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Assessing spatial deposition of aquatic subsidies by insects emerging from agricultural streams

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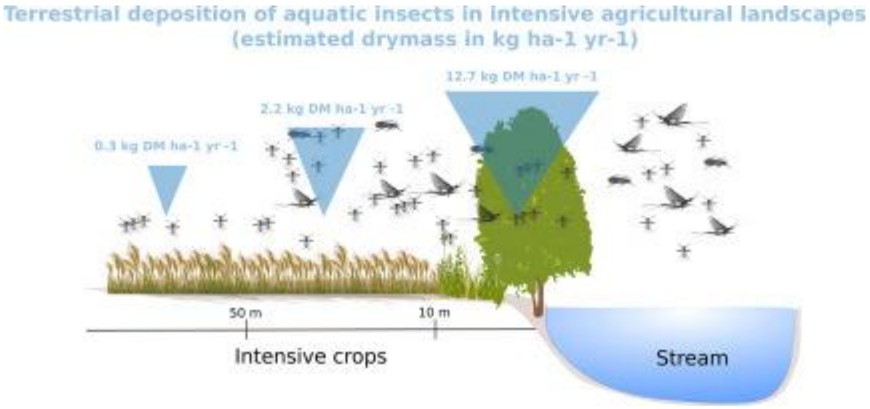
Abstract :

The role of winged aquatic insects that emerge from streams and subsidize terrestrial ecosystems has been demonstrated for natural forest landscapes, but almost no information is available for intensive agricultural landscapes. This study is the first to estimate aquatic subsidies provided by flying insects that emerge from streams and land on cropland. We investigated three major groups of aquatic insects - Trichoptera, Ephemeroptera and Chironomidae (Diptera) - that emerged from 12 third-order temperate, agricultural streams. We simultaneously monitored their emergence using floating traps and their terrestrial dispersal using passive interception traps. We estimated that the annual aquatic emerging dry mass (DM) of these groups varied from 1.4–7.5 g m−2 yr−1, depending on the stream. We used a Bayesian approach to estimate parameters of the terrestrial dispersal function of each group. We combined emerging DM and the dispersal parameters to estimate how terrestrial deposition of aquatic insect DM varied with increasing distance from streams. The results highlighted that emerging DM and dispersal to land could be higher in intensive agricultural landscapes than that previously described in natural settings. We estimated that 12.5 kg ha−1 yr−1 of winged aquatic insect DM fell to the ground 0–10 m from stream edges, composed mainly of Ephemeroptera and Trichoptera. We also estimated that 2.2 kg DM ha−1 yr−1 fell 10–50 m from the stream, especially small-bodied species of Chironomidae, throughout the year, except for the coldest weeks of winter. By influencing aquatic insect communities that emerge from streams, intensive agricultural practices change the magnitude and spatial extent of aquatic subsidy deposition on land. Implications for terrestrial food webs and ecosystem services provided to agriculture are discussed.

Graphical abstract



Highlights

► We show that aquatic insects dispersed farther in agricultural than forest streams. ► 12.5 kg ha^{-1} yr^{-1} of winged aquatic insect drymass fell at 0–10 m from stream. ► Ephemeroptera and Trichoptera are dominant at the stream vicinity. ► 50% of emerging Chironomidae dispersed farther than 25 m inland. ► Such aquatic insect deposition on land could influence the terrestrial food web.

Keywords : winged stream insects, agroecosystems, emergence, resource pulse, dry mass

1 Introduction

Connections between adjacent ecosystems have attracted ecologists' attention in recent decades due to their importance in maintaining biodiversity in terrestrial and aquatic landscapes. Energy and matter that cross ecosystem boundaries, referred to as allochthonous inputs or subsidies, ultimately fuel food webs in the receiving ecosystem and influence its functioning (Polis et al. 1997). This phenomenon has been intensively investigated between aquatic and terrestrial ecosystems, likely because interconnections between land and water are common across the planet. Polis et al. (1997) listed several processes involved in the transport of subsidies across land-water ecotones, including physical vectors such as wind and water flow, or biotic vectors such as movement of prey and consumers. Focusing on the flow of invertebrate prey between stream and forest ecosystems, Nakano and Murakami (2001) demonstrated how two adjacent ecosystems could benefit from the alternating seasonal contrast between *in situ* prey availability and allochthonous prey supply. The biomass of aquatic subsidies to land is generally lower than that of terrestrial subsidies to water, but their average contributions to receiving food webs can be equivalent (Bartels et al. 2012). For instance, several studies in the literature highlight the presence of aquatic prey in the diets of birds (Nakano and Murakami 2001), lizards (Sabo and Power 2002), bats (Hagen and Sabo 2011) or spiders (Hoekman et al. 2019). Aquatic insect prey contain physiologically essential fatty acids and provide critical resources for both stream and riparian consumers (Twining et al. 2019).

As adults, many winged aquatic insects disperse to riparian ecosystems to mate (*e.g.* for Chironomidae, Armitage et *al.* 1995), and a small percentage ultimately return to the water, especially females for oviposition (Baxter et al. 2017). Previous studies have estimated that less than 5% of total emerging biomass ultimately returns to the stream (Jackson and Fisher 1986), suggesting that most of it enters terrestrial food webs. Dreyer et al. (2015) estimated that up to 100 kg ha^{-1} yr^{-1} of dry mass (DM) of midges in subarctic lakes fell 0-50 m from the shoreline. Similarly, Walters et al. (2018) found that stonefly emergence in the most productive western USA streams resulted in a mean annual export of 10 g of carbon per m of streambank to riparian ecosystems. In a review of the spatial dispersal of winged stream insects, Muehlbauer et al. (2014) showed that among the aquatic insects that emerge (i.e. Ephemeroptera, Plecoptera, Trichoptera and Diptera), some can disperse up to 50 m or more from streams. However, most recent studies of adult stream insects have been conducted in natural settings (i.e. forest streams), but rarely on streams highly impacted by human activity (but see Carlson et al. 2016, Raitif et al. 2018).

Several factors can explain why dispersal of winged adult stream insects to land differs between agricultural landscapes and natural ecosystems (Raitif et al. 2019). First, intensive agricultural streams can be highly productive, and their annual flow of emerging insects is among the highest recorded to date (reviewed in Raitif et al. 2018). Second, agricultural intensification profoundly changes aquatic insect communities. The decrease in larger and more sensitive aquatic insects (Ephemeroptera, Plecoptera and Trichoptera) in favor of small-bodied taxa (Diptera, especially Chironomidae) in agricultural streams (Greenwood and Booker 2016; Stenroth et al. 2015) may change the distance to which emerging aquatic insect communities disperse. Third, once emerged, winged stream insects experience environmental conditions that may promote their dispersal toward agricultural land. Notably, the lack of riparian 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).

