatory variable and the response variable
214 (as in GLM or GAM models). This approach is entirely data-driven and reduces the associated variance

215 of the prediction (Breiman 2001). Therefore, within the limit of the data, random forest which
216 maximizes the reduction of deviance is more suitable for prediction than GLM or GAM (Guisan et al.
217 2017).

218 The response variables were the occurrences of EPT orders and the explanatory variables were
219 the environmental factors and the sampling sessions. We used the occurrence of different orders
220 because it allows us to validate our prediction, and to compare our results with other studies. We
221 followed the procedure described by Genuer and Poggi (2020). According to this procedure, the
222 number of trees was fixed at 10,000. The number of factors tested at each division minimizing the out-
223 of-bag error (OOB error estimates of the prediction error using the unselected observations in a
224 bootstrap sample as test data, Genuer and Poggi 2020) was chosen. For each order, we kept a session
225 when the occurrence rate was higher than 10% to have enough occurrences to calibrate the models
226 (Fig. 2). We used the dataset from 2020 to calibrate the model because the predictions were better
227 compared to 2021 (Supplementary information, Fig. S4).

228 For predictions, we used the *VSURF* function from the *VSURF* package (Genuer et al. 2015). It
229 is a three-step variable selection procedure based on random forests. The first step is dedicated to
230 eliminating irrelevant variables from the dataset according to the Mean Decrease Accuracy, a measure
231 that expresses how much accuracy the model losses by excluding each variable. The second step aims
232 to select all variables related to the response for interpretation purposes. The model is built with
233 variables selected in the first step and variables with the lowest OOB errors. The third step refines the
234 selection by eliminating redundancy in the set of variables selected by the second step, for prediction
235 purposes. Variables are kept if the OOB error decreases more than the average variation, thus limiting
236 the correlations between the variables. Finally, the remaining variables are added in order of increasing
237 importance. Model validation was made using the area under curve (AUC) criteria. AUC is a standard
238 measure often applied to random forest (Guisan et al. 2017). It measures the discrimination (i.e., the

239 ability to distinguish between occupied and unoccupied sites, Guisan et al. 2017) by comparing the
240 order of occurrences observed in 2021 with the predictions of the model based on environmental
241 variables in 2021. AUC ranges in value from 0 to 1. A model whose predictions are 100% wrong has
242 an AUC of 0, and one whose predictions are 100% correct has an AUC of 1. An AUC of 0.5 suggests
243 no discrimination, 0.7 to 0.8 is considered acceptable and 0.8 to 0.9 is considered excellent (Guisan et
244 al. 2017).

245 Finally, for the whole area, we created predictive maps of the probability of ETPs occurrences
246 based on the explanatory factors selected by the *VSURF* procedure. To obtain predictive maps of the
247 whole area, we computed for each selected factor its map in 2021. Distance maps (for woodland and
248 water) were calculated using Chloé software v. 4.1 (Boussard and Baudry 2017). Maps of density,
249 mean and variance (for woodland, potential insolation, and elevation) were calculated using moving
250 windows. A moving window assigns to each pixel the value of a function (e.g., mean, variance) in a
251 window centered on each of these pixels, using the *focal* function from the *terra* package (Hijmans et
252 al. 2023). Moving windows sizes and shapes were identical to the three scale buffers so that the pixel
253 values are comparable to the corresponding factor values for each of the sticky traps. All the maps
254 were resampled at 5 m resolution using the nearest neighbor method, *aggregate* function, in the *terra*
255 package.

