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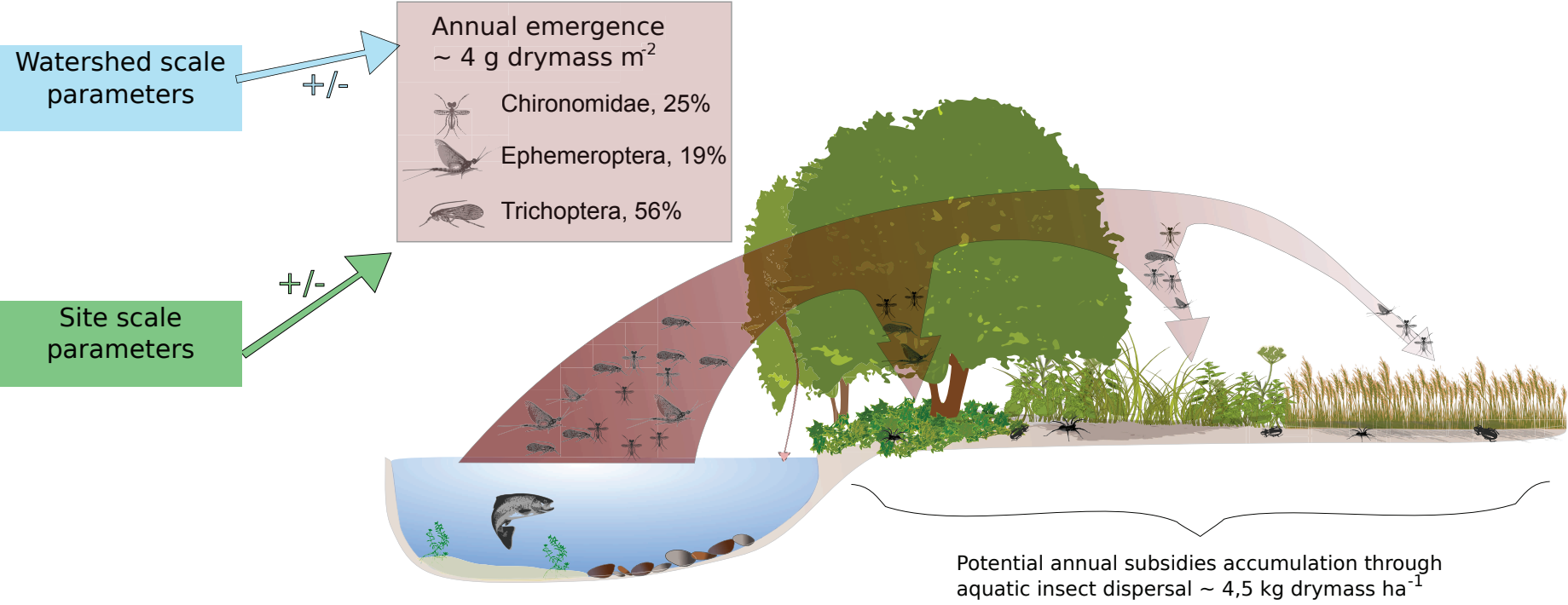
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AGROECOSYSTEMS



Highlights

- Aquatic insects emergence reaches 4 g drymass (DM).m⁻².y⁻¹ in agricultural streams
- Trichoptera contributed the most, followed by Chironomidae then Ephemeroptera
- Emergence happened throughout the year with taxon-specific patterns
- Several parameters linked to agriculture influenced emerging DM of aquatic insects
- We estimated potential deposit of aquatic subsidies on land at 4.5 kg DM.ha⁻¹.y⁻¹

Seasonal and spatial variations of stream insect emergence in an intensive agricultural landscape

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1 *Abstract*

2 A growing amount of literature exists on reciprocal fluxes of matter and energy between
3 ecosystems. Aquatic subsidies of winged aquatic insects can affect terrestrial ecosystems
4 significantly, but this issue is rarely addressed in agroecosystems. By altering the production
5 of benthic macroinvertebrates, agricultural practices could increase or decrease the strength of
6 aquatic subsidies and subsequently the provision of several ecosystem services to agriculture.
7 Effects of seasons and environmental variables on aquatic insect emergence were investigated
8 in third-order agricultural streams in northwestern France. Most emerging dry mass (DM) of
9 caught insects belonged to Trichoptera (56%), Chironomidae (25%) and Ephemeroptera
10 (19%). We estimated that annual emerging dry mass of aquatic insects ranged between 1,445
11 and 7,374 mg/m²/y depending on the stream. Seasonal variations were taxon-specific, with
12 Ephemeroptera emerging only in spring, Trichoptera emerging in spring and early summer,
13 and Chironomidae emerging throughout the year. The percentage of watershed area covered
14 by agriculture, ammonium concentration and hypoxia positively influenced emerging DM of
15 Chironomidae but negatively influenced Ephemeroptera. Emerging DM of Trichoptera and
16 Ephemeroptera increased significantly as water conductivity and temperature increased.
17 Channel openness increased the emerging DM of all taxonomic groups, but Chironomidae
18 were more abundant in narrow, incised streams. Assuming that the biomass of aquatic
19 invertebrates ultimately disperse toward terrestrial habitats, nutrient accumulations on land
20 near streams were estimated to reach 0.5-2.3 kg C ha⁻¹ y⁻¹, 0.1-0.5 kg N ha⁻¹ y⁻¹ and 0.005-
21 0.03 kg P ha⁻¹ y⁻¹, depending on the stream. This suggests a significant flux of aquatic
22 nutrients to agroecosystems and the need for future studies of its potential influence on the
23 ecosystem services provided to agriculture.

24

25 Keywords: agroecosystems; winged stream insects; emergence; aquatic subsidies;
26 environmental factors; seasonal variations

27 1 Introduction

28 Riverine ecosystems host a rich but endangered biodiversity (Naiman and and Décamps 1997;
29 Dudgeon *et al.* 2006) that could play a significant role in providing ecosystem services. In a
30 recent review, Hanna *et al.* (2017) listed more than 30 types of services that riverine
31 ecosystems provide, and observed a potential distinction between the location and the spatial
32 extent at which these services are produced and delivered. Growing evidence indicates that
33 ecosystems that were previously considered unrelated can interact. Several studies have
34 demonstrated the existence of reciprocal exchanges of matter and energy between aquatic and
35 terrestrial habitats (e.g. Polis *et al.* 1997, Richardson *et al.* 2010, Bartels *et al.* 2012). These
36 “aquatic subsidies” can significantly influence the functioning of terrestrial ecosystems
37 (Jackson and Fisher 1986; Havik *et al.* 2014; Dreyer *et al.* 2015), but this is poorly
38 documented for agricultural landscapes. Aquatic subsidies can also influence several
39 ecosystem services supplied to agriculture (Raitif *et al.*, in revision), and future studies are
40 required to estimate the magnitude of their influence.

