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

Short title: aquatic insect distribution in agricultural landscape

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Abstract

Context.

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

Objectives.

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

Methods.

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

Results.

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

Conclusions.

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

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

Introduction

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

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

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

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

Methods

Study area

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

Sampling

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

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

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

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

Selected landscape features as explanatory factors

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

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

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

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

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

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

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

Statistical analyses

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

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

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

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

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

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

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

Results

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

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

Factors explaining occurrences of aquatic insects

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

Prediction

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

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

Discussion

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

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

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

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

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

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

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

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

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Author contributions

RGer, CP, JMR and BB conceived the ideas and designed methodology; RGer, CP, JMR, RGeo, JR and BB collected the data; TH performed UAV flights; RGer, RGeo, TH, and BB analyzed the data; Rger, CP, JMR and BB led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Declarations

Competing interests

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

Data availability

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

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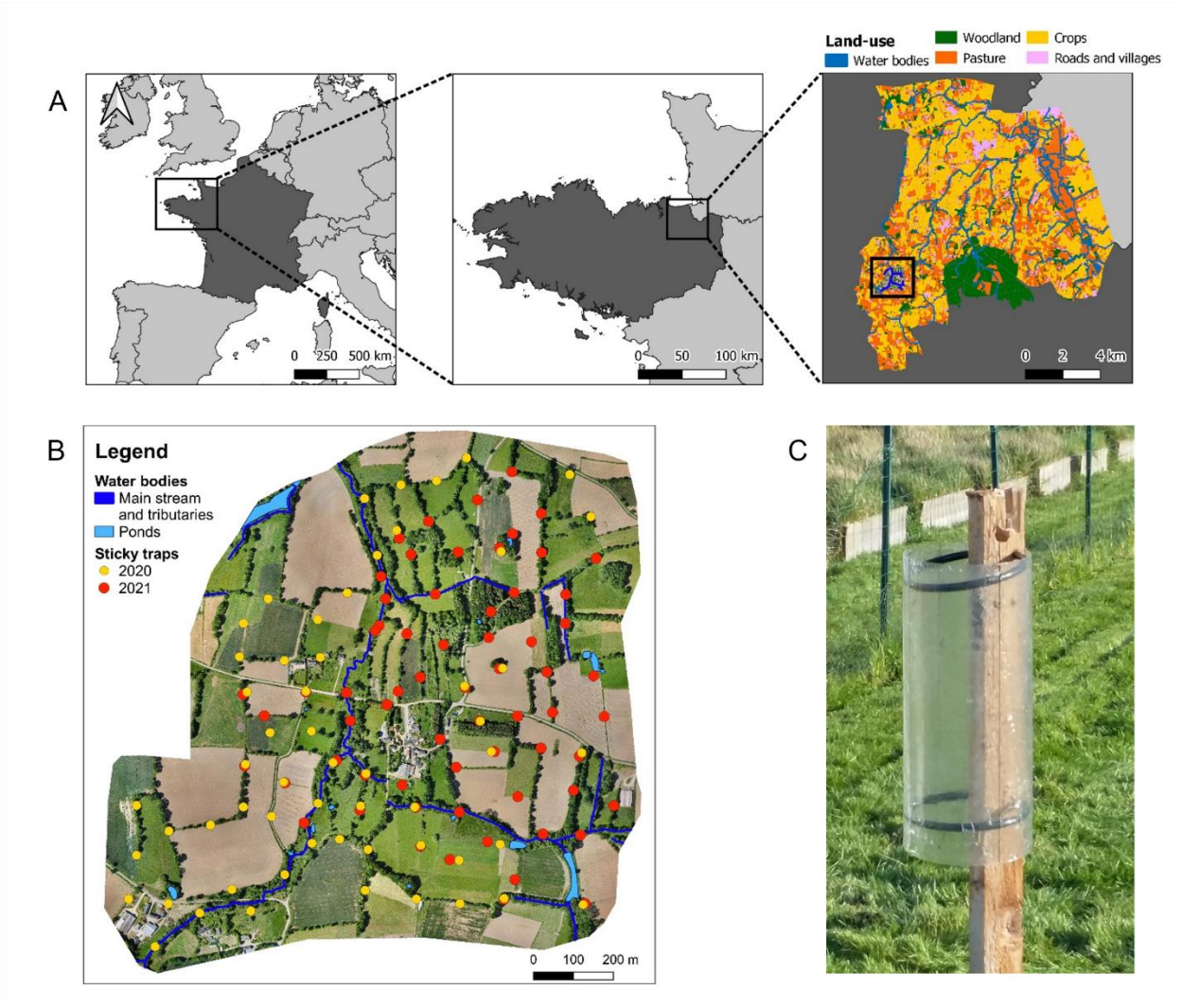
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605