256 All statistical analyses were performed using the R software v. 4.2.1 (R Core Team 2021).

257

258

259 **Results**

260 A total of 748 adult aquatic insects (EPTs) were sampled. Among Ephemeroptera, 91
261 individuals were counted and 6 species identified. The most represented species was *Habrophlebia*
262 *fusca* (80.2%). The distances at which the abundance of Ephemeroptera was at 50% and 10% of its

263 near-water source levels were 1.1 and 6.5 m, respectively. Among Plecoptera, 484 individuals were
264 counted and 6 species identified. The three most abundant species were *Nemoura cinerea* (60.33%),
265 *Nemoura lacustris* (15.49%) and *Amphinemoura standfussi* (13.42%). The distances at which the
266 abundance of Plecoptera was at 50% and 10% of its near-water source levels were 2.5 and 109 m,
267 respectively. Among Trichoptera, 128 individuals were counted and 9 species identified. The four main
268 species were *Stenophylax lateralis* (26.56%), *Beraea pullata* (25%), *Limnephilus centralis* (20.31%)
269 and *Limnephilus sparsus* (10.15%). The distances at which the abundance of Trichoptera was at 50%
270 and 10% of its near-water source levels were 3.4 and 304 m, respectively.

271

272 ***Factors explaining occurrences of aquatic insects***

273 Distance from water consistently ranked within the top three variables controlling the
274 distribution of EPTs (Fig. 3). For Ephemeroptera, two correlated variables (Supplementary
275 information, Fig. S3) stood out in addition to distance from water: woodland density and the mean of
276 PISR in a 5 to 25 m ring. For Plecoptera, the top three variable controlling the distribution were the
277 distance from water and average PISR at 5 m and to a lesser extent the woodland density in a 5 to 25
278 m ring. For Trichoptera, the session was the main variable followed by the variance of PISR in a 25 to
279 50 m ring and the distance from water.

280

281 ***Prediction***

282 For Trichoptera, the variance of PISR in a 25 to 50 m ring was retained for prediction through
283 the *VSURF* procedure. For Ephemeroptera, the distance from water and the woodland density in 5 to
284 25 m were retained. For Plecoptera, the distance from water and the mean of PISR in a 5 m buffer were
285 retained. Predictions were good for Ephemeroptera (AUC = 0.86, Fig. 4) and nearly acceptable for

286 Plecoptera (AUC = 0.68, Fig. 4). For Trichoptera, the model gave poor predictions (AUC = 0.43, Fig.
287 4). Thus, prediction maps were made for Ephemeroptera and Plecoptera (Fig. 5). The prediction map
288 of Ephemeroptera showed visually three levels of probability of occurrence. The highest one represents
289 areas close to the water with riparian forests (from 0.75 to 1) and occupies 16 % of the study area,
290 including the hydrographic network (0.4 % of the area). Then, the probability is medium for wooded
291 patches without or with small water bodies or for an area close to the water without riparian forests
292 (from 0.25 to 0.75, occupying 16 % of the study area). Finally, the probability of occurrence is very
293 low in the fields (from 0 to 0.25) which occupy 68 % of the study area. The prediction of Plecoptera
294 exhibited a very high probability of occurrence in an approximately 12 m buffer around water bodies
295 (> 0.9 of occurrence probability, 13 % of the study area, including the hydrographic network, i.e., 1.1%
296 of the area). Most of the values from 0.75 to 0.9 (33 % of the study area) are in a 12 m to 50-60 m
297 buffer from the water bodies.

298

299 **Discussion**

300 In this study, we highlighted the distribution extent of EPTs in terrestrial environments. Aquatic
301 ecosystems are often considered physically well-defined. However the biological width of a stream or
302 stream signature (which encompasses the aquatic insect subsidies on the terrestrial ecosystem) has
303 been recently acknowledged (Muehlbauer et al. 2014; Gurnell et al. 2016; Kopp and Allen 2019). In
304 this study, we considered not only streams but all the water bodies which can produce aquatic insects
305 (e.g., pond, ditch, temporary tributaries) within a landscape mosaic. We included both the aquatic
306 habitat for insect production and the terrestrial environment where the insects spread. We showed that
307 aquatic insect fluxes to terrestrial environments cover the entire surrounding land, even for site located
308 relatively far from water (several hundred meters). Furthermore, random forest analyses confirmed
309 that the spatial distribution of adult EPTs is explained differently for each order.