41 Adult aquatic winged insects are effective vectors of aquatic subsidies (Bartels *et al.* 2012)
42 since they are abundant in almost all freshwater ecosystems, and their ability to disperse is
43 substantial (Muehlbauer *et al.* 2014). Several studies have demonstrated their role as prey for
44 terrestrial predators (e.g. birds, Gray 1993; carabids, Hering and Plachter 1997; spiders,
45 Paetzold *et al.* 2005), providing a valuable source of nutrients for entire terrestrial ecosystems
46 (Dreyer *et al.* 2015). Agricultural practices can regulate the production of benthic
47 macroinvertebrates in streams by modifying water chemistry, eutrophication processes and
48 pollution (Sallenave and Day 1991; Liess and Von Der Ohe 2005; Cross *et al.* 2006; Davis *et*
49 *al.* 2010; Johnson *et al.* 2013a; Beketov *et al.* 2013); changing the flow regime and aquatic
50 habitats (Rabení *et al.* 2005; Kennedy and Turner 2011; Wagenhoff *et al.* 2011; Magbanua *et*
51 *al.* 2016); and modifying riparian vegetation (Deegan and Ganf 2008) and water temperature

52 (Nagasaka and Nakamura 1999; Sponseller *et al.* 2001). Consequently, the influence of
53 agriculture in watersheds on the emergence of stream winged insects could increase or
54 decrease the strength of aquatic subsidies provided to terrestrial ecosystems. For instance,
55 stream insect communities are usually dominated by small taxa with greater ability to disperse
56 by flight in agricultural landscapes (Stenroth *et al.* 2015; Carlson *et al.* 2016; Greenwood and
57 Booker 2016). While insect emergence depends on season and weather conditions (Corbet
58 1964), few studies quantify these influences or analyze their variability in agricultural
59 landscapes. For instance, Shieh *et al.* (2003) and Gücker *et al.* (2011) published seasonal
60 variations of aquatic insect production in two agricultural streams, but not emergence data.
61 However, information on spatial and temporal variation in the emerging biomass of aquatic
62 insect taxa is essential to accurately estimate the amount of aquatic subsidies annually
63 produced by agricultural streams.

64 In this study, we quantified the spatial and seasonal emergence of aquatic insects in 12 sites
65 located in intensive agricultural landscapes. We aimed to (i) assess temporal variation in dry
66 mass (DM) for the main emerging aquatic insect taxa and (ii) highlight the influence of
67 environmental parameters at different spatial scales on emergence patterns. We hypothesized
68 that agriculture intensification would drive emergence of aquatic insects at both local and
69 watershed scales, and notably enhance Chironomidae (Diptera) that could emerge throughout
70 the year.

71 2 Methods

72 2.1 Study sites

73 The study was performed in the Ille-et-Vilaine county (Brittany), western France. This area
74 sits on sedimentary rocks (schist and sandstone) with occasional layers of aeolian loam
75 deposits. The climate is oceanic, with a mean annual temperature of 10.5-12.5°C and

76 cumulative annual rainfall of approximately 700 mm (peaking in fall and winter) (Météo
77 France 2017). Mean annual discharge of third-order streams in this part of Brittany is 0.65 m^3
78 s^{-1} , ranging from $0.06 \text{ m}^3 \text{ s}^{-1}$ in September (end of summer) to $2.23 \text{ m}^3 \text{ s}^{-1}$ in March (end of
79 winter).

80 Intensive agricultural practices that rely on large amounts of inputs (fertilizers and pesticides)
81 and extreme modifications of the landscape have altered terrestrial and aquatic ecosystems for
82 decades (Piscart *et al.* 2009). Stream banks, deeply incised into thick arable ground, are
83 destabilized by clearcutting of riparian vegetation, which results in sloughing, bank erosion,
84 siltation and homogenization of stream substratum. Twelve sites were selected from 8
85 watersheds: Champagne, Roncelinçais, Jardière, Rocher, Tertre, Ourmais, Bray, Ormal,
86 Moulin, Fèvre, Vallée and Sauvagère (Table S1). Selection criteria was based according to (1)
87 third-order permanent streams (Strahler classification), and (2) approximately 6 m wide and
88 flowing along small-grain cereal fields (winter wheat or barley). We chose third-order streams
89 to avoid summer drying of lower-order streams and fall and winter floods in higher-order
90 streams, which would have impeded aquatic insect sampling. A drought occurred in 2016,
91 resulting in very low discharge in winter 2016/2017 ($1 \text{ m}^3 \text{ s}^{-1}$). Mandatory grass strips (~8 m
92 wide) separated streams from fields. This highly enriched buffer zone was dominated by
93 nitrophilous plants belonging to a variety of families (Poaceae, Urticaceae, Apiaceae, *etc.*).
94 Riparian vegetation near the stream bank consisted of shrubs, small trees (*Salix* sp.), and
95 occasional larger trees (*Quercus* sp., *Alnus* sp.).

96 2.2 Aquatic insect sampling

97 We estimated aquatic insect emergence by deploying two emergence traps at each site. The
98 traps consisted of a floating pyramidal tent (1 m^2 at its base) made of nylon mesh and
99 anchored to shorelines with ropes. Because substratum and water velocity strongly affect
100 aquatic insect communities (Tachet *et al.* 2010), one trap was set in a deep and silty habitat

101 and the other in a shallow gravel-pebble habitat to reflect the natural habitat heterogeneity of
102 each site. Adult insects were collected in a plastic bottle placed at the top of the trap and filled
103 with a mix of water, concentrated detergent and propylene glycol (approx. 20%) to preserve
104 insects. Upon collection, aquatic insects were stored in alcohol (70%).

105 Six campaigns of sampling were performed in 2016 and 2017: 17 - 26 May; 6 - 15 June; 27
106 June – 6 July; 12 - 21 September; 28 November - 5 December; 27 February – 9 March. At
107 each site, emergence trap was collected after 7 consecutive days and nights. Ten days per
108 campaign were necessary to proceed the 12 sites because of travel time between sites. The
109 timeline was designed to match aquatic insect emergence in such streams, which occurs
110 mainly in spring (March to June), to a lesser extent in summer and early fall (July to October),
111 and almost stops during cold and high-discharge winter months (Corbet 1964). Sampling was
112 carried out in December 2017 to confirm that insects do not emerge in coldest times at the end
113 of fall or during winter, but only at one site, to avoid damaging the equipment in windy and
114 flooded conditions. A total of 111 samples, totaling 777 days of aquatic insect emergence,
115 were collected; 11 samples were lost due to strong winds, flash floods or vandalism.

116 2.3 Emergence abundance, dry mass and secondary production

117 A stereomicroscope was used (1) to identify adult aquatic insects to the order level for
118 Ephemeroptera, Plecoptera, and Trichoptera, and (2) to separate Chironomidae from other
119 Diptera, the most abundant taxon in our sampling. Other insects, mainly Diptera, were not
120 considered because their contribution to total DM was low and did not justify the time-
121 consuming work required for identification. For Chironomidae, sub-samples (1/2, 1/4 or 1/8)
122 were obtained with a Motoda splitter (Motoda, 1959) when abundance was too high. Insects
123 were then dried at 60 °C for at least 24 h. After cooling in a desiccator for another 24 h, each
124 sample of each taxon was weighed to the nearest 0.2 mg (on a Mettler Toledo AG). Insect
125 abundance ($\text{ind m}^{-2} \text{d}^{-1}$) and DM ($\text{mg DM m}^{-2} \text{d}^{-1}$) were recorded for each site separately and

126 then averaged (all sites combined) on a daily basis. Mean daily values obtained for each
127 campaign were prolonged to adjacent days (both forward and backward) to fill temporal gaps
128 between campaigns. Daily values were then summed to calculate cumulative seasonal
129 emerging DM ($\text{mg DM m}^{-2} \text{ season}^{-1}$) using solstice and equinox dates as reference. We
130 calculated cumulative annual emerging DM as the sum of all seasonal values ($\text{mg DM m}^{-2} \text{ y}^{-1}$).
131 Biomass of emerging insects was then transformed to estimate secondary production at
132 each site using the mean Emergence:Production (E:P) ratio of 0.183 calculated by Poepperl *et*
133 *al.* (2000) for a similar agricultural stream. This ratio is relatively constant across taxa and
134 stream ecosystems (Statzner and Resh 1993; Gratton and Zanden 2009).