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

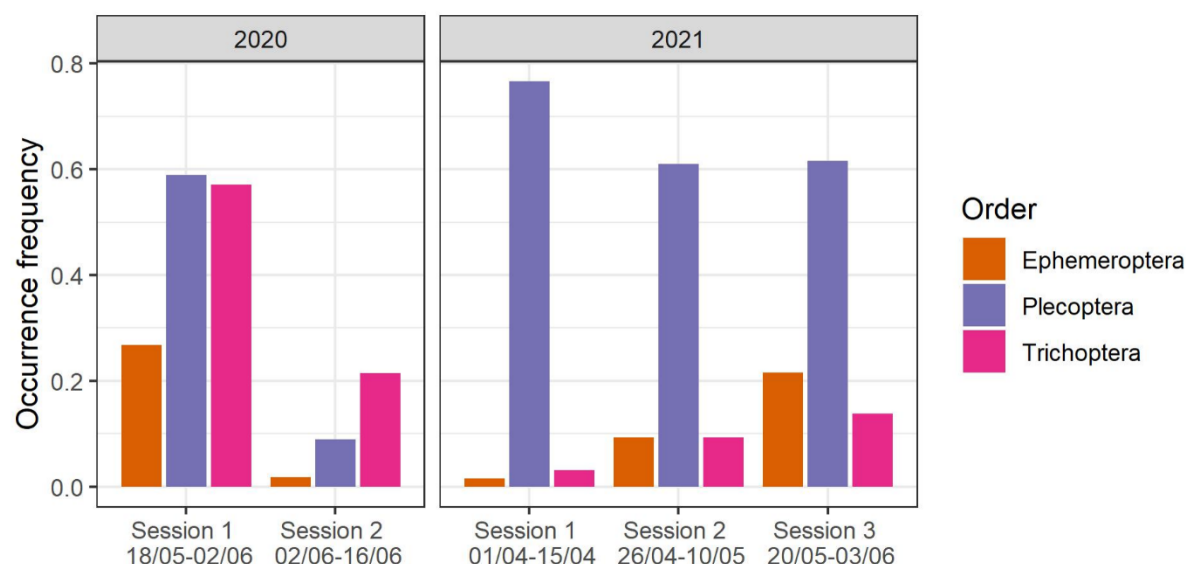


Fig. 2. Occurrence frequency per session and order. The occurrence frequency is the number of sticky traps with individuals of the considered order divided by the total number of sticky traps for a session.

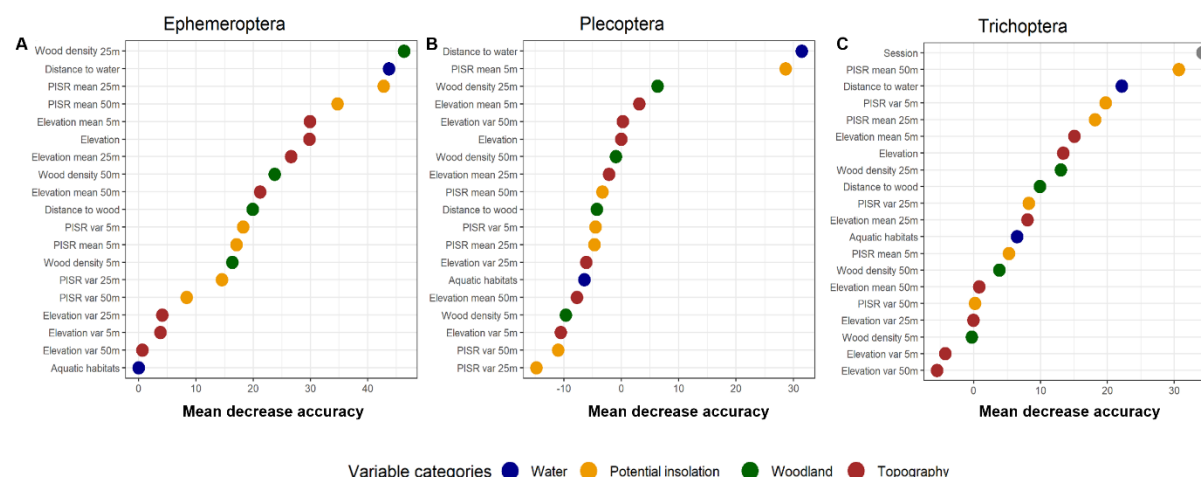


Fig. 3 Plot of variable importance selected from random forest models for Ephemeroptera (A), Plecoptera (B) and Trichoptera (C). The mean decrease accuracy is a measure of variable importance and expresses how much accuracy the model losses by excluding each variable. It represents the average increase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