In this study, we sought to provide the first estimates of the spatial deposition of aquatic subsidies through the dispersal of winged adult insects emerging from streams in intensive agricultural landscapes. We simultaneously monitored the flow of emerging aquatic insects using floating traps and their terrestrial dispersal using passive interception (i.e. “sticky”) traps along 12 agricultural streams in western France. Because we expected different dispersal distances and seasonal contrast in the phenology of emergence, we considered three dominant groups (Ephemeroptera, Trichoptera and Chironomidae) separately to estimate annual budgets. Our objectives were to (i) assess the pattern of inland dispersal of adult stream insects and (ii) estimate how the biomass of aquatic flying insects on agricultural land decreases with increasing distance from the stream. We hypothesized that in intensive agricultural landscapes, both the amount and distance of aquatic insect deposition would be larger than those previously reported in natural landscapes. We also hypothesized that the taxonomic composition of the emerging communities would influence the extent of the terrestrial deposition of aquatic subsidies.

2 Materials & Methods

2.1 Site selection

The study was conducted in Brittany, France. The climate is temperate, with a mean annual temperature of 10.5-12.5°C and cumulative annual rainfall of ca. 700 mm. Intensive farming dominates the landscape, involving large amounts of fertilizers and pesticides and significant modification of the landscape. In 8 watersheds, we selected sites on 12 third-order perennial streams (Strahler 1952), with a mean width of 6 m, that flowed along crop fields (winter wheat or barley). A grass strip (5-12 m wide) in each field separated the stream from the crop field (Figure 1). In selected sites, streams are greatly polluted by agriculture practices. In a companion study, Raitif et al. (2019) highlighted for all sites high concentrations of nitrates through the year (mean = 20.4 mg NO_3^{-} L^{-1} ± 6.6). Each watershed’s water chemistry and landscape characteristics are described in Supplementary Material S1 and further detailed in Raitif et al. (2019).

2.2 Estimating the amount of aquatic insect deposition on land

2.2.1 Sampling period

The study was conducted from spring 2016 to winter 2017 (Table 1). Adult aquatic insects were trapped during 7-day periods. We targeted the main months of aquatic insect emergence in temperate latitudes (i.e. in spring and, to a lesser degree, in summer and early autumn). Due to the risk of equipment damage, aquatic emergence and dispersal were assessed at only one site in winter (December 2017). We observed no emergence or dispersal then, which confirmed the results of Corbet (1964), who observed negligible aquatic insect activity during the coldest period of the year (i.e. end of autumn to the end of winter). We collected 111 emergence samples, totaling 777 days of trapping (10% of the samples were damaged by extreme weather events or suspected vandalism). At the same time, 590 sticky traps were collected (3% of the samples were lost for the same reasons).

2.2.2 Emergence

At each site, we measured aquatic emergence by setting up two floating emergence tents (basal area = 1 m², Figure 1). Each tent was secured to the shoreline with ropes. One tent was set in a pool habitat of the river and the other in a riffle to consider the influence of aquatic habitat on aquatic insects. A plastic container was installed outside the peak of the tent to collect adult flying insects. It was filled with propylene glycol (ca. 20%) and water to preserve the insects. After collection, aquatic insects were kept in 70% alcohol. In the laboratory, a stereomicroscope was used to sort and count insects from three taxonomic groups: Ephemeroptera, Trichoptera and Chironomidae. Other aquatic insects, especially Plecoptera and Megaloptera, usually emerge by crawling on land (Hynes 1976; Elliott 1996). Consequently, their emergence cannot be accurately assessed using floating emergence traps, and they were excluded from the analysis. Insects were dried at 60°C for at least 24 h and weighed to the nearest 0.2 mg (for more details on methods, see Raitif et al. 2018).

We calculated mean emerging insect DM, expressed in g DM m^{-2} d^{-1}, at each site for each sampling date using data from the two emergence traps. Mean daily values obtained for each campaign were extrapolated forward and backward to adjacent days to fill temporal gaps between campaigns. Daily emergence was then summed to estimate cumulative annual emerging DM (g DM m^{-2} yr^{-1}) at each site and for each taxonomic group (Ephemeroptera, Trichoptera and Chironomidae).

2.2.3 Dispersal to land

Sticky traps (Figure 1) were used to monitor terrestrial dispersal of winged stream insects. They are simple to use in the field and are reported not to attract flying insects (Smith et al. 2014). Each trap was made from a sheet of transparent film (29.7×42 cm) to which we applied a non-drying, odorless and colorless adhesive (Tangle-trap^{TM}). The coated transparent sheets were attached to a transparent plastic panel and installed vertically on a pole 1 m above the ground. Each site contained two lines of five sticky traps: the first trap was located on the riverbank 1 m from the stream. The remaining traps were randomly and individually installed within four distances – 2-7, 8-15, 16-30 and 31-50 m – to capture the dispersal gradient from the stream edge to the crops (Figure 1). We chose a maximum distance of 50 m from the edge since most adult aquatic insects, except for Chironomidae, usually disperse less than 50 m from their emergence site (Muehlbauer et al. 2014). We also wanted to avoid the potential influence of other aquatic ecosystems (permanent or temporary). For instance, ditches around crop fields provide habitats for aquatic insects (Delettre and Morvan 2000). When collected, each sticky trap was detached, wrapped in plastic film and frozen at -20°C until the insects on it were counted in the laboratory. They were then sorted into three groups: Ephemeroptera, Trichoptera and Chironomidae. Like with the emergence traps, other aquatic insects were not considered due to their low contribution to the total abundance captured.

2.2.3.1 Data processing

We assumed that data collected using the sticky traps were dispersal decay-function observations. Data consisted of the abundance of each taxonomic group (Ephemeroptera, Trichoptera and Chironomidae) for each site and sampling date at multiple distances from the stream. For all insect groups, count data showed overdispersion and, for Ephemeroptera and Trichoptera, an excess of zero values (40% and 55%, respectively). We used a negative binomial distribution to accommodate overdispersion in the observed abundance of Chironomidae and a zero-inflated negative binomial distribution to accommodate the high frequency of zeros observed in abundances of Ephemeroptera and Trichoptera. When fewer than 100 individuals of a given taxonomic group had been captured during a given sampling campaign (all sites combined), the data for that group were discarded. Similarly, for a given site and campaign, when fewer than 6 individuals had been captured (all traps combined), the entire sample from this site was discarded. Consequently, we used dispersal data from sampling campaigns 1-5 for Chironomidae, 1-2 for Ephemeroptera and 2-4 for Trichoptera. Few Chironomidae were caught during the 6th campaign (late fall) on the sticky traps, but an abnormal dispersion pattern was observed: more individuals were caught as distance to stream increased. Raitif et al. (2019) previously highlighted that emergence of stream insects, including Chironomidae, was almost inexistent at this time of year. We assumed that this dispersal was due to terrestrial sources of emergence (Delettre 1992), such as ephemeral puddle of waters or ditches nearby our study streams, and discarded the associated data from the analysis.