135 2.4 Water quality, land use and habitat assessment

136 Water quality data were provided for each study stream by the *Agence de l'Eau Loire-*
137 *Bretagne* (2017). Information on water temperature ($^{\circ}\text{C}$), turbidity (Formazin Nephelometric
138 Units, FNU), conductivity ($\mu\text{S cm}^{-1}$), nitrate ($\text{mg NO}_3^- \text{ L}^{-1}$), ammonium ($\text{mg NH}_4^+ \text{ L}^{-1}$),
139 phosphorus (P) (mg total P L^{-1}), suspended matter (mg DM L^{-1}) and oxygen saturation (%)
140 were collected to reflect water quality at the watershed scale. Monthly values observed from
141 February 2016 to March 2017 were averaged to account for seasonal variations (Table S1).
142 Similarly, mean annual discharge was estimated for each stream using QGIS (QGIS
143 Development Team 2009), based on information available from the *Réseau Hydrographique*
144 *Théorique* (Pella *et al.* 2012). Watershed-scale variables also included watershed area and
145 land use (% of agricultural, artificial and natural area), which were estimated using QGIS and
146 Corine Land Cover (CLC 2012). For each study site, local habitat features were measured or
147 visually assessed at mid-channel every 5 m along a 20-m reach on both sides of each trap:
148 surface water velocity (cm s^{-1}), water depth (cm), depth of soft sediments on the bottom (cm),
149 stream width (cm), bank height (cm), channel openness (%) and substrate size (Table S1).
150 Substrate size was visually estimated following a modified Wentworth classification

151 (Cummins 1962). A substrate score was calculated by multiplying mean particulate size of
152 each class by its observed proportion. Substrate heterogeneity was assessed by calculating the
153 Shannon index of the proportions of each substrate size class. The embankment score (stream
154 width divided by bank height) was used to estimate stream incision and erosion risk.

155 2.5 Statistical analyses

156 To study the temporal pattern of emergence, we fitted a linear mixed model (LMM) with a
157 Gaussian distribution, considering the sampling campaign as a fixed effect. The campaign
158 from 28 Nov to 5 Dec 2016 was ignored since data were available for only one site. To study
159 effects of environmental variables on emerging insect DM, another LMM with a Gaussian
160 distribution was applied. The small sample size precluded including both site- and watershed-
161 scale variables in a single model. Consequently, two separate models were fitted to the dataset
162 to assess effects of each set of variables.

163 The *corvif()* function of R software (R Core Team 2013) was used to verify correlations
164 between variables before model computation (Zuur *et al.* 2009). Variables were removed
165 when r coefficient of correlation exceeded 0.8 and the variance inflation factor exceeded 4.5.
166 Accordingly, the following variables were selected and considered as fixed effects at the
167 watershed scale: water temperature, turbidity, conductivity, oxygen saturation, ammonium
168 nitrate concentrations and the percentage of watershed area covered by agriculture (cropland,
169 pastures). At the site scale, the variables selected were water depth, stream width, substratum
170 score, embankment score and channel openness. Prior to modeling, DM was log-transformed
171 ($\log x + 1$) to better meet assumptions of normality. Since quantitative explanatory variables
172 were at different scales, we standardized them (mean=0, $\sigma = 0.5$) using the *standardize()*
173 function of the R package *arm* (Gelman A. and Hill J. 2007). Samplings were nested in
174 *site/watershed* and *campaign*; these effects were thus included in the random part of temporal

175 and spatial models respectively. When a random effect was non-significant (*i.e.* when
176 deviance explained was null), the model was re-run excluding it.

177 To identify variables that significantly influenced insect emergence, *model averaging* was
178 preferred to a *best model* strategy. Indeed, *best model* strategy select only one model with one
179 or several parameters and thus potentially exclude other model with different parameters
180 having a similarly good fit (Whittingham *et al.* 2006). In an explanatory approach, *model*
181 *averaging* is more appropriate as it produces estimates of parameters derived from multiple
182 weighted models. The model-averaging method (Burnham and Anderson 2003) was applied
183 at each spatial scale separately. Full models without interactions were used as starting models
184 for the *dredge* function of the R package *MuMIn* (Barton K. 2016). We retained all models
185 whose Akaike Information Criterion (AIC) corrected for small sample size (AICc; Grueber *et*
186 *al.* 2011) differed by less than 4 from the best model. We also checked for correlation
187 between fixed effects during the dredge process, but found no high correlation (all $r < 0.7$).
188 We performed model averaging on the selected subset using the *model.avg* function of the R
189 package *MuMIn*. We considered explanatory variables significant when their associated 90%
190 parameter confidence interval (CI) excluded zero (Arnold 2010). We assessed the significance
191 of their effect on variations in DM of each taxon by considering their effect intensity through
192 parameter estimates (*i.e.* effect size). Finally, the goodness-of-fit of all best averaged models
193 (R^2) was assessed using the procedure developed by Nakagawa and Schielzeth (2013) for
194 mixed models using only significant explanatory variables. R^2_{marginal} approximates the
195 variance explained by the fixed part of the model and $R^2_{\text{conditional}}$ the variance explained by the
196 complete model (fixed and random parts). All models were fitted using the R package *lme4*
197 (Bates *et al.* 2015). The same datasets were used for temporal and environmental modeling.
198 This allowed us to compare the AICc and R^2 of models for each taxon.

199 3 Results

200 3.1 Variations in environmental characteristics

201 Stream discharge in 2016 peaked after heavy rainfall in March, two months before the first
202 sampling campaign at all sites. Discharge rapidly decreased in April and May ($< 0.5 \text{ m}^3 \text{ s}^{-1}$ for
203 all streams), followed by a slight increase in June. No further rainfall increased stream
204 discharge until February 2017, resulting in a low regime ($< 0.1 \text{ m}^3 \text{ s}^{-1}$) for all streams from
205 late summer to early winter. After some rainfall events in fall and winter, turbidity and
206 suspended matter concentrations increased sharply to a mean of 16 FNU and 15 mg DM L^{-1} ,
207 respectively. Mean water temperature (± 1 standard deviation) ranged from $17.4 \text{ }^\circ\text{C}$ ($\pm 2.0 \text{ }^\circ\text{C}$)
208 in early summer to $4.1 \text{ }^\circ\text{C}$ ($\pm 1.5 \text{ }^\circ\text{C}$) in winter. Mean water conductivity was highest in fall
209 ($1,103 \text{ } \mu\text{S cm}^{-1} \pm 1,043$) and peaked at $3,370 \text{ } \mu\text{S cm}^{-1}$ in Garun. Oxygen saturation ranged
210 from 75% in summer to 100% in spring, with distinct annual variations among sites (Table
211 S1). Mean nitrate concentration was high throughout the year ($20.4 \text{ mg NO}_3^- \text{ L}^{-1} \pm 6.6$), with
212 minimum values recorded at Illet and Veuvre and maximum values at Yaigne. Similarly,
213 ammonium and total P concentrations varied greatly among streams. Agriculture dominates
214 the landscape, covering a mean of 85% of the total watershed area, but variations in local
215 habitat characteristics were observed among sites. For instance, the channel was narrow with
216 dense riparian vegetation at Ormal but wider and almost completely open (no tree or shrub) at
217 Ronceliniais. At Tertre, the stream flowed very slowly ($< 0.1 \text{ m s}^{-1}$), with an accumulation of
218 fine sediment on the bottom, whereas at Jardière and Bray, water velocity, depth and
219 substratum were more heterogeneous. Mean annual values of site- and watershed-scale
220 variables are listed in Table S1.

221 3.2 Characteristics of aquatic insect emergence

222 We caught 64,027 insects in emergence traps during the study, equaling 13.1 g of total DM
223 (all taxa combined). Chironomidae dominated total abundance (91%) and contributed 25% of
224 total caught DM. Trichoptera contributed the most to total DM (56%) for only 6% of total
225 abundance. Ephemeroptera represented 19% of total DM and 3% of total abundance.
226 Plecoptera were rarely captured (only 23 individuals, 33.4 mg DM) and thus were not
227 considered for further analysis. Total emerging DM caught in all sampling campaigns differed
228 among sites and ranged from 435 (at Jardière) to 2,091 mg DM (at Vallée) (Table S2).