310 Our results confirm that distance from water is a key factor explaining the inland distribution of
311 aquatic insects and is one of the top three factors for all orders. Indeed, EPTs are more abundant near
312 water bodies (Carlson et al. 2016; Peredo Arce et al. 2021). However, our analysis also highlights that
313 while distance to water is a key parameter, other landscape factors also help explain the predictions for
314 each order. For Ephemeroptera, the density of woodland within 25 m stands out. One explanation
315 would be that the larvae of *Habrophlebia fusca*, the main species in our study, are shredders that
316 consume leaf litter and are therefore common in wooded areas (Bauernfeind and Soldán 2013). The
317 scale of 25 m for woodlands could therefore be related to larval habitat, as this species is known for its
318 poor dispersal capability (Sarremejane et al. 2020). Ephemeroptera distribution also appears sensitive
319 to potential insolation (PISR) between 5 and 25 m. This result is consistent with the hypothesis that an
320 open environment promotes inland dispersal of aquatic insects. In an open environment, the absence
321 of tall vegetation and exposure to higher wind speeds could lead to farther inland dispersal than that in
322 forested landscapes (Delettre and Morvan 2000; Carlson et al. 2016). Potential insolation is also
323 important for Trichoptera and Plecoptera, suggesting that open environments may also favor inland
324 dispersal for these orders. This factor, which has not been examined in previous studies, may provide
325 an interesting explanation for the inland movement of aquatic insects, probably because of its influence
326 on flight. The amount of potential insolation may be stronger in open environments as is it highly
327 negatively correlated with woodland density ($\rho = -0.7$, Supplementary information, Fig. S3). In
328 forest, insolation values are very low and homogeneous due to the tree cover, which reduces its impact
329 on insect distribution. For Trichoptera, we noticed a significant impact of the sampling session during
330 the study. This result is probably due to the high diversity of species with very different biological
331 traits and emergence times (Singh et al. 1984). The emergence of different species between each
332 session may induce temporal and spatial heterogeneity between sessions which induces noise in our
333 analyses.

334 To our knowledge, for the first time, we have provided a predictive map of the occurrence of
335 some aquatic insects (i.e., Ephemeroptera and Plecoptera) at the landscape scale, thereby emphasizing
336 the extent of stream influence (Gurnell et al. 2016; Gounand et al. 2018). According to the meta-
337 analysis from Muehlbauer et al. (2014), these two orders have a similar extent (10 % of abundances at
338 140 m for Plecoptera and 160 m for Ephemeroptera), but Ephemeroptera tends to stay closer than
339 Plecoptera (50 % of abundances at 2.7 m for Plecoptera and 0.9 m for Ephemeroptera). However, our
340 models predict a highly divergent distribution of adult Plecoptera and Ephemeroptera at the landscape
341 scale. The probability of occurrence decreases rapidly for Ephemeroptera but does not stabilize at low
342 values to zero, in contrast to other studies (Muehlbauer et al. 2014; Raitif et al. 2022), while the extent
343 for Plecoptera is large and the probability of occurrence remains high even away from water. This
344 difference may be explained by several factors. For Ephemeroptera, almost all species included in the
345 Muehlbauer et al. (2014) meta-analysis are good dispersers and are more likely to be found far from
346 water, unlike *Habrophlebia fusca* (Sarremejane et al. 2020), which dominated the Ephemeroptera
347 assemblages in our study. This low dispersal capability of this species is also congruent to its body
348 stores consisting primarily of triglycerides for reproduction and less glycogen and proteins for long-
349 distance flight (Gerber et al. 2022b). Another possibility is the unsuitable sampling methods used to
350 study dispersal and distribution at the landscape scale. Indeed, most emergence studies have sampled
351 along transects from stream to terrestrial habitats. This protocol is efficient to study the linear dispersal
352 from the stream but does not account for i) alternative sources of insects (pool, ditch, temporary
353 running waters) (Gerber et al. 2022a) and ii) erratic insect movements due to wind and other landscape
354 elements (e.g., woodland density). For example, in Muehlbauer et al. (2014), most studies were
355 conducted in forests with homogeneous conditions that may favor dispersal over a longer distance from
356 streams. Raitif et al. (2022) conducted a similar study but their furthest sampling point from the aquatic
357 source was 50 m. They cannot therefore conclude anything about the real dispersal distance of

358 individuals beyond 50 m. Our sampling strategy was chosen to be suitable for studying dispersal at the
359 landscape scale (i.e., beyond 50 m).