2.2.3.2 Models

Plotting the raw dispersal data revealed two distinct patterns: an exponential decrease in abundance with increasing distance (Petersen et al. 2004) for Ephemeroptera and Trichoptera, but a different pattern for Chironomidae, previously described by Dreyer et al. (2015), with an initial plateau or moderate decrease near the stream edge, followed by an exponential decrease.

Accordingly, a classic exponential decay model was fitted to Ephemeroptera and Trichoptera data (Eq. 1), while an alternative model inspired by Dreyer et al. (2015) was fitted to Chironomidae data (Eq. 2) for each site (s) and date (t):

$$Abundance_{s,t} = b \cdot e^{-a \cdot X} \qquad (Eq.\ 1)$$

$$Abundance_{s,t} = b_{s,t} \cdot e^{-a_{s,t} \cdot X} + d \cdot X \cdot e^{-c_{s,t} \cdot X} \qquad (Eq.\ 2)$$

For both models, *b* is the abundance of insects at the stream edge (i.e. X = 0) and *a* is the slope of exponential decrease in abundance with increasing distance from the stream. For the alternative model (Eq. 2), parameters *c* and *d* determine the slope and the shape of the potential plateau with increasing distance from the stream. Several models were fitted to the data to assess whether the dispersal function depended on the site, the date or both (Table 2).

2.2.3.3 Parameter inference

No information was available to generate informative priors for parameters. We assessed the sensitivity of the models to different sets of weakl informative priors and hyperpriors distributions and values (Supp.Mat S5 for further details). Posterior estimates of total aquatic insect dry mass were not sensitive to the prior distributions and values tested and we therefore retained configuration V3 (Supp.Mat S5, table S5.1), commonly used in hierarchical models (Gelman 2014), in the subsequent analysis.

Posterior distributions of parameters were estimated using Monte Carlo Markov Chain methods in the *Rjags* package of R software (www.Rproject.org). We ran three chains independently, with 600 000 iterations each. For each chain, the first 100 000 iterations were discarded. Posterior distributions were obtained by keeping 1 out of every 50 iterations, which yielded 10 000 iterations per chain.

2.2.3.4 Validation and model selection

To assess convergence, we used the Gelman-Rubin diagnostic (Brooks and Gelman 1998) in the R *coda* package. In addition, to check the ability of the model to replicate a posteriori data similar to those observed, we calculated Bayesian p-values from chi-square discrepancies tests (Gelman et al. 2014). In this study, the prediction/observations couple were the abundance of individuals within each taxonomic group at various distances from stream. Bayesian p-value should be close to 0.50 for good model, but in practice, p-value between 0.1 and 0.9 are accepted (Royle et al. 2014) and lack of fit is pinpoint when *p-value* ranged between 0.05 and 0.95 (Conn et al. 2018).

Alternative hierarchical models were compared using the Watanabe-Akaike information criterion (WAIC) (Watanabe 2013). The best model was the one with the lowest WAIC, and we considered that a model performed better than another when its WAIC was at least 5 points lower.

2.2.4 Calculating the deposition of dry mass on land

We estimated annual terrestrial deposition of aquatic insects with increasing distance from the stream edge by combining the decay function with the estimated annual DM of emerging insects at each site. We assumed that (i) aquatic insects dispersing from the stream and collected on a sticky trap would have fallen on the ground close to it, and (ii) the abundance of insects on a sticky is a good indicator of terrestrial deposition. For each taxonomic group, we used the dispersal model with the lowest WAIC and predicted the number of captures from 0-150 m from each stream using the Bayesian posterior distribution of parameters of the selected model. We then estimated the relative deposition rate with increasing distance from the stream by calculating the fitted area under the curve (AUC) divided by the total AUC (from 0-150 m). We then calculated the deposition rate for seven ranges of distance: 0-1, 1-5, 5-10, 10-20, 20-50, 50-100 and 100-150 m. We used the R *pracma* package (Brochers 2018) to calculate AUC using the trapezoidal rule.

Finally, we multiplied these deposition rates by total annual emerging DM to estimate the annual DM of aquatic insect deposition with increasing distance from a 6 m-wide stream for each site. The resulting deposition rates were combined for each distance from 0-100 m from the stream to obtain an average profile of the annual terrestrial deposition of DM of aquatic insects emerging from a third-order stream in an intensive agricultural landscape (in kg DM ha^{-1} yr^{-1}).

3 Results

3.1 Aquatic insect emergence

In total, more than 64 000 insects were captured in emergence traps during the study, of which 91% were Chironomidae, 6% were Trichoptera and 3% were Ephemeroptera. As expected, due to their emergence behavior, Plecoptera were rarely captured (< 0.1%) and thus excluded from further analysis. Chironomidae emerged throughout the year, except in winter. Trichoptera and Ephemeroptera emergence peaked in spring and then decreased in summer (see Supplementary Material S2 for detailed results for all campaigns). Trichoptera contributed the most to annual emerging DM, followed by Chironomidae and Ephemeroptera (2.1, 1.1 and 0.7 g DM m^{-2} yr^{1}, respectively). Estimates of annual emerging DM ranged from 1.4-7.4 g DM m^{-2} yr^{-1} among sites, with a mean of 3.8 g DM m^{-2} yr^{-1} (Figure 2).

3.2 Dispersal of adult aquatic insects

3.2.1 Captures

We captured 416 783 insects on sticky traps during the study. More than 90% of them were terrestrial (Diptera, Hymenoptera, Coleoptera) and were thus discarded. Aquatic insects accounted for ca. 8% of total captures (32 406 insects), and 7% were Chironomidae, 0.1% were Ephemeroptera and 0.2% were Trichoptera. Megaloptera were also captured (704 specimens) on sticky traps, but Plecoptera were extremely rare (< 0.01%). Because their emerging DM could not be estimated using the floating emergence traps, Plecoptera and Megaloptera were excluded from further analysis. Chironomidae dispersal was detected during all campaigns and peaked in April (campaign 1), accounting for nearly 50% of total captures (Figure 3). Ephemeroptera dispersed mainly in May (campaign 2) and April (67% and 19% of Ephemeroptera captures, respectively). Trichoptera captures peaked in May (campaign 2, 42% of captures) but remained abundant in June and early July (campaigns 3 and 4), accounting for 20% and 23% of captures, respectively. Total annual captures varied greatly among sites, ranging from 706-5125 for Chironomidae, 23-131 for Ephemeroptera and 19-298 for Trichoptera (Figure 3, Supplementary Material S3).