229 3.3 Temporal dynamics of insect emergence

230 Daily emergence varied by taxon among sampling campaigns (Fig. 1a). That of Trichoptera
231 increased in spring and early summer (up to $19.35 \text{ mg DM m}^{-2} \text{ d}^{-1}$), then decreased sharply
232 and remained low until the end of the study ($R^2_{\text{marginal}} = 34\%$). Daily emergence of
233 Trichoptera varied greatly among sites in July, ranging from 2.62 to $79.53 \text{ mg DM m}^{-2} \text{ d}^{-1}$ at
234 Jardière and Fèvre, respectively (Table S3). Mean daily emergence of Chironomidae varied
235 less among sampling campaigns ($R^2_{\text{marginal}} = 11\%$), ranging from 2.89- $6.44 \text{ mg DM m}^{-2} \text{ d}^{-1}$,
236 with two distinct emergence peaks in May and July. Ephemeroptera emergence decreased
237 continuously ($R^2_{\text{marginal}} = 34\%$) from spring (max. $8.2 \text{ mg DM m}^{-2} \text{ d}^{-1}$) to winter. No
238 emergence was observed for Ephemeroptera and Trichoptera in December, and it was very
239 low for Chironomidae ($\sim 0.17 \text{ mg DM m}^{-2} \text{ d}^{-1}$). Cumulative DM varied by taxon and season
240 (Fig. 1b). Over the entire study, that of Trichoptera was highest ($2,050 \text{ mg DM m}^{-2}$), followed
241 by those of Chironomidae ($1,120 \text{ mg DM m}^{-2}$) and Ephemeroptera (670 mg DM m^{-2}). For all
242 taxa combined, cumulative DM reached $3,840 \text{ mg DM m}^{-2} \text{ y}^{-1}$, ranging from 1,445 to $7,374$
243 $\text{mg DM m}^{-2} \text{ y}^{-1}$ at Jardière and Fèvre, respectively. Using the Poepperl E:P ratio (2000), mean
244 secondary production was estimated at $21 \text{ g DM m}^{-2} \text{ y}^{-1}$, ranging from 7.9 to $40 \text{ g DM m}^{-2} \text{ y}^{-1}$
245 at Jardière and Roncelinais, respectively.

246 3.4 Influence of environmental characteristics on insect emergence

247 The environmental variables in the spatial models explained a significant percentage of the
248 variation in emerging insects DM, and noticeable differences were observed among taxa
249 (Table 1). For Chironomidae, the spatial models performed better ($R^2_{\text{marginal}} = 15.9\%$ and
250 21.4% at the site and watershed scale, respectively) than the temporal model ($R^2_{\text{marginal}} =$
251 10.9%). Among spatial models, the model with watershed-scale variables fit the data better
252 but was less parsimonious than that with site-scale variables. Conversely, the temporal model
253 explained emerging Trichoptera and Ephemeroptera DM best ($R^2_{\text{marginal}} \sim 34\%$), the spatial
254 models R^2_{marginal} ranging from 11.6 to 23.9%, with watershed-scale variables explaining
255 Ephemeroptera better and site-scale variables explaining Trichoptera better.

256 Among the watershed-scale variables (Fig. 2a), the percentage of watershed area covered by
257 agriculture positively and significantly influenced emerging Chironomidae DM. Emerging
258 Chironomidae DM also increased significantly with increasing ammonium concentration and
259 decreasing dissolved oxygen concentration. Conversely, emerging Ephemeroptera DM was
260 significantly and negatively influenced by the percentage of watershed area covered by
261 agriculture and, although not significantly, negatively influenced by ammonium concentration
262 and positively influenced by dissolved oxygen concentration. Emerging Trichoptera and
263 Ephemeroptera DM increased significantly with increasing water conductivity and
264 temperature, but that of Trichoptera decreased with increasing turbidity. Among the site-scale
265 variables (Fig. 2b), channel openness positively and significantly influenced emerging DM of
266 all taxa. Emerging Trichoptera and Ephemeroptera DM increased significantly with
267 decreasing stream incision (higher embankment scores), while that of Chironomidae increased
268 significantly with decreasing stream width. Finally, emerging DM of Trichoptera increased
269 significantly with increasing proportion of coarse substrate (*i.e.* higher substratum scores).

270 4 Discussion

271 We measured the biomass of aquatic insects emerging from third-order streams that drain
272 agricultural landscapes in western France. Mean total emerging DM of the three dominant
273 taxonomic groups living in temperate streams – Chironomidae, Ephemeroptera, and
274 Trichoptera – equaled approximately $4.0 \text{ g DM m}^{-2} \text{ y}^{-1}$, ranging from $1.4\text{-}7.4 \text{ g DM m}^{-2} \text{ y}^{-1}$
275 depending on the stream. These results fall within the range of those reported in previous
276 studies for emerging aquatic insects in streams (listed in Table 2), although exceptionally
277 larger masses ($> 20 \text{ g DM m}^{-2} \text{ y}^{-1}$) have been observed in desert streams in Arizona, United
278 States (US) (Jackson and Fisher, 1986). In similar agricultural streams in Germany, Poepperl
279 (2000) reported lower annual biomass of emerging aquatic insects, especially for Trichoptera
280 and Ephemeroptera. The benthic biomass estimated by Gucker *et al.* (2011) was
281 approximately 20% that observed in this study. The high biomass estimates in our streams are
282 similar to those in other agriculture-dominated streams in several US states (Berg and
283 Hellenthal 1991; Shieh *et al.* 2003; Johnson *et al.* 2013b). Compared to other forest-
284 dominated streams, the biomass we estimated were four times greater for all taxa (combined)
285 than in a third order stream in China (Yuen and Dudgeon 2016), but five times smaller for
286 Chironomidae production than in a second order stream in Alabama (US) (Reynolds and
287 Benke 2012).

288 The influence of water temperature on benthic invertebrate production and emergence (Huryn
289 and Wallace 2000) was confirmed in our study by its positive correlation with Ephemeroptera
290 and Trichoptera emergence, but not that of Chironomidae. Since Chironomidae species
291 tolerate variations in water temperature better (Sponseller *et al.* 2001), the temperature range
292 observed in the study may not have been wide enough to influence their biomass. This study
293 confirmed that several agriculture-related variables can regulate the biomass of emerging
294 stream insects (Allan *et al.* 1997). Indeed, proportion of agricultural land in catchment is often

295 associated with a decrease of emerging biomass of more sensitive taxa such as Ephemeroptera
296 and Trichoptera (Piscart *et al.* 2009, 2011) and the enhancement of tolerant taxa such as
297 Chironomidae (Lemly 1982). Sponseller *et al.* (2001) also reported that such pattern is
298 correlated with a higher algal biomass in agricultural catchments of second to third order
299 streams. At site scale in our study, the alteration of channel morphology by intensive
300 agriculture practices, approximated by stream width and embankment score, was detrimental
301 for Ephemeroptera and Trichoptera, while favoring Chironomidae biomass as reported in
302 previous studies (Quinn and Hickey 1990, Kennedy and Turner 2011). Accumulation of silt is
303 commonly reported in such altered streams (Wagenhoff *et al.* 2011). Filter-feeding taxa (*i.e.*
304 Chironomidae and some Trichoptera) usually take advantage of fine sediment on the river
305 bed, while shredders and scrapers (*i.e.* most Ephemeroptera and some Trichoptera) are
306 hindered by these less favorable trophic conditions (Quinn and Hickey 1990, Compin and
307 Céréghino 2007). Conversely, we observed that biomass of emerging Ephemeroptera and
308 Trichoptera increased with increasing water conductivity. High conductivity is detrimental to
309 benthic macroinvertebrate biomass and diversity (Johnson *et al.* 2013b), but high nutrient
310 loads promote biofilm growth on stream substrate. Since biofilm is a major food source for
311 Ephemeroptera and some Trichoptera, their biomass may have increased at sites with both
312 high nutrient load and conductivity (Piscart *et al.* 2009). The positive correlation between
313 channel openness and emergence further corroborates this hypothesis. Incident light enhances
314 primary production in streams, favoring taxa that feed on algae and diatoms (Dance and
315 Hynes 1980) in each taxonomic groups (e.g. *Baetis* or *Serratella* mayflies, Glossomatid
316 caddisflies and many chironomids).

