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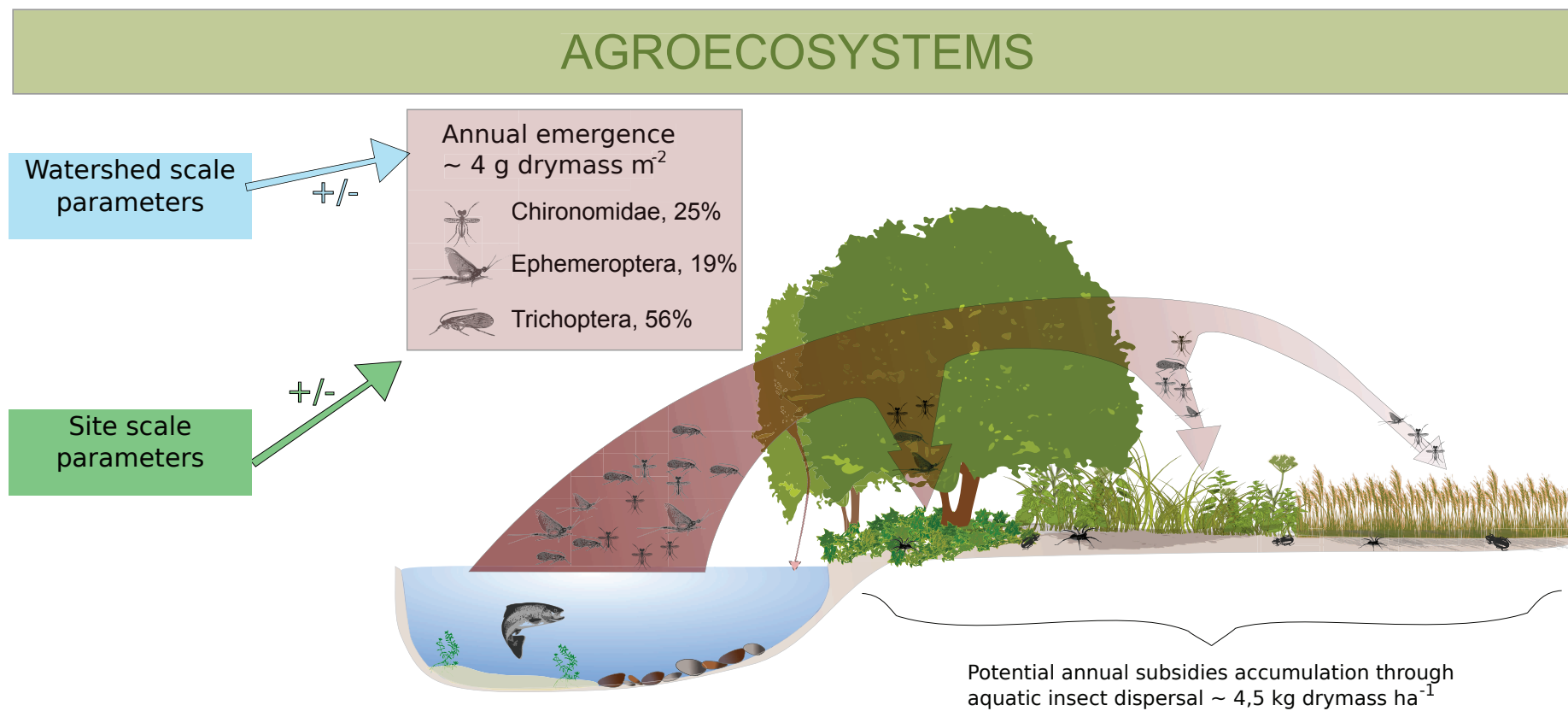
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Highlights

- 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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Abstract

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

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

1 Introduction

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

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

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

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

2 Methods

2.1 Study sites

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

cumulative annual rainfall of approximately 700 mm (peaking in fall and winter) (Météo France 2017). Mean annual discharge of third-order streams in this part of Brittany is $0.65 \text{ m}^3 \text{ s}^{-1}$, 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 winter).