360 For Plecoptera, we found a very large extent of inland occurrence. The probability of occurrence
361 could be relatively high up to 60 m around each water body. This result is surprising because most of
362 Plecoptera species tend to be weak dispersers (Sarremejane et al. 2020). This result suggests that
363 Plecoptera may disperse farther from the water than previously thought. As with Ephemeroptera, this
364 difference with the literature may be explained by our sampling protocol, which is more adapted to
365 studying spatial distribution at the landscape scale. Furthermore, this result is also in line with the
366 higher fuels for flight in Plecoptera than in Ephemeroptera found by Gerber et al. (2022b).

367 The quality of the predictions differed strongly between Trichoptera, Plecoptera, and
368 Ephemeroptera. Predictions for Plecoptera and Ephemeroptera were strong but remained weak for
369 Trichoptera. We can make three suggestions to explain this. First, we observed that between the two
370 sampling periods (i.e., 2020 and 2021), the taxonomical composition changed significantly for
371 Trichoptera (11 species belonging to 9 genera in 2020 and only 4 belonging to 3 genera in 2021) and
372 to a lesser extent for Plecoptera (the proportion of *Amphinemoura standfussi* strongly increased in 2021
373 while the proportion of *Nemoura lacustris* decreased in samples). Within an order, different species
374 may vary in flight ability (Goldsworthy and Wheeler 1989), behavior (Steyn et al. 2016), biological
375 traits (Gerber et al. 2022b) and larval habitats (Tachet et al. 2000). These differences could explain the
376 poor quality of predictions for Trichoptera. Second, the quality of the prediction could depend on the
377 movement ability of the organisms. Indeed, most of the Trichoptera are considered good dispersers
378 (Sarremejane et al. 2020), good flyers (Graham et al. 2017) and are frequently found far from water
379 (Peredo Arce et al. 2021). In contrast, when organisms like Ephemeroptera and Plecoptera remain close
380 to water (Muehlbauer et al. 2014), their distribution can be more easily modeled. Third, some
381 explanatory variables could still be missing or need to be refined. For instance, hedgerow permeability,

382 defined by vegetation structure and density, could limit insect dispersal differently from one species to
383 another. The use of other sensors, such as Lidar, would be highly contributive to provide additional
384 explanatory variables. In the same way, measurements of surface temperature using a thermal camera
385 may be interesting to explore. PISR could also be refined from one period to another by accounting for
386 irradiance measurements available from weather station near the study site. Indeed, as shown,
387 insolation seems to influence EPTs distribution although we did not account for real insolation during
388 each of the sampling sessions. One sunny/cloudy period may positively or negatively affect the
389 magnitude of EPTs distribution compared to another. One way to improve our predictions would be to
390 adjust the resolution of our models, the sampling strategy (e.g., by considering later emergence periods)
391 or even the drone flight surveys according to the flight ability of the species, as we did with the best
392 hydrographic network for each sampling session. Indeed, in highly mobile organisms, the choice of
393 spatial and temporal resolution greatly influences distribution models (Guisan et al. 2017). However,
394 to our knowledge, no studies have attempted to model inland distribution of aquatic insects, limiting
395 the information available on which resolution to use.

396 In conclusion, our results show that the spatial extent of emergent aquatic EPTs is much wider
397 than expected in the literature, likely because sampling along linear transects is not suitable for
398 studying the distribution of aquatic insect at the landscape scale with multiple aquatic sources.
399 Moreover, the analysis of new landscape elements in our study confirms the role of distance to the
400 water, independent of aquatic habitat type and of woodland for some species. It also highlights the role
401 of new and untested variables such as the PISR. Finally, our models have been successfully used to
402 predict the distribution of Ephemeroptera and Plecoptera at the landscape scale. This opens the door to
403 studying their impacts in terrestrial ecosystems in terms of fertilization, pollination, or as food source
404 for terrestrial predators at the landscape scale.