317 While Trichoptera emerged from early spring to summer, Ephemeroptera emerged only in
318 spring. When sorting samples in the lab, we observed at least 15 morphospecies of
319 Trichoptera (not taxonomically identified), suggesting that it had higher diversity than

320 Ephemeroptera. Since each species has its own timing of emergence, the longer emergence
321 period for Trichoptera could have resulted simply from higher specific diversity.
322 Chironomidae were caught almost continuously except in the coldest period in December,
323 indicating that they emerged throughout the year, and were dominant taxa of emerging insects
324 in fall, winter and early spring. These temporal patterns suggest that stream insects can
325 subsidize surrounding agroecosystems for almost the entire year.

326 For accurate estimation of aquatic insect deposition on land, it is necessary to take into
327 account the flux of winged aquatic insects returning to streams. Notably, females of several
328 taxa lay their eggs at the surface or in water and died by drowning afterward (Baxter *et al.*
329 2017). Nonetheless, several studies estimated that terrestrial mortality of female aquatic
330 insects before oviposition is very high and exceeding 95% on average (reviewed by Huryn
331 and Wallace 2000). This was reported for caddisfly, mortality of adult females reaching up to
332 80% for Limnephilidae (Trichoptera, Enders and Wagner 1996) and 98.8% for Baetidae
333 (Ephemeroptera, Werneke and Zick 1992), two families commonly found in agricultural
334 streams (Friberg *et al.* 2009). These observations confirm other investigations on the low
335 percentage of aquatic insects that could ultimately return to the stream (1-3%, Jackson and
336 Fisher 1986, Gray 1989).

337 Based on the range of invertebrate production in our study, a stream section 100 m long \times 6 m
338 wide could produce 0.9-4.5 kg DM y^{-1} of emerging insects. Assuming that most winged
339 aquatic insects disperse up to 50 m from the stream on each bank, aquatic insect deposition on
340 land could reach 0.9-4.5 kg DM $ha^{-1} y^{-1}$. Using conversion factors of Evans-White *et al.*
341 (2005), this could result in accumulation of 0.5-2.3, 0.1-0.5 and 0.005-0.03 kg $ha^{-1} y^{-1}$ of
342 carbon (C), nitrogen (N) and P on land, respectively, mainly in spring and summer. These
343 subsidies are similar to reciprocal fluxes reported for other ecosystems (see Landry and
344 Parrott 2016), notably the subsidies that carnivorous birds provide to freshwater or that deer

345 provide from fields to forests. In addition, terrestrial net secondary production can reach 1.9-
346 4.0 kg C ha⁻¹ y⁻¹ in temperate grasslands (Gratton and Zanden 2009), *i.e.* approximately twice
347 that expected along a stream 6 m wide. No estimate of secondary production exists for
348 temperate cropland, but some studies highlighted that terrestrial insect communities are less
349 diverse and abundant in agricultural areas (Benton *et al.* 2002; Batáry *et al.* 2012).

350 Taken together, these aspects suggest that aquatic subsidies provided by winged aquatic
351 insects could play a significant role in agroecosystem functioning near streams. Chironomidae
352 emerge throughout the year and can easily disperse over land (Muehlbauer *et al.* 2014),
353 potentially providing a valuable source of nutrients (C, N, P) to receiving agroecosystems at
354 critical times of the year. Recent studies highlighted the importance of aquatic insects in
355 providing essential fatty acids to terrestrial consumers (Martin-Creuzburg *et al.* 2017; Popova
356 *et al.* 2017). Many terrestrial predators (e.g. birds, Nakano and Murakami, 2001; spiders and
357 carabids, Stenroth *et al.*, 2015) likely feed on aquatic prey and could later shift to terrestrial
358 prey, including crop pests, as previously observed between fields and uncultivated areas
359 (Rand *et al.* 2006).

360 5 Conclusion

361 Multiple influences on aquatic insect emergence were identified at the local and watershed
362 scales, and some were directly related to agricultural practices. Our results suggest that
363 emergence and dispersal of aquatic insects could substantially influence terrestrial ecosystem
364 functioning in landscapes with a dense waterway network. More studies are required on the
365 dispersal of aquatic winged insects and their deposition in terrestrial ecosystems to better
366 understand and quantify the ecological processes involved. This will help to assess effects of
367 the aquatic subsidies that streams provide on ecosystem services supplied to agriculture, such
368 as fertilization, biological control and pollination.

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Table 1. Comparison of temporal and spatial fitted mix-models for each taxon. Summarizing statistics are: Akaike Information Criterion score corrected for small sample size (AIC_c), the variance explained by fixed parameters (marginal R^2) and both fixed and random parameters (conditional R^2) of the model. Null models are intercept-only models, which have no fixed parameter and the same random structure as fitted models. They are used as bases of comparison against fitted models for AIC_c and R^2 . For a given taxon and scale (*i.e.* temporal or spatial), lower AIC_c indicates a better fit of the model to the data, higher marginal/conditional R^2 indicate greater goodness-of-fit (the amount of variance explained).

Taxon	Statistic	Temporal model		Spatial models		
		Null	Sampling campaign	Null	Watershed	Site
Chironomidae	AIC_c	305.1	298.6	301.8	294.9	293.5
	Marginal/conditional R^2	0.0/22.0	10.9/34.9	0.0/32.7	21.4/32.5	15.9/41.9
Trichoptera	AIC_c	323.6	285.4	294.3	292.2	272.0
	Marginal/conditional R^2	0.0/13.3	34.1/52.4	0.0/52.5	11.6/50.5	23.9/57.2
Ephemeroptera	AIC_c	225.3	196.1	204.2	195.7	201.7
	Marginal/conditional R^2	0.0/11.4	33.9/52.1	0.0/51.8	18.8/50.9	11.9/43.5

Table 2. Mean annual dry mass (with range of values in brackets when available) of emerging aquatic insect or secondary production. Values in italics correspond to estimates based on the Poepperl (2000) Emergence:Production ratio. EPT = Ephemeroptera, Plecoptera and Trichoptera.