3.2.2 Dispersal functions

For Ephemeroptera and Trichoptera, the best model was an exponential decay model with parameters depending on *Site* only (Table 2). Mean P values for Trichoptera (0.29) and Ephemeroptera (0.37) confirmed that models fitted the data accurately (SuppMat S4). Plotting *P values* as a function of distance from the stream revealed that some of the best models fit poorly for distances greater than 20 m (ca. 7.5% and 6.5% of *P values* were less than 0.05 for Trichoptera and Ephemeroptera, Supplementary Material S4). The alternative model (Eq. 2) best explained the dispersal of Chironomidae, with parameters depending on both Site and

Date (Table 2, Supplementary Material S4). The mean *P value* of 0.50 (± 0.20) confirmed that the model fit the observed data accurately.

The abundance of Ephemeroptera decreased to 50% at a mean distance of 8 m from the edge (range: 3-25 m among sites) (Figure 4). It decreased to 10% at 35 m (10-78 m) and 1% at 86 m (27-130 m). For Trichoptera, the mean distances corresponding to 50%, 10% and 1% of abundance were 5 m (2-36 m among sites), 22 m (5-36 m) and 51 m (10-71 m), respectively (Figure 4). For Chironomidae, the mean distances corresponding to 50%, 10% and 1% of abundance were 25 m (6-34 m), 66 m (49-71 m) and 114 m (98-117 m), respectively (Figure 4).

3.3 Annual deposition of winged aquatic insect dry mass on land

Approximately 52% of the total aquatic DM fell 0-10 m from the stream, 40% from 10-50 m and 8% from 50-100 m (Figure 5). On average, 2.3 kg DM ha^{-1} yr^{-1} of Ephemeroptera, Trichoptera and Chironomidae fell to the ground on a 100 meters wide strip of land, ranging from 0.9-4.4 kg DM ha^{-1} yr^{-1}. The amount of total aquatic dry mass deposited varied greatly among the ranges of distance from the stream, with a mean of 12.5 kg DM ha^{-1} yr^{-1} from 0 to 10 m (range: 4.4- 24.9 kg DM ha^{-1} yr^{-1} among streams). Similarly, 2.19 and 0.32 kg DM ha^{-1} yr^{-1} (range: 0.82-4.20 and 0.12-0.62 kg DM ha^{-1} yr^{-1}) of aquatic insect DM was estimated to fall from 10-50 m and 50-100 m, respectively. Deposition of DM from 100-150 m was negligible (< 0.05 kg DM ha^{-1} yr^{-1}).

4 Discussion

While dispersal of aquatic insects has been assessed for several decades (*e.g.* Williams and Hynes 1976; Hershey et al. 1993), inland dispersal and terrestrial deposition of winged aquatic insects emerging from streams are not well known. Because most studies of dispersal of adult aquatic insects (reviewed by Muehlbauer et al. 2014) were conducted in forested areas, information from intensive agricultural contexts is rare. In a companion study (Raitif et al. 2018), we showed that insect biomass emerging from streams in intensive agricultural landscapes was greater than most of those reported for more pristine systems. For Chironomidae, we highlighted the propensity of agricultural streams to produce and deliver large amounts of aquatic subsidies to surrounding terrestrial ecosystems (Raitif et al., 2018). Notably, increasing agricultural pressure in a watershed, water pollution due to nitrate leaching after fertilizer application, alteration of stream banks and a decrease in riparian vegetation strongly promote the emergence of small aquatic dipterans such as Chironomidae. Stenroth et al. (2015) confirmed that the proportion of agricultural land in the landscape positively correlates with the emergence of small aquatic insects, especially Chironomidae. Conversely, Raitif et al. (2018) highlighted that biomass of Ephemeroptera and Trichoptera emerging from water significantly decreased in streams strongly impacted by agriculture. Chironomidae are frequently associated with farther terrestrial dispersal (Muehlbauer et al. 2014), in particular due to their ability to be carried away by the wind because of their low individual mass (Delettre and Morvan 2000). Consequently, by promoting shifts in assemblages of stream insect species, intensive agricultural practices could greatly alter the magnitude and spatial extent of aquatic subsidies delivered to land.

To our knowledge, the present study is the first to model inland dispersal of winged insects emerging from streams in an intensive agricultural context. Our results suggest that aquatic insects dispersed much farther than expected, based on previous observations of forest streams (Muehlbauer et al. 2014). Half of the emerging Trichoptera and Ephemeroptera dispersed farther than 5 and 8 m from the stream edge, respectively. This distance was observed to be only 1 m along forest streams (Muehlbauer et al. 2014). Similarly, half of the Chironomidae dispersed farther than 25 m from our agricultural streams, which is nearly twice the distance observed by Muehlbauer et al. (2014) along forest streams. Thus, according to Muehlbauer et al.'s definition, the "biological width" of a stream, as opposed to its hydro-geomorphic width, is broader in agricultural contexts than in forest contexts. The recent study of Carlson et al. (2016) observed shorter dispersal distances of emerging insects from agricultural streams in Sweden than those we observed. Agriculture was less prominent in their study landscape, with a higher percentage of forest (49% ± 10%) than in our study (8% ± 9%), and much wider strips of riparian vegetation (26 ± 23 m). Delettre and Morvan (2000) showed that riparian vegetation could act as a natural barrier that strongly restricts inland dispersal of Chironomidae that emerge from streams. Because adult Chironomidae (Frouz and Paoletti 2000) and other taxa (e.g. Trichoptera, Petersen et al. 1999) can take shelter in riparian habitats, agricultural intensification and alteration of riparian vegetation may modify inland dispersal of winged aquatic insects by increasing landscape permeability to aerial movement.

We observed between-site variations in dispersal distances for all groups of aquatic insects, suggesting that local environmental parameters influence dispersal. Riparian vegetation density was visually assessed by measuring channel openness (Raitif et al. 2018), which varied among stream channels (Supplementary Material S1). We calculated correlations between this proxy of riparian density/structure and dispersal results estimated for each taxonomic group, but none of them were strong or significant (results not shown). Accurately assessing the influence of riparian vegetation on aquatic insect dispersal will require more detailed studies that examine the density, structure and diversity (i.e. species composition) of riparian vegetation over space and time (i.e. seasons). Regional or local weather conditions may also have an influence. For instance, most Chironomidae are passive dispersers that are frequently blown away from streams by the wind. Conversely, Sabo and Hagen (2012) showed that their dispersal could be restricted by wind blowing along the stream channel. A similar reduction in Chironomidae dispersal was observed along steeper banks (Carlson et al., 2016). Finally, species composition of the adult Chironomidae community is likely to change throughout the year, mainly due to changes in water temperature. Among Chironomidae, the Orthocladiinae subfamily can emerge in spring and autumn, while the Chironominae and Tanyponinae subfamilies can emerge in summer (Eggermont and Heiri 2012). Changes in the community can thus result in changes in dispersal distances, which would be amplified by differences in mean body and wing sizes among subfamilies (Delettre 1988).