405

406

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410 **Author contributions**

411 RGer, CP, JMR and BB conceived the ideas and designed methodology; RGer, CP, JMR, RGeo,

412 JR and BB collected the data; TH performed UAV flights; RGer, RGeo, TH, and BB analyzed the

413 data; Rger, CP, JMR and BB led the writing of the manuscript. All authors contributed critically to the

414 drafts and gave final approval for publication.

415

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419 **Declarations**

420 **Competing interests**

421 The authors have no relevant financial or non-financial interests to disclose.

422

423 **Data availability**

424 The data are available from the corresponding author on reasonable request.

425

426 **References**

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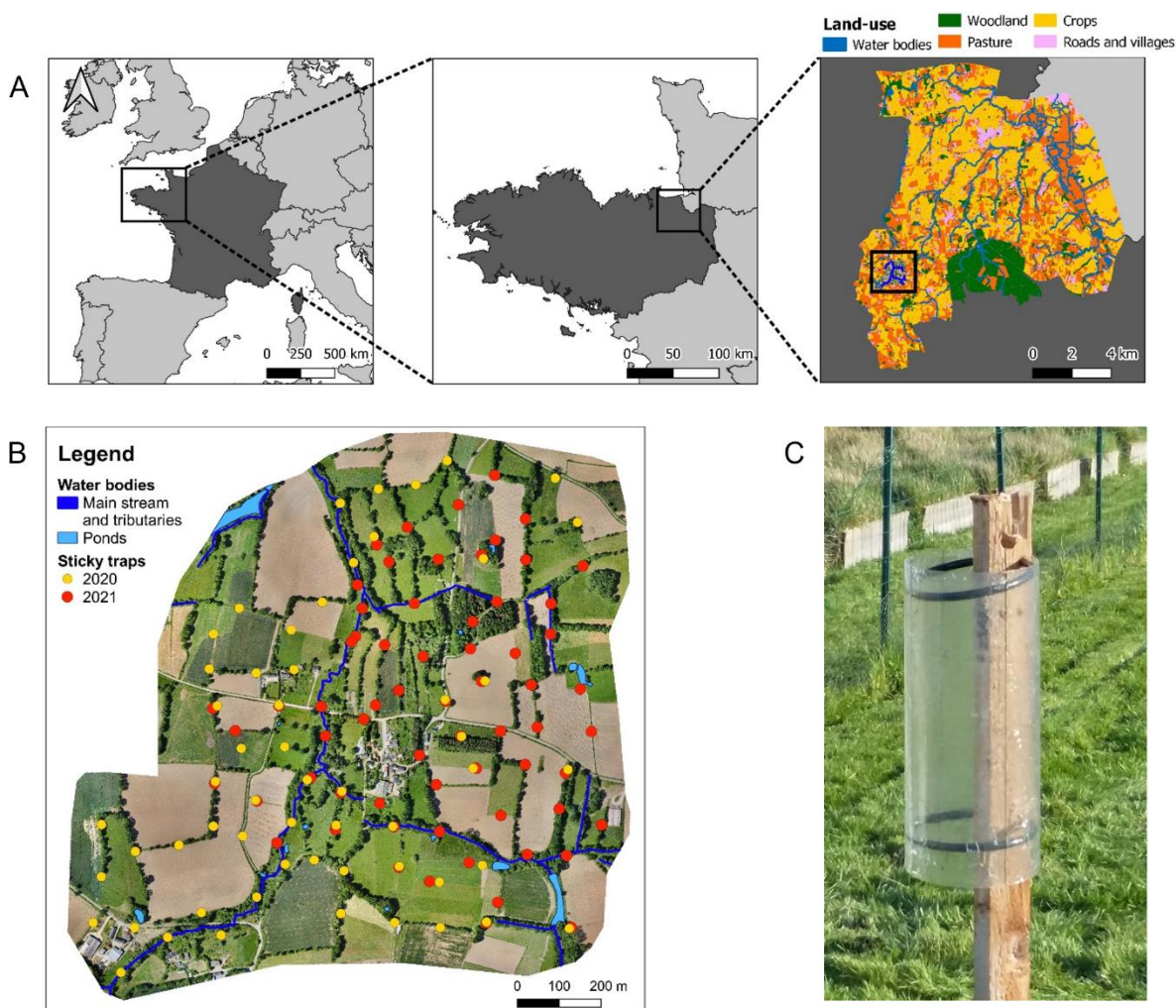
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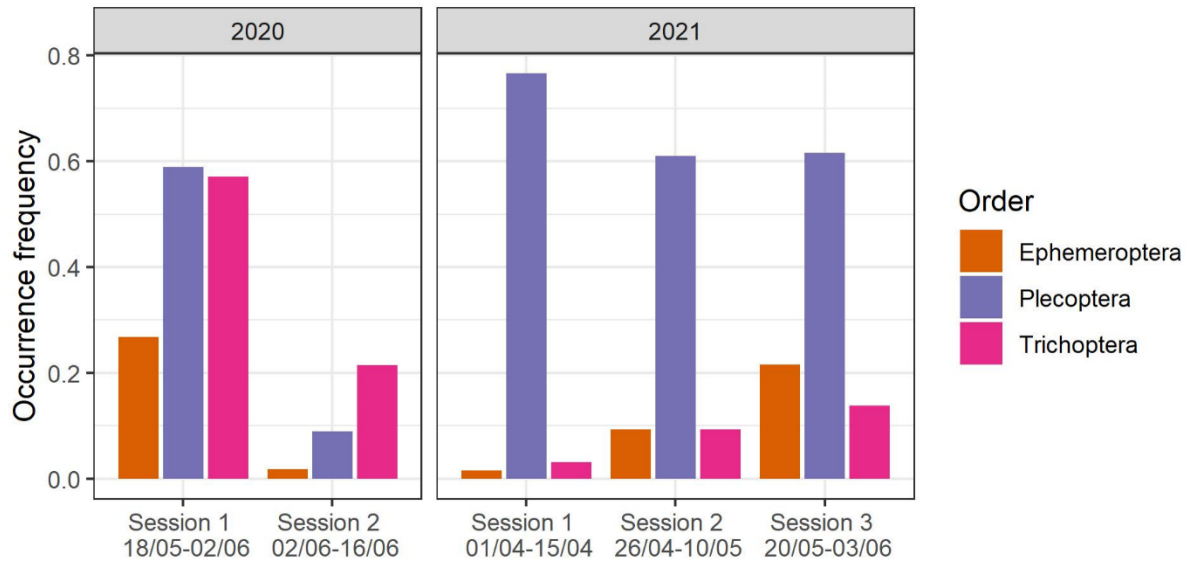
606 Fig. 1 Sampling site. A: Location of Brittany, the Zone Atelier Armorique (ZAAR) and the study site.