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

2.2 Aquatic insect sampling

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

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

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

2.3 Emergence abundance, dry mass and secondary production

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

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

2.4 Water quality, land use and habitat assessment

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

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

2.5 Statistical analyses

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

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

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

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

3 Results

3.1 Variations in environmental characteristics

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

3.2 Characteristics of aquatic insect emergence

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

3.3 Temporal dynamics of insect emergence

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

3.4 Influence of environmental characteristics on insect emergence

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

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

4 Discussion

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

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

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

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

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

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

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

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

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

5 Conclusion

Multiple influences on aquatic insect emergence were identified at the local and watershed scales, and some were directly related to agricultural practices. Our results suggest that emergence and dispersal of aquatic insects could substantially influence terrestrial ecosystem functioning in landscapes with a dense waterway network. More studies are required on the dispersal of aquatic winged insects and their deposition in terrestrial ecosystems to better understand and quantify the ecological processes involved. This will help to assess effects of the aquatic subsidies that streams provide on ecosystem services supplied to agriculture, such 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
Shieh <i>et al.</i> 2003	Colorado, USA	fifth order	Agriculture	4.2 [3.3-5]	23.2 [17.9-27.2]	Chironomidae
				0.4 [0-0.7]	2.4 [0.02-3.7]	Ephemeroptera
				1.7 [0.4-2.2]	9.5 [2.3-12]	Trichoptera
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

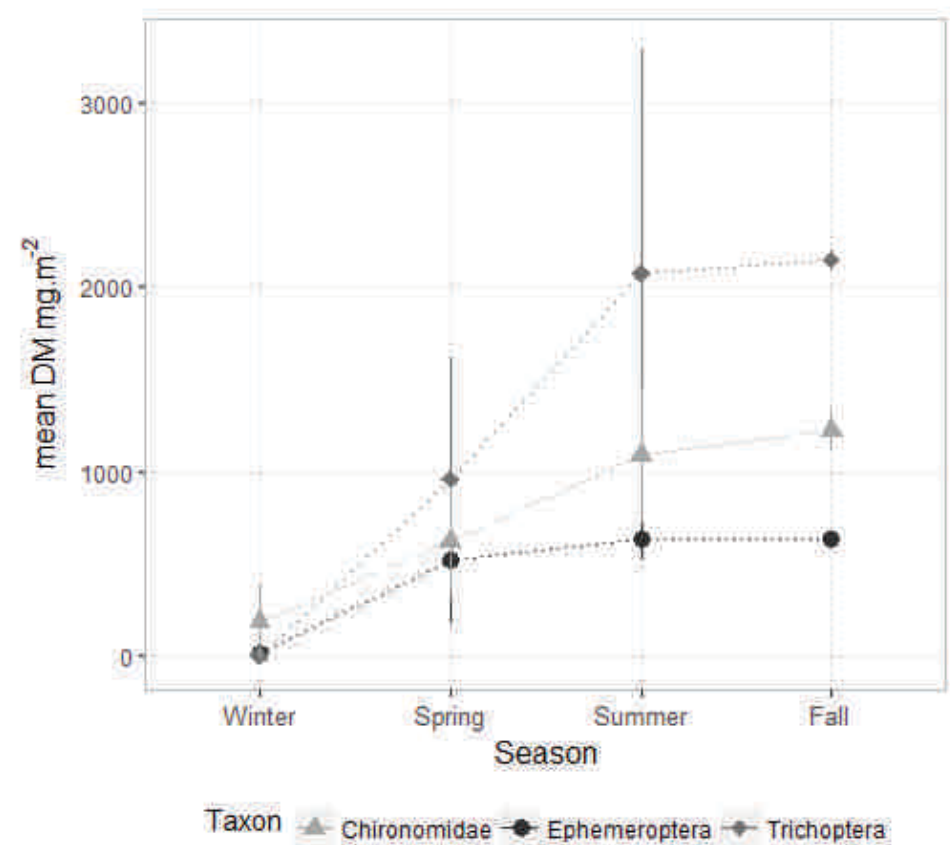
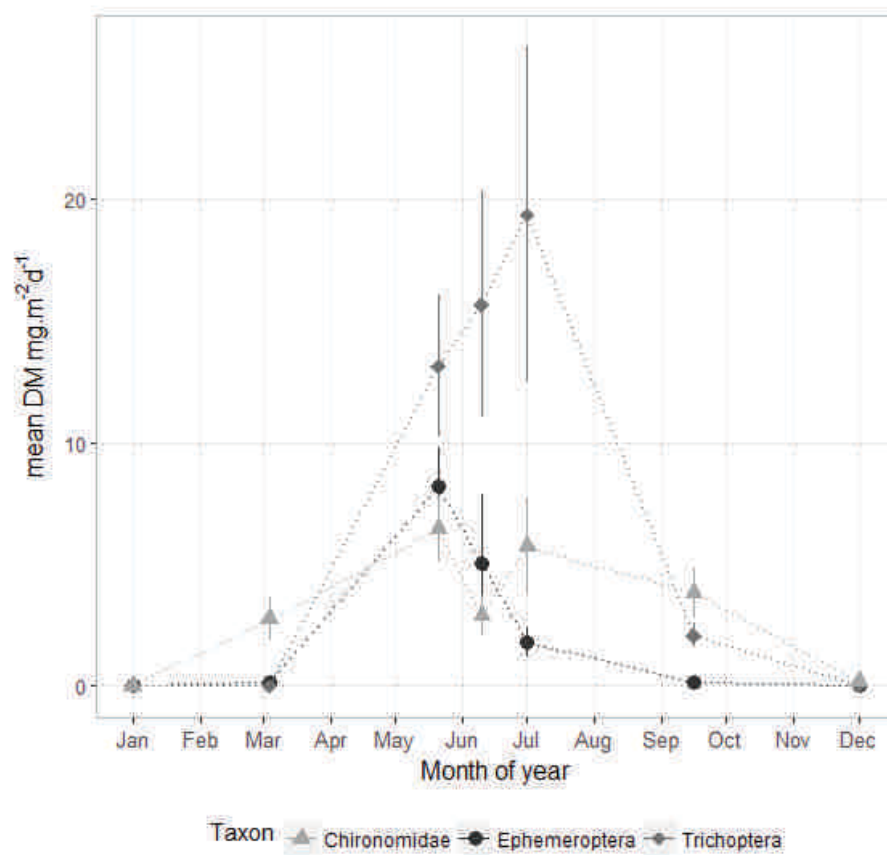