The mean estimated annual deposition of aquatic insects was 12.5 kg DM ha^{-1} yr^{-1} from 0-10 m from the stream, reaching 24.9 kg DM ha^{-1} yr^{-1} along the most productive stream. A large amount of aquatic insect biomass fell 10-50 m from the streams (mean: 2.2 kg DM ha^{-1} yr^{-1}, range: 0.8-4.2), in crop fields in the sites of this study. In addition, we observed many Megaloptera (*Sialis lutaria*) on the sticky traps located near the streams, but none on emergence traps. Consequently, we could not calculate their resulting terrestrial deposition. It is thus likely that we underestimated the terrestrial deposition of aquatic insect DM. These results highlight how streams can subsidize agroecosystems greatly through aerial dispersal and inland deposition of winged adult aquatic insects.

Insect communities that emerge from temperate streams provide a variety of subsidies to agroecosystems. Large-bodied taxa (e.g. Trichoptera, Ephemeroptera and Megaloptera) provide great amount of aquatic-derived biomass to a narrow strip of land along streams within a short period of time (spring and early summer). The spatial distribution and temporal availability of resources influence ecosystem functioning greatly (Polis and Strong 1996), especially through resource pulses, which have been described for many ecosystems (Noy-Meir 1973, Connell 1978, Nakano and Murakami 2001). A short period of substantial emergence of insects has been shown to fuel the community of soil decomposers (Lovett and Ruesink 1995) or the activity of a diverse macroarthropod community (e.g. Carabidae and Staphylinidae, Yang 2006). Moreover, stream-derived subsidies in agricultural landscapes contain abundant small-bodied dipteran taxa (especially Chironomidae) that disperse far from streams nearly all year round (except in the middle of winter), which diversifies the prey available to terrestrial consumers. Recently, Twining et al. (2019) demonstrated that aquatic insects supply terrestrial ecosystems with essential amino and fatty acids. By entering terrestrial food webs in early spring and late autumn, when terrestrial secondary production is low, with a diverse prey community of high nutritional quality, aquatic subsidies may function as a resource pulse and sustain multiple communities of terrestrial predators near streams (Larsen et al. 2016). Finally, several terrestrial predators that feed on aquatic insects help to regulate crop pests at different times of the year (e.g. spiders, Riechert and Lockley 1984; birds, Maas et al. 2013). Our results suggest that these aquatic subsidies could drive the spillover of several terrestrial predators from areas near streams to crops at different times of year. This effect has been shown to be significant in sustaining ecosystem services, such as biocontrol, in terrestrial agricultural landscapes (Tscharntke et al. 2005).

5 *Conclusion*

Based on a unique dataset, our results indicate that aquatic insect deposition on land could provide abundant, diverse and high-quality resources to terrestrial predators over a broad temporal and spatial scale. In an agriculture landscape in which streams run along crop fields, this deposition of aquatic DM could complement several ecosystem services, such as soil fertilization with labile organic matter that stimulates microbial soil activity, or biological control by supplying alternative prey to sustain natural enemy populations. From an agroecological perspective, a complex and abundant insect community is necessary in agricultural landscapes. The involvement of aquatic subsidies in providing ecosystem services to agriculture is a new topic of research that requires further study.

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Table 1. Sampling campaigns of aquatic insect emergence and dispersal

Campaign	**Emergence**	**Dispersal**
1	-	April 25 to May 4 (2016)
2	May 17 to 26 (2016)	May 17 to 26
3	June 6 to 15	June 6 to 15
4	June 27 to July 6	June 27 to July 6
5	September 12 to 21	September 12 to 21
6	November 28 to December 5	November 28 to December 5
7	February 27 to March 9 (2017)	-

Table 2. Results of model evaluation. Ephemeroptera and Trichoptera models were exponential decay models with increasing distance from the stream. The Chironomidae model was an alternate exponential model. Bold text indicates the results of the best models (i.e. lowest Watanabe-Akaike information criterion or *WAIC*).

Taxon	**Hierarchy level**	**WAIC**
Ephemeroptera	None	761
	Site	**728**
	Date	752
	Site & Date	740
Trichoptera	None	913
	Site	**886**
	Date	905
	Site & Date	892
Chironomidae	None	5072
	Site	4949
	Date	4784
	Site & Date	**4373**

Figure 1. Photographs of (a) sticky traps set up from the streambank to a cereal field and across the grass strip, (b) sticky traps lined up perpendicular to the stream and (c) an emergence tent set up in the stream.

Figure 2. Estimate of annual emerging dry mass (in g m^{-2}) of aquatic insects at each site. The estimate for the Ormal site is missing because one sampling session (in autumn) could not be performed due to farm operations.

Figure 3. Log-transformed abundance of insects of three taxonomic groups captured on sticky traps at each site (sum of all dates and distances from the stream)

Figure 4. Decaying dispersal functions for (a) Trichoptera by site, (b) Ephemeroptera by site and (c) Chironomidae by site/campaign combination

Figure 5. Estimates of total aquatic insect dry mass (sum of biomass of Chironomidae, Ephemeroptera and Trichoptera) deposited on land 1-100 m from the stream edge, in kg DM ha^{-1} yr^{-1}. Percentages indicate the percentage of total deposition from 0-10 m, 10-50 m and 50-100 m. The boxplot at each distance shows inter-site variation in median deposition estimated using Bayesian posterior distribution of parameters.