607 B: Sticky trap locations. The colors represent the sampling years (yellow: 2020, 56 traps; red: 2021,

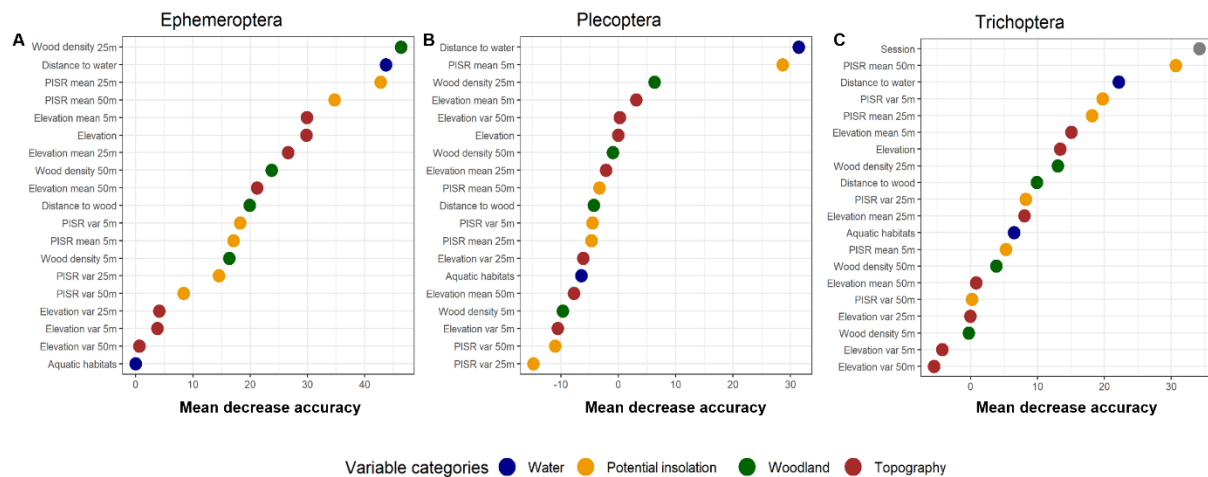
608 64 traps). The elements indicated in blue are the water bodies (dark blue: main stream, Le Guyoult and

609 its tributaries, light blue: ponds). C: Picture of a sticky trap.

610



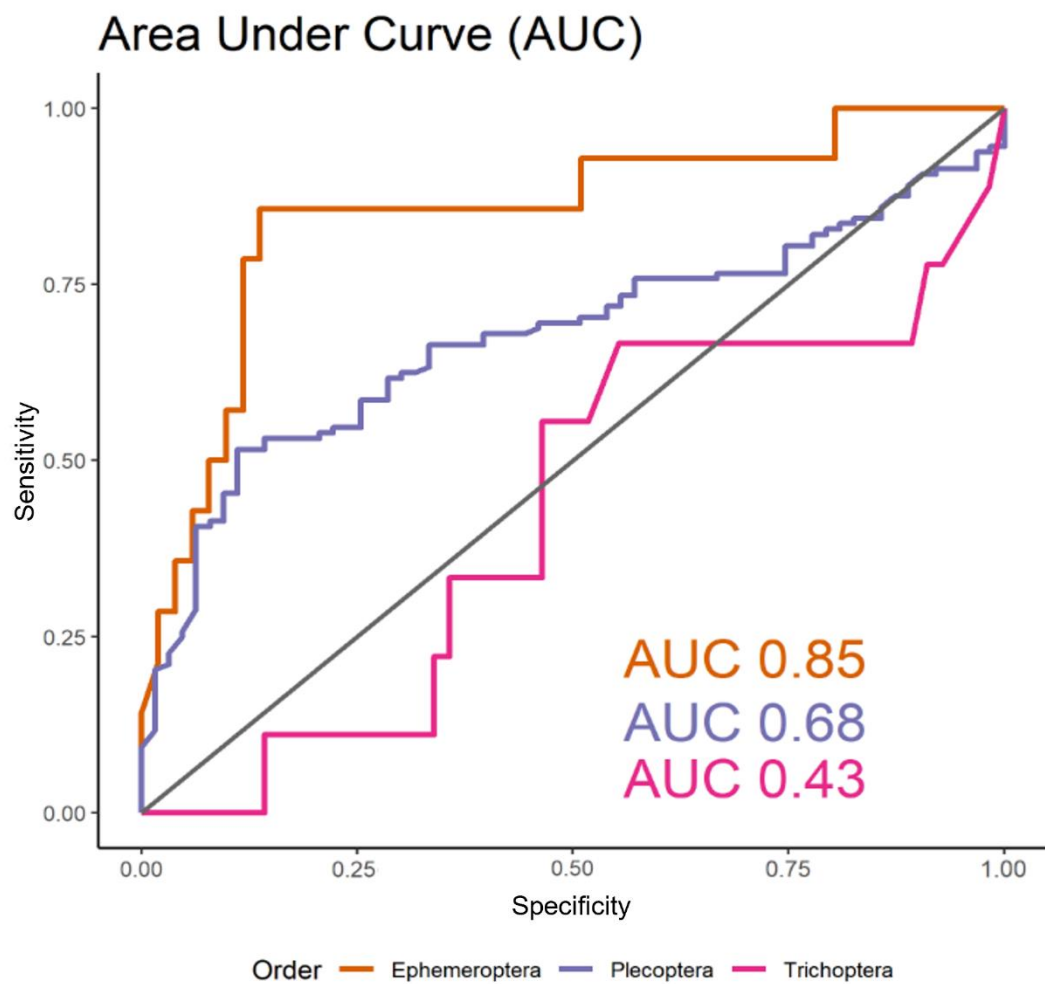
611
 612 Fig. 2. Occurrence frequency per session and order. The occurrence frequency is the number of sticky
 613 traps with individuals of the considered order divided by the total number of sticky traps for a session.
 614