References	Location	Stream order or width	Landscape	Annual emergence g m^{-2}	Annual secondary production g m^{-2}	Taxa
Jackson & Fisher 1986	Arizona, USA	3-4 m	Desert	13.8	58.3	Chironomidae
				4.4	55.5	Ephemeroptera
				2.9	3.6	Trichoptera
Berg & Hellenthal 1991	Indiana, USA	third order	Agriculture/Forest	5.4	29.7	Chironomidae
Sallenave et Day, 1991	Ontario, Canada	2-4 m	Agriculture/Forest	2.9 [1.1-4.7]	15.6 [5.8-25.4]	Trichoptera
Poepperl 2000	Schleswig-Holstein, Germany	6 m	Agriculture	1.1 [0.6-1.3]	5.3 [3-6.1]	Diptera
				0.1 [0.01-0.1]	0.6 [<0.1-0.9]	Ephemeroptera
				0.5 [0.3-0.6]	1.9 [1-2.1]	Trichoptera
				4.2 [3.3-5]	23.2 [17.9-27.2]	Chironomidae
Shieh <i>et al.</i> 2003	Colorado, USA	fifth order	Agriculture	0.4 [0-0.7]	2.4 [0.02-3.7]	Ephemeroptera
				1.7 [0.4-2.2]	9.5 [2.3-12]	Trichoptera
				-	3.9 [0.4-70.9]	EPT + Chironomidae + other taxa
Gücker <i>et al.</i> 2011	Berlin, Germany	3-4 m	Agriculture	-	3.9 [0.4-70.9]	EPT + Chironomidae + other taxa
Reynolds & Benke 2012	Alabama, USA	second order	Forest	5.3 [1.4-12.5]	29.2 [7.8 - 68.3]	Chironomidae
Johnson <i>et al.</i> 2013	Kentucky, USA	6 m	Agriculture/Forest	-	21.8	EPT + Chironomidae + other taxa
		6 m	Agriculture/Forest	1.4	7.5	EPT
Yuen & Dudgeon 2016	Hong Kong, China	third or fourth order	Forest	0.9 [0.7-1.2]	4.9 [3.8-6.6]	EPT + Chironomidae + other taxa
This study	Brittany, France	third order	Agriculture	3.8 [1.4-7.4]	21 [7.9-40.2]	EPT + Chironomidae
				1.1 [0.2-2.2]	6.1 [1.3-11.8]	Chironomidae
				0.7 [0.1-1.6]	3.7 [0.4-7.6]	Ephemeroptera
				2.1 [0.7-4.9]	11.2 [2.9-24.8]	Trichoptera

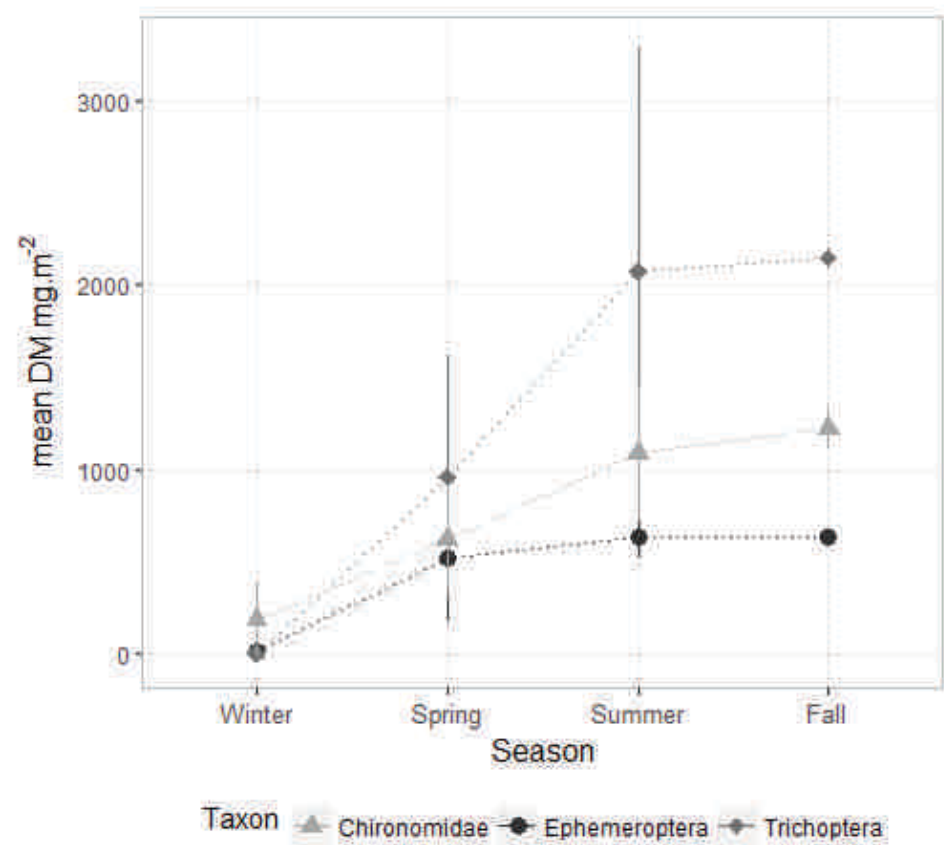
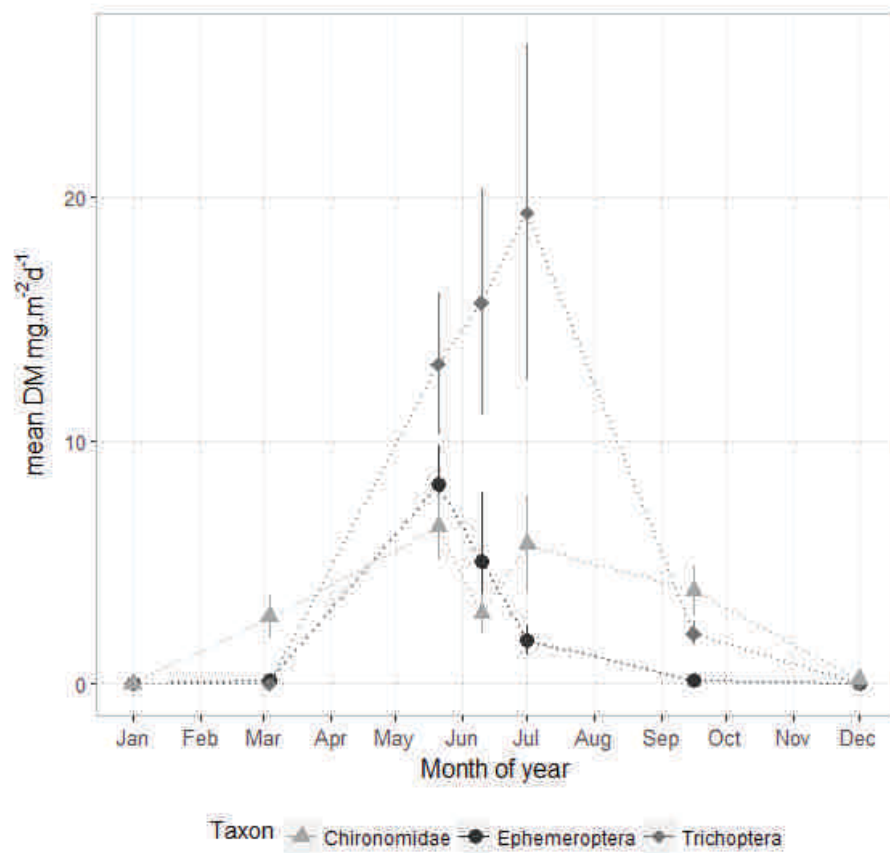


Figure 1. Emergence of aquatic insects dry mass (DM) all sites combined. Left panel shows mean (± 1 standard deviation SD) daily values for each sampling date and taxonomic group. Right panel shows the mean (± 1 SD) cumulative emergence by season (see text for details).