Figure 1. Emergence of aquatic insects dry mass (DM) all sites combined. Left panel shows mean (± 1 standard deviation SD) daily values for each sampling date and taxonomic group. Right panel shows the mean (± 1 SD) cumulative emergence by season (see text for details).

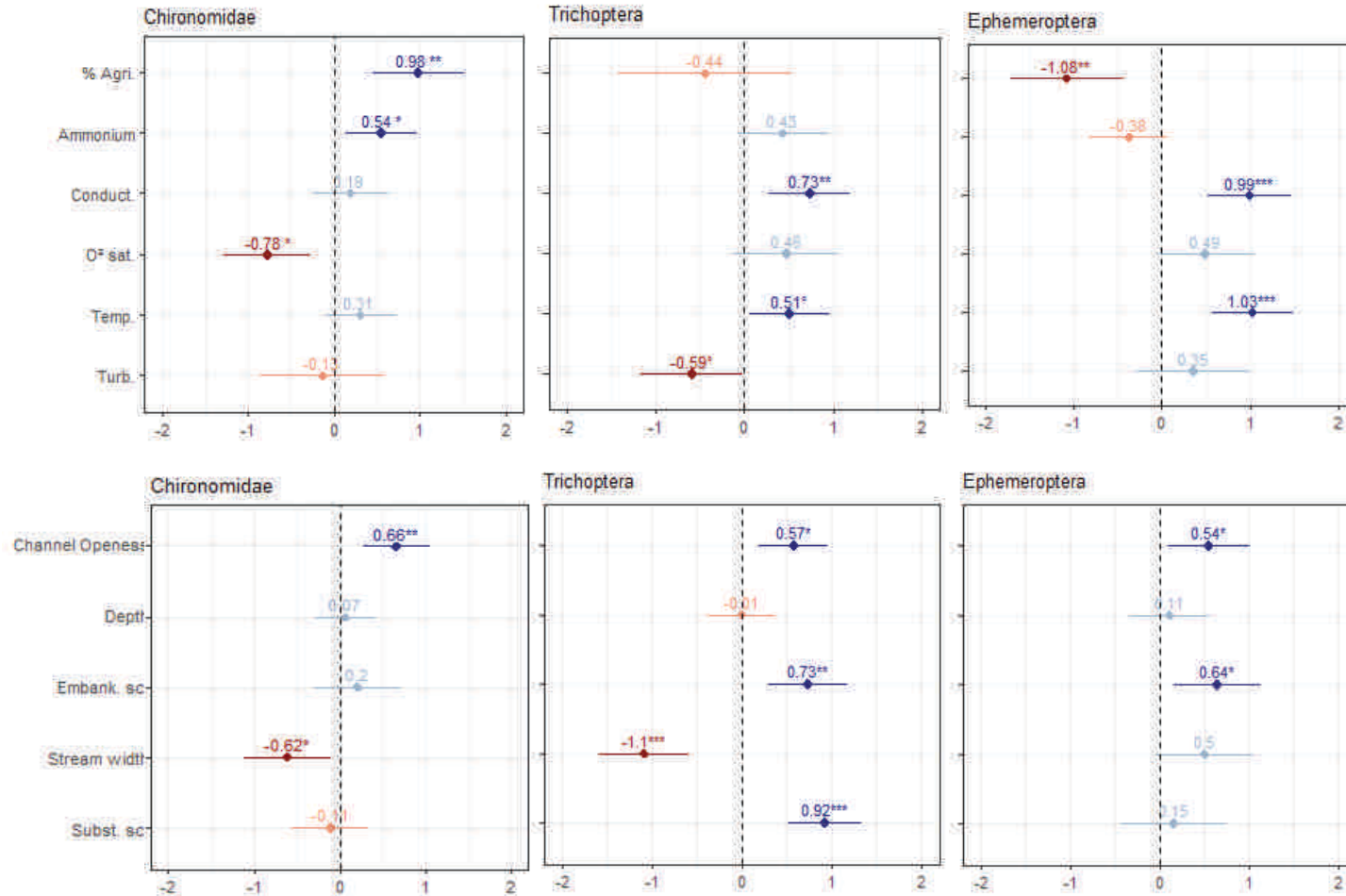


Figure 2. Standardized effect of environmental variables (mean effect size \pm 90% confidence interval) at watershed and site scales on emerging biomass of Chironomidae (left), Trichoptera (middle) and Ephemeroptera (right). Upper panel: Watershed-scale variables; % Agri = Percentage of watershed area covered by agriculture (cropland and pasture), Ammonium = Ammonium (NH_4^+) concentration in water, Conductivity =

Water conductivity, O² Sat. = Oxygen saturation, Temp. = Water temperature, Turb. = Water turbidity. Lower panel: Site-scale variables;

Channel Openness = Proportion of non-canopy cover over the stream channel, Depth = Water depth, Embank. Sc. = Stream width divided by bank height, Stream width = channel width, Subst. sc. = Substratum score, based on modified Wenworth classification (Cummins, 1962).

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).

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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
Shieh <i>et al.</i> 2003	Colorado, USA	fifth order	Agriculture	4.2 [3.3-5]	23.2 [17.9-27.2]	Chironomidae
				0.4 [0-0.7]	2.4 [0.02-3.7]	Ephemeroptera
				1.7 [0.4-2.2]	9.5 [2.3-12]	Trichoptera
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