615
 616 Fig. 3 Plot of variable importance selected from random forest models for Ephemeroptera (A),
 617 Plecoptera (B) and Trichoptera (C). The mean decrease accuracy is a measure of variable importance
 618 and expresses how much accuracy the model losses by excluding each variable. It represents the
 619 average increase in the error of a tree in the forest when random permutations are made in the out-of-

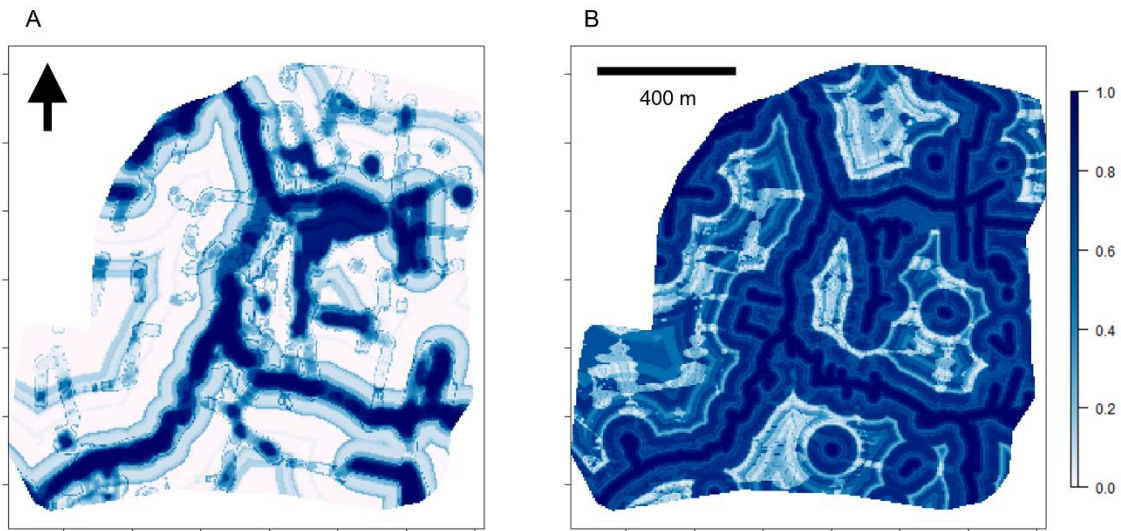
620 bag (OOB) samples. The greater the increase in the error generated by the random permutations of an
621 explanatory variable, the more important the variable is.

622



623 Fig. 4 Area
624 under the curve (AUC). For each order, models were calibrated using a random forest algorithm on the
625 dataset 2020. The AUC was calculated from the predicted model on environmental variables and order
626 occurrence of 2021. Sensitivity is the proportion of true occurrence. Specificity is the proportion of
627 true absence.

628



629

630 Fig. 5 Prediction of the probability of occurrence for Ephemeroptera (A) and Plecoptera (B). Dark blue
631 areas represent high probabilities of occurrence and white areas represents low probabilities of
632 occurrence.

633