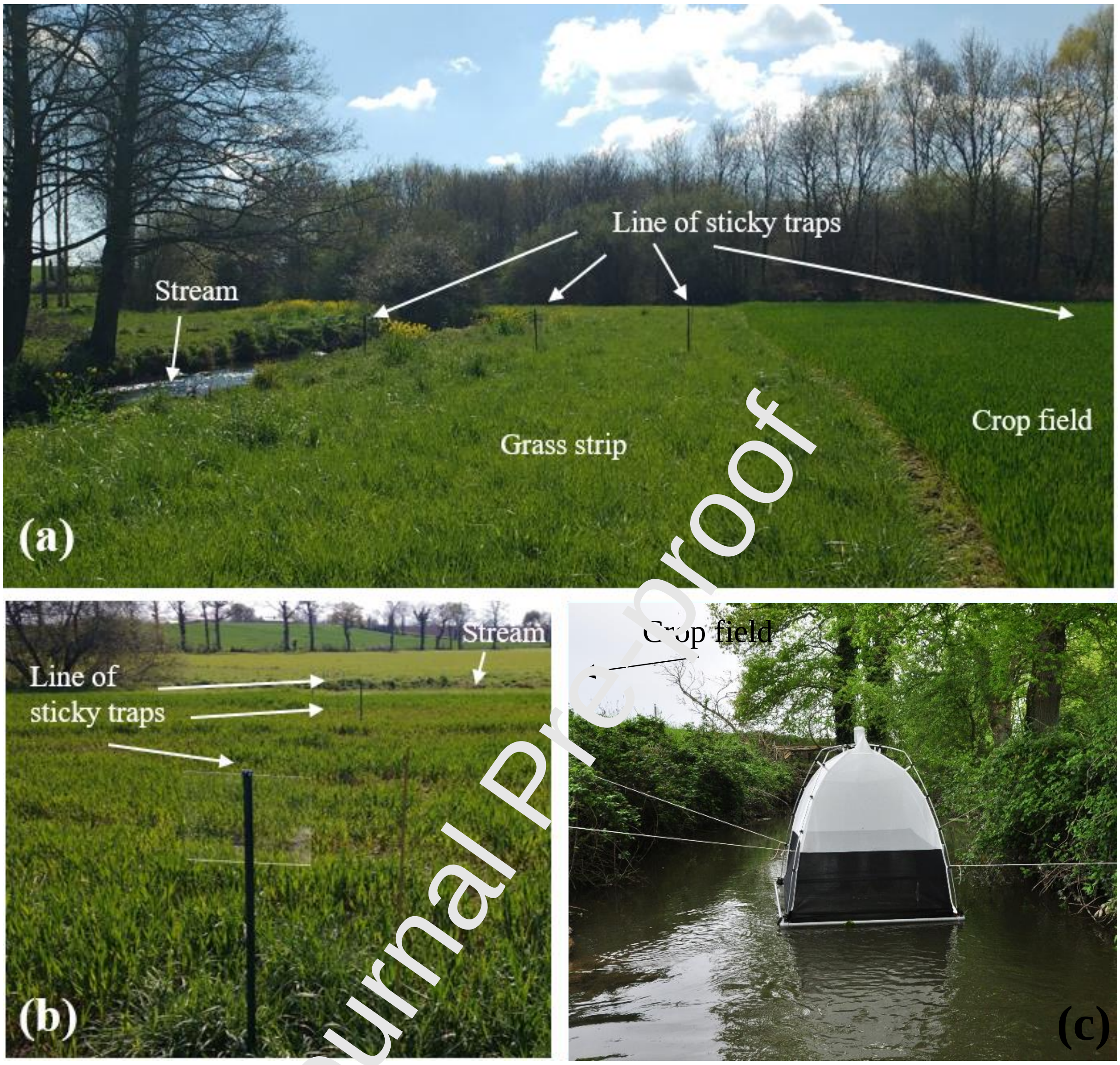

Line of sticky traps
Stream
Grass strip
Crop field
(a)
Line of
sticky traps
Stream
(b)
Crop field
(c)

Figure 1

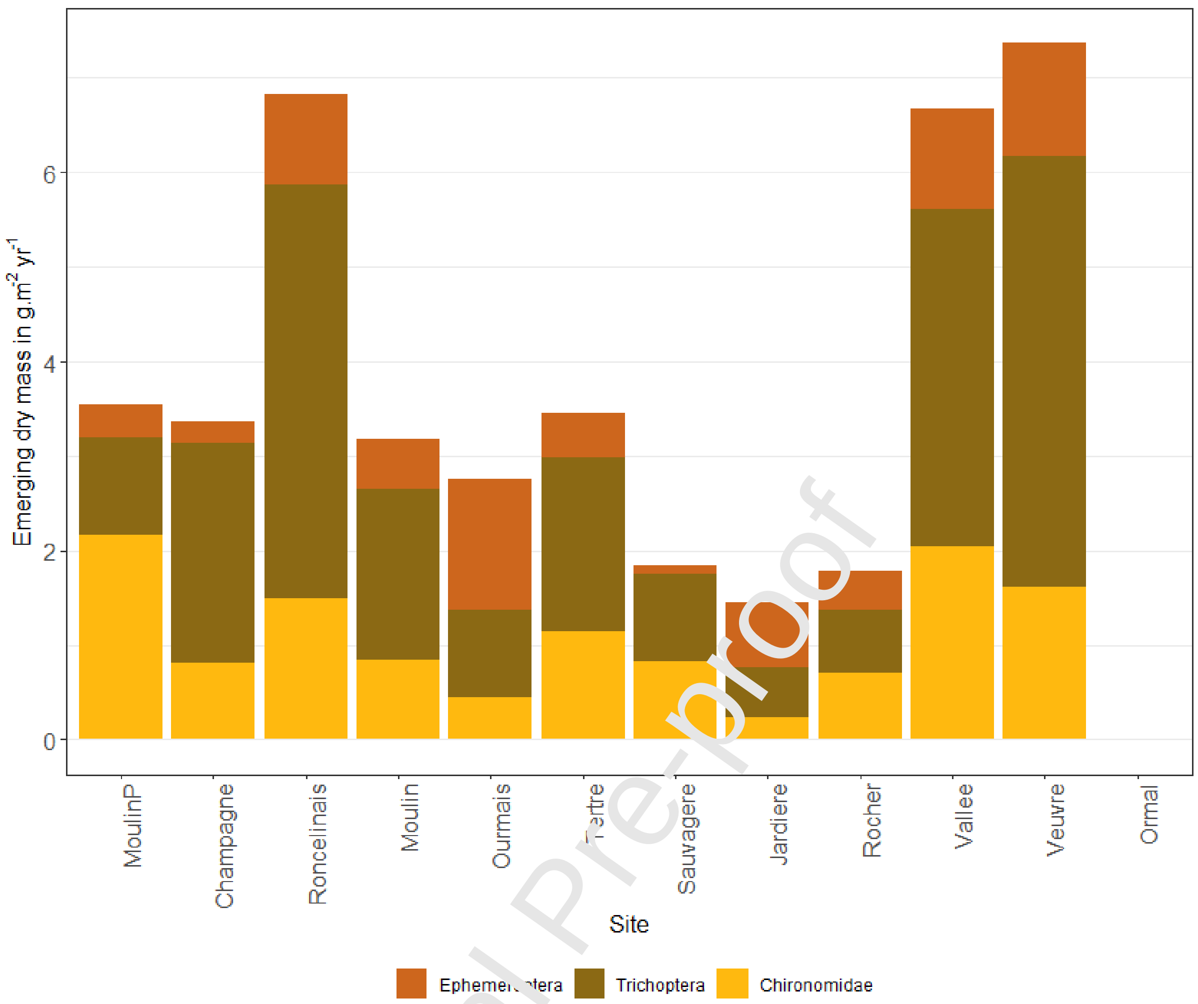

Emerging dry mass in g.m^{-2} yr^{-1}
0
2
4
6
MoulinP
Champagne
Roncelinais
Moulin
Ourmais
Tertre
Sauvagere
Jardiere
Rocher
Vallee
Veuvre
Ormal
Site
Ephemeroptera
Trichoptera
Chironomidae