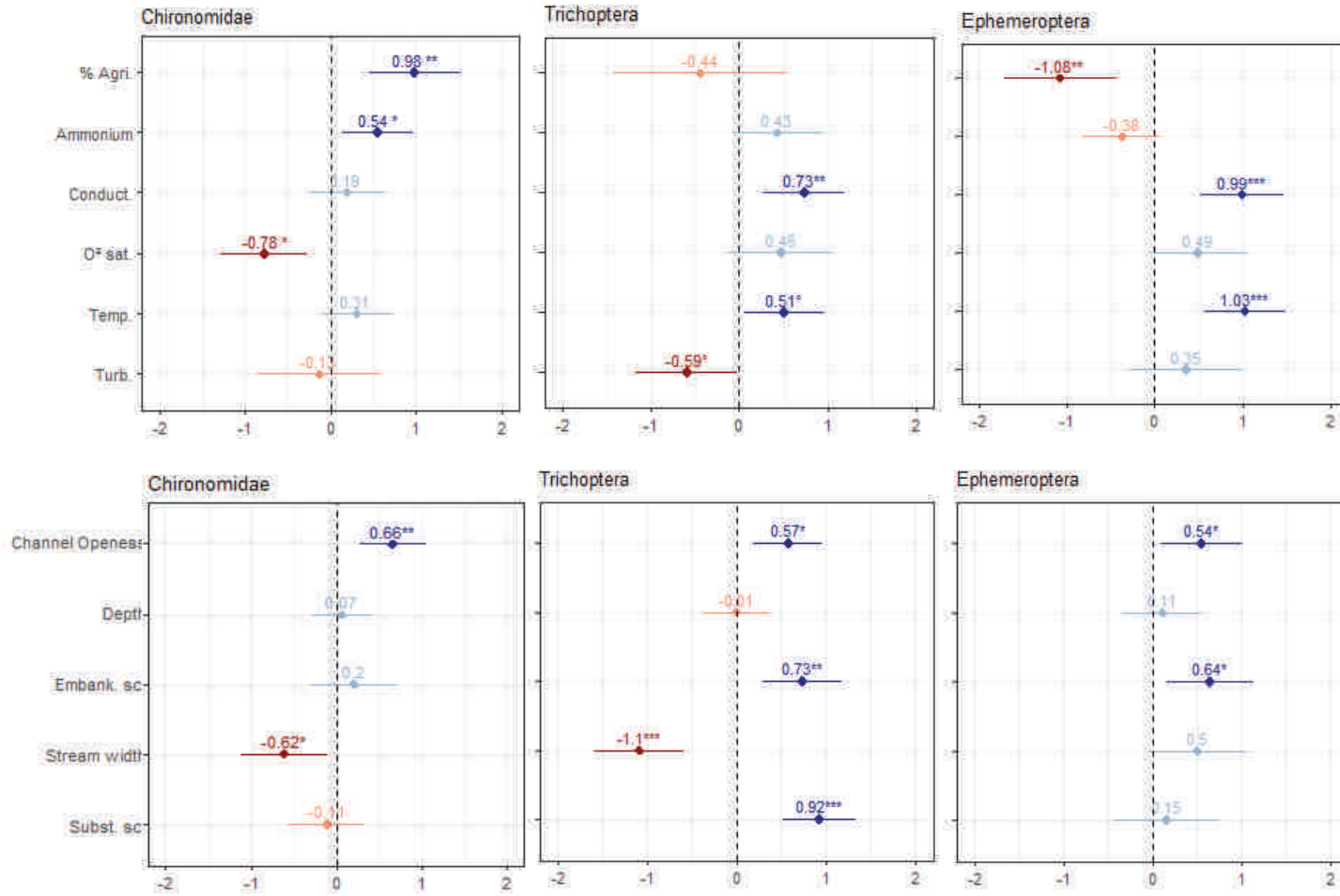


Figure 2. Standardized effect of environmental variables (mean effect size \pm 90% confidence interval) at watershed and site scales on emerging biomass of Chironomidae (left), Trichoptera (middle) and Ephemeroptera (right). Upper panel: Watershed-scale variables; % Agri = Percentage of watershed area covered by agriculture (cropland and pasture), Ammonium = Ammonium (NH₄⁺) concentration in water, Conductivity =

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Colors indicate degree of positive or negative effect. ° = $p < 0.10$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

Table 1. Comparison of temporal and spatial fitted mix-models for each taxon. Summarizing statistics are: Akaike Information Criterion score corrected for small sample size (AIC_c), the variance explained by fixed parameters (marginal R^2) and both fixed and random parameters (conditional R^2) of the model. Null models are intercept-only models, which have no fixed parameter and the same random structure as fitted models. They are used as bases of comparison against fitted models for AIC_c and R^2 . For a given taxon and scale (*i.e.* temporal or spatial), lower AIC_c indicates a better fit of the model to the data, higher marginal/conditional R^2 indicate greater goodness-of-fit (the amount of variance explained).

Taxon	Statistic	Temporal model		Spatial models		
		Null	Sampling campaign	Null	Watershed	Site
Chironomidae	AIC_c	305.1	298.6	301.8	294.9	293.5
	Marginal/conditional R^2	0.0/22.0	10.9/34.9	0.0/32.7	21.4/32.5	15.9/41.9
Trichoptera	AIC_c	323.6	285.4	294.3	292.2	272.0
	Marginal/conditional R^2	0.0/13.3	34.1/52.4	0.0/52.5	11.6/50.5	23.9/57.2
Ephemeroptera	AIC_c	225.3	196.1	204.2	195.7	201.7
	Marginal/conditional R^2	0.0/11.4	33.9/52.1	0.0/51.8	18.8/50.9	11.9/43.5

Table 2. Mean annual dry mass (with range of values in brackets when available) of emerging aquatic insect or secondary production. Values in italics correspond to estimates based on the Poepperl (2000) Emergence:Production ratio. EPT = Ephemeroptera, Plecoptera and Trichoptera.

References	Location	Stream order or width	Landscape	Annual emergence g m^{-2}	Annual secondary production g m^{-2}	Taxa
Jackson & Fisher 1986	Arizona, USA	3-4 m	Desert	13.8	58.3	Chironomidae
				4.4	55.5	Ephemeroptera
				2.9	3.6	Trichoptera
Berg & Hellenthal 1991	Indiana, USA	third order	Agriculture/Forest	5.4	29.7	Chironomidae
Sallenave et Day, 1991	Ontario, Canada	2-4 m	Agriculture/Forest	2.9 [1.1-4.7]	15.6 [5.8-25.4]	Trichoptera
Poepperl 2000	Schleswig-Holstein, Germany	6 m	Agriculture	1.1 [0.6-1.3]	5.3 [3-6.1]	Diptera
				0.1 [0.01-0.1]	0.6 [<0.1-0.9]	Ephemeroptera
				0.5 [0.3-0.6]	1.9 [1-2.1]	Trichoptera
				4.2 [3.3-5]	23.2 [17.9-27.2]	Chironomidae
Shieh <i>et al.</i> 2003	Colorado, USA	fifth order	Agriculture	0.4 [0-0.7]	2.4 [0.02-3.7]	Ephemeroptera
				1.7 [0.4-2.2]	9.5 [2.3-12]	Trichoptera
				-	3.9 [0.4-70.9]	EPT + Chironomidae + other taxa
Gücker <i>et al.</i> 2011	Berlin, Germany	3-4 m	Agriculture	-	3.9 [0.4-70.9]	EPT + Chironomidae + other taxa
Reynolds & Benke 2012	Alabama, USA	second order	Forest	5.3 [1.4-12.5]	29.2 [7.8 - 68.3]	Chironomidae
Johnson <i>et al.</i> 2013	Kentucky, USA	6 m	Agriculture/Forest	-	21.8	EPT + Chironomidae + other taxa
		6 m	Agriculture/Forest	1.4	7.5	EPT
Yuen & Dudgeon 2016	Hong Kong, China	third or fourth order	Forest	0.9 [0.7-1.2]	4.9 [3.8-6.6]	EPT + Chironomidae + other taxa
This study	Brittany, France	third order	Agriculture	3.8 [1.4-7.4]	21 [7.9-40.2]	EPT + Chironomidae
				1.1 [0.2-2.2]	6.1 [1.3-11.8]	Chironomidae
				0.7 [0.1-1.6]	3.7 [0.4-7.6]	Ephemeroptera
				2.1 [0.7-4.9]	11.2 [2.9-24.8]	Trichoptera