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

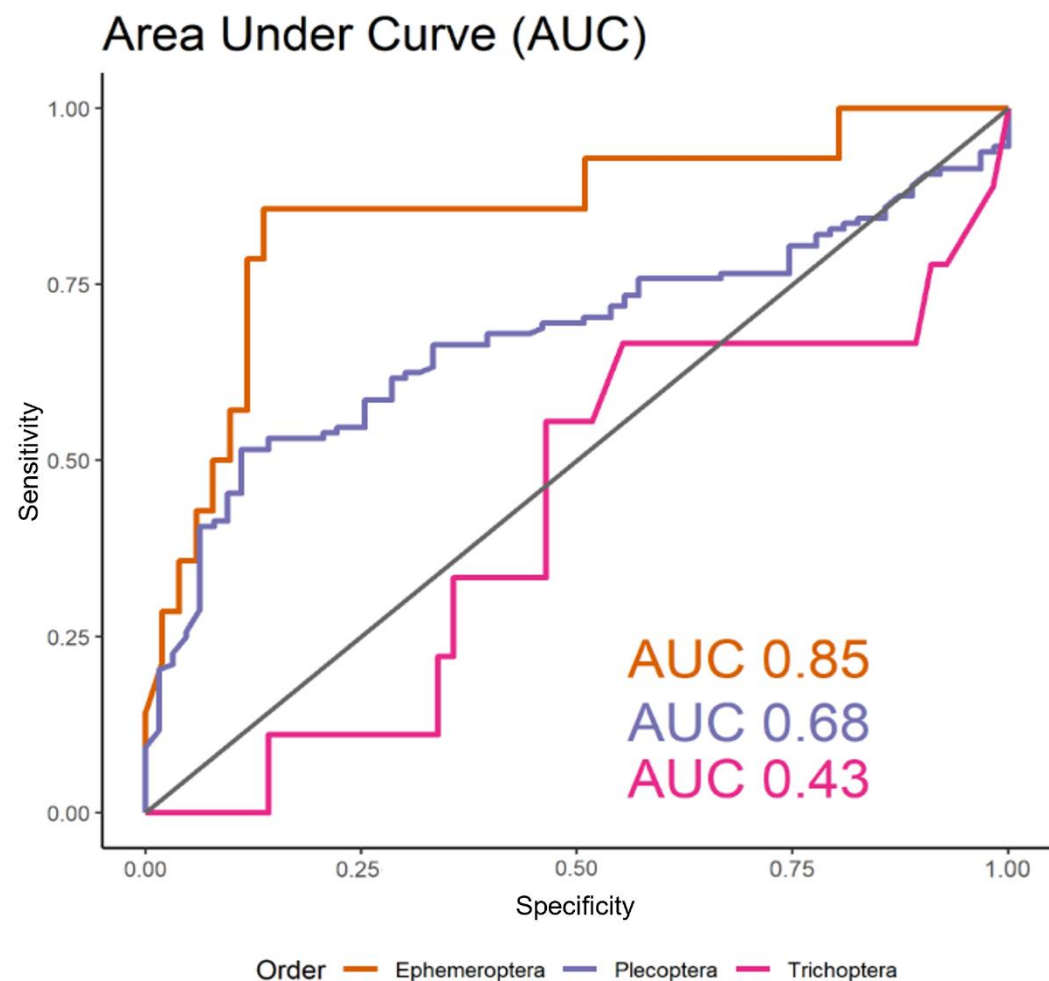


Fig. 4 Area

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

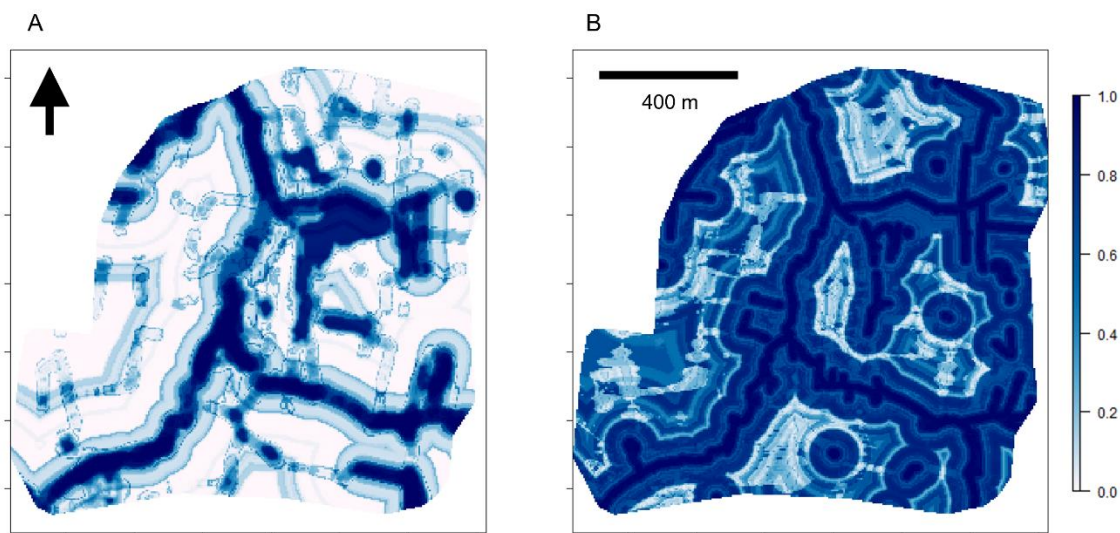


Fig. 5 Prediction of the probability of occurrence for Ephemeroptera (A) and Plecoptera (B). Dark blue areas represent high probabilities of occurrence and white areas represents low probabilities of occurrence.