Figure 2

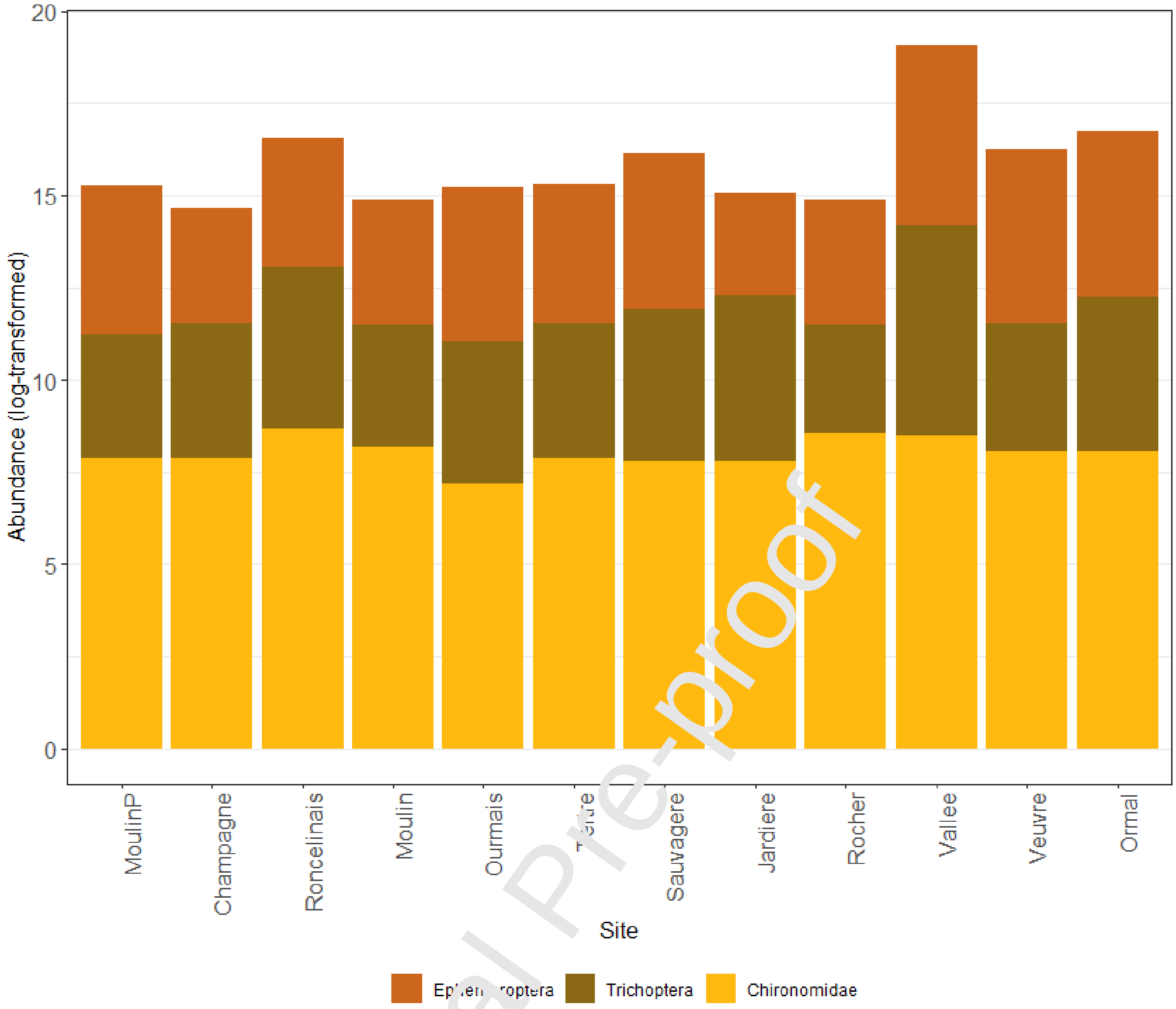

20
15
10
5
0
Abundance (log-transformed)
MoulinP
Champagne
Roncelinais
Moulin
Ourmais
Terre
Sauvagere
Jardiere
Rocher
Vallee
Veuvre
Ormal
Site
Ephemeroptera
Trichoptera
Chironomidae