Figure

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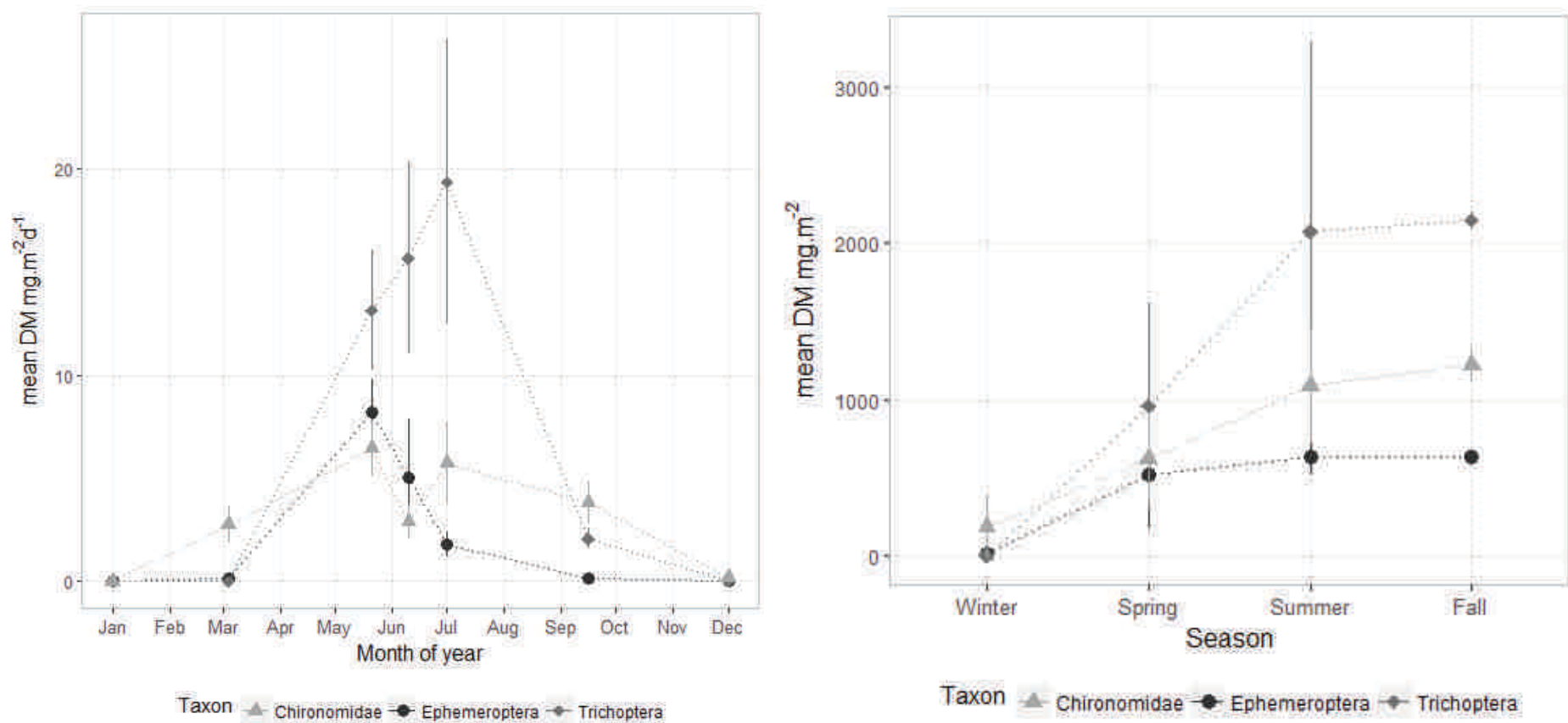


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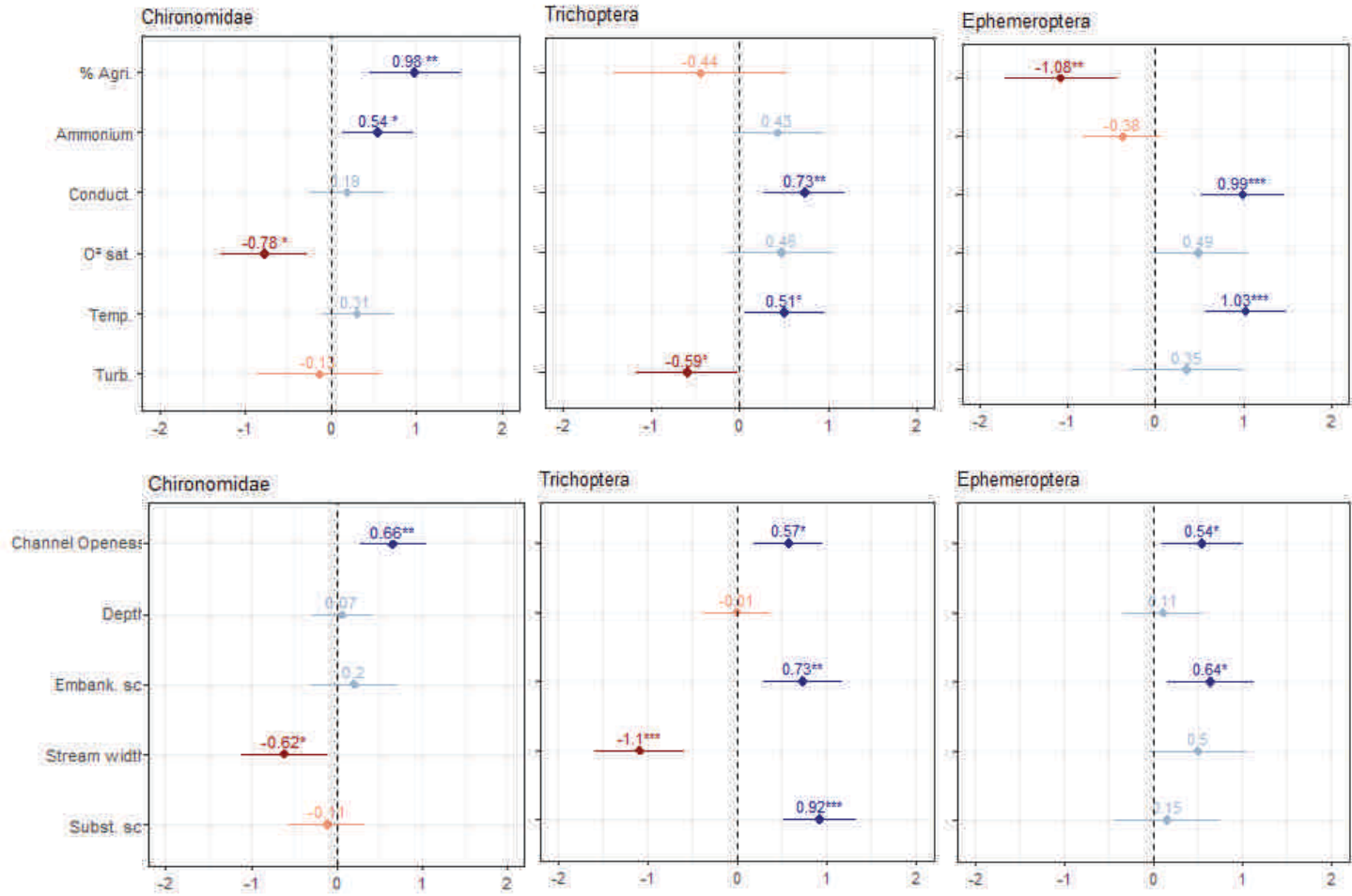


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