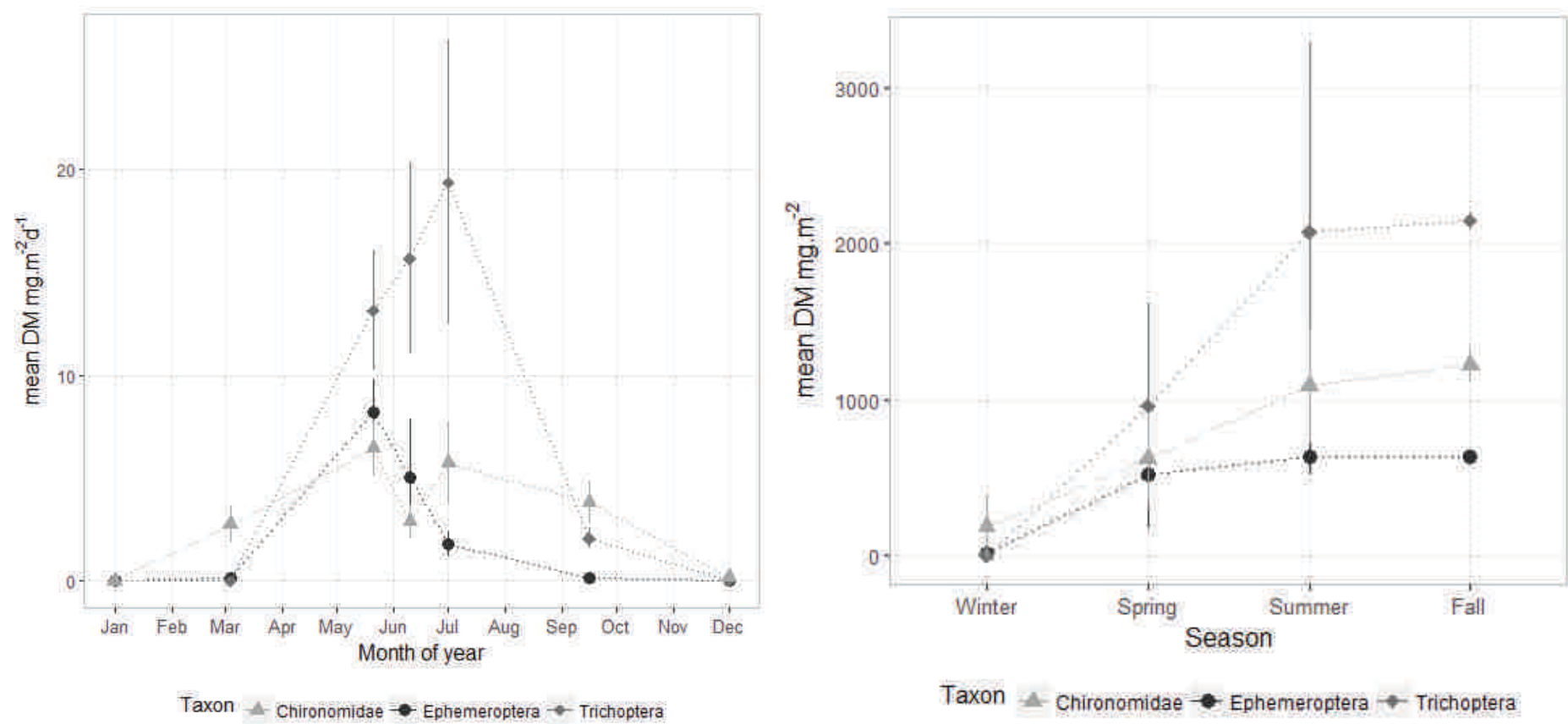


Figure 1. Emergence of aquatic insects dry mass (DM) all sites combined. Left panel shows mean (± 1 standard deviation SD) daily values for each sampling date and taxonomic group. Right panel shows the mean (± 1 SD) cumulative emergence by season (see text for details).