Figure 3

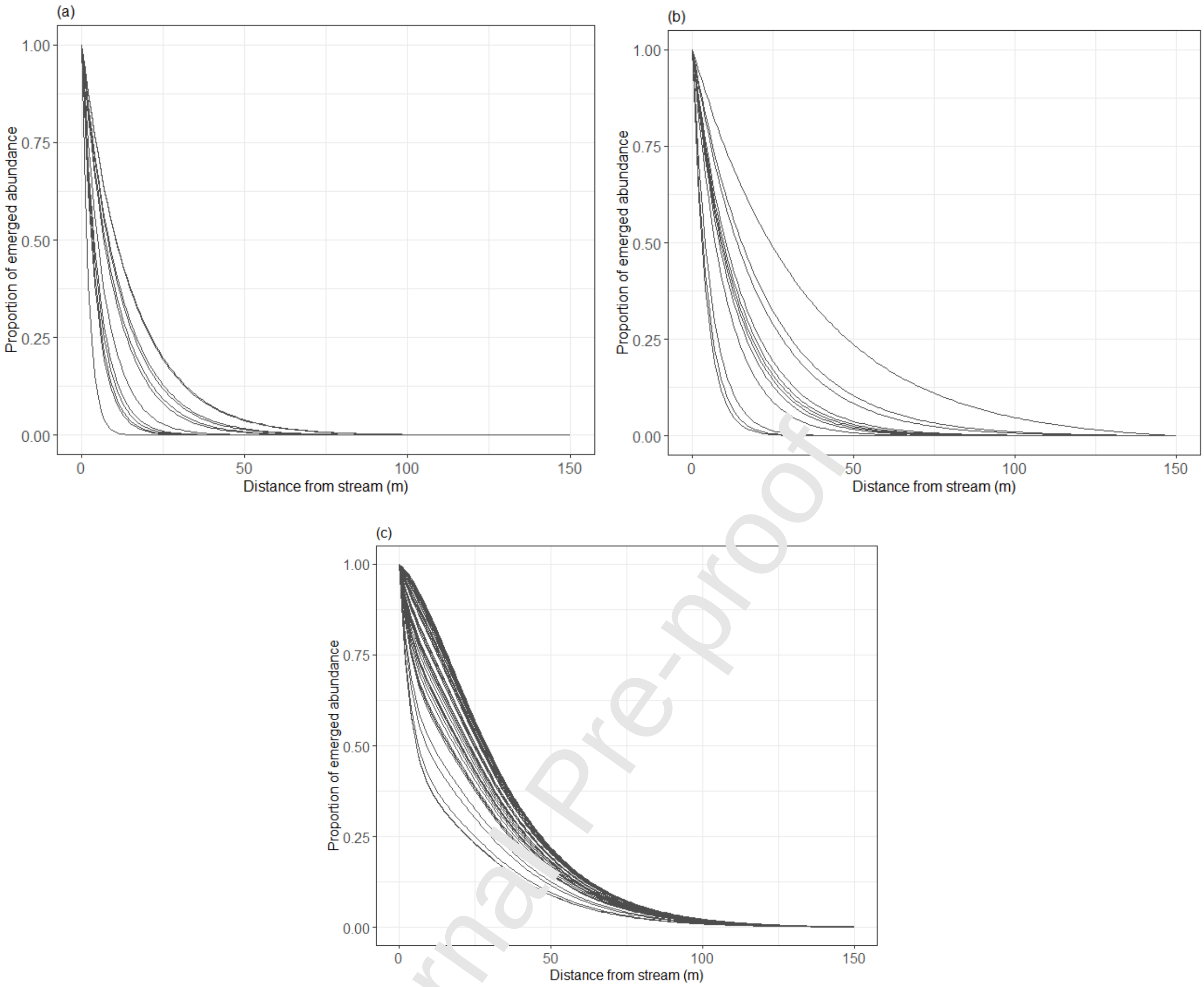

(a)
Proportion of emerged abundance
1.00
0.75
0.50
0.25
0.00
0
50
100
150
Distance from stream (m)
(b)
Proportion of emerged abundance
1.00
0.75
0.50
0.25
0.00
0
50
100
150
Distance from stream (m)
(c)
Proportion of emerged abundance
1.00
0.75
0.50
0.25
0.00
0
50
100
150
Distance from stream (m)

Figure 4

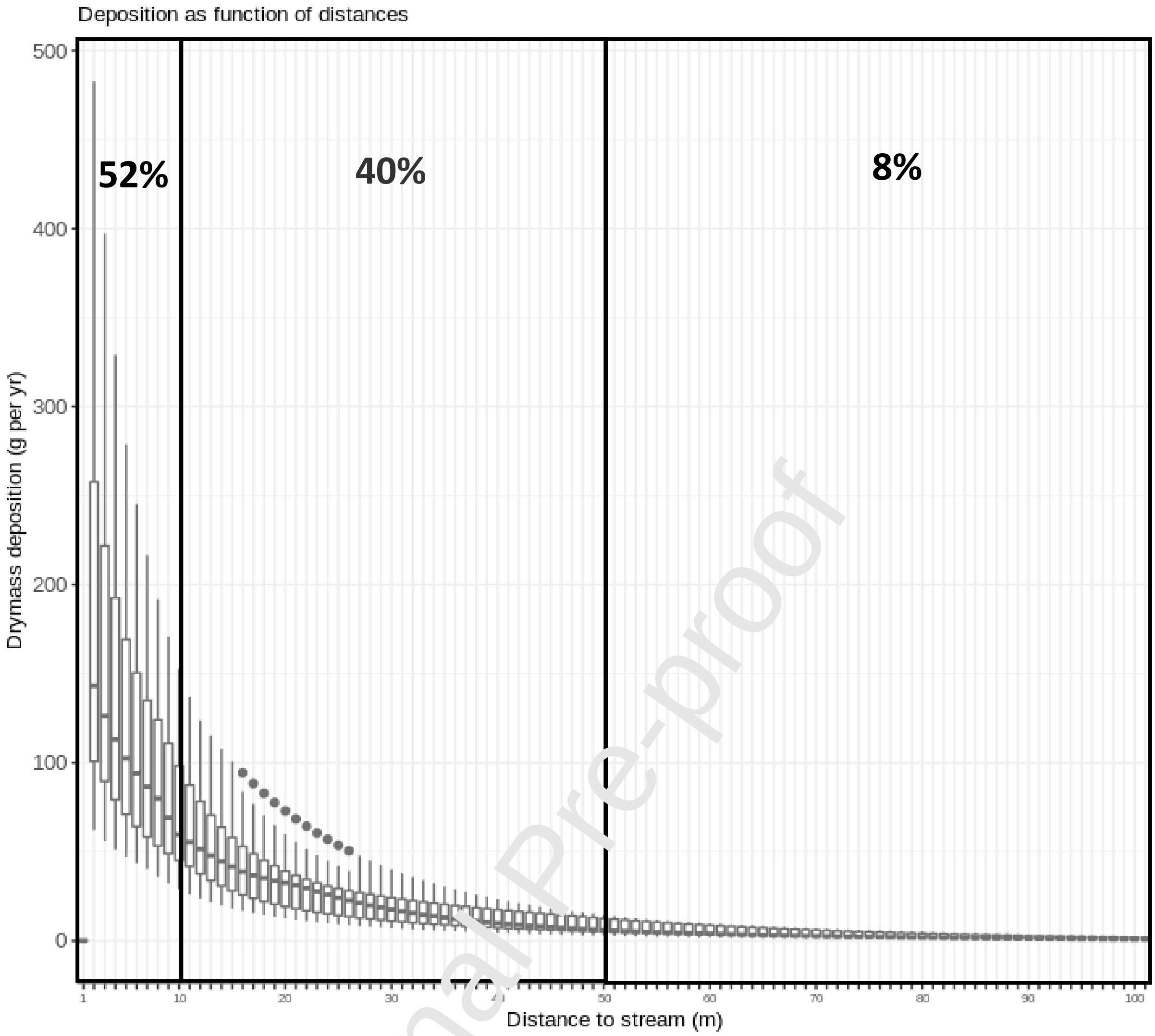

Deposition as function of distances
52%
40%
8%
Drymass deposition (g per yr)
0
100
200
300
400
500
Distance to stream (m)
1
10
20
30
40
50
60
70
80
90
100

Figure 5

Credit authorship contribution statement