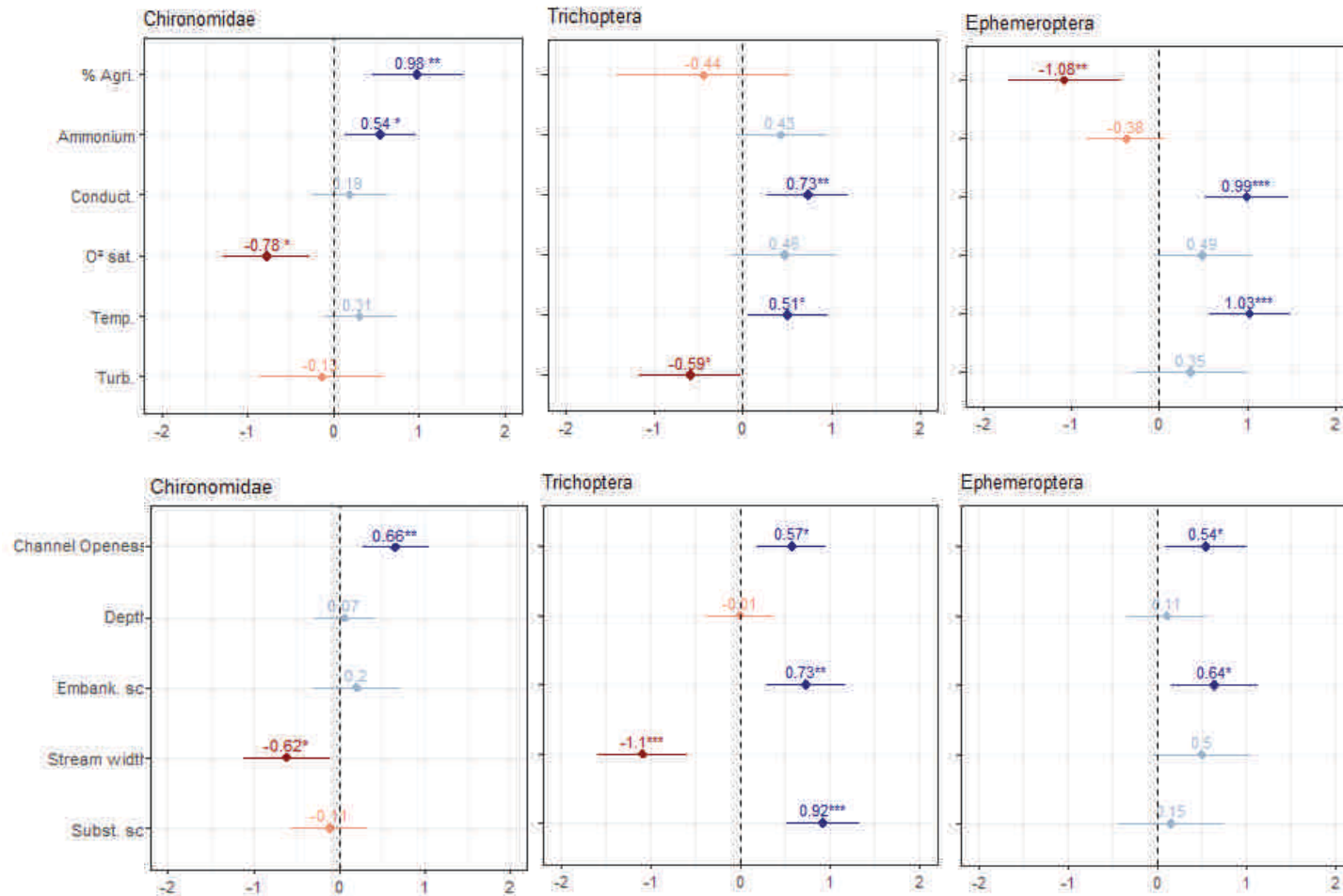


Figure 2. Standardized effect of environmental variables (mean effect size \pm 90% confidence interval) at watershed and site scales on emerging biomass of Chironomidae (left), Trichoptera (middle) and Ephemeroptera (right). Upper panel: Watershed-scale variables; % Agri = Percentage of watershed area covered by agriculture (cropland and pasture), Ammonium = Ammonium (NH_4^+) concentration in water, Conductivity =

Water conductivity, O² Sat. = Oxygen saturation, Temp. = Water temperature, Turb. = Water turbidity. Lower panel: Site-scale variables;

Channel Openness = Proportion of non-canopy cover over the stream channel, Depth = Water depth, Embank. Sc. = Stream width divided by bank height, Stream width = channel width, Subst. sc. = Substratum score, based on modified Wenworth classification (Cummins, 1962).

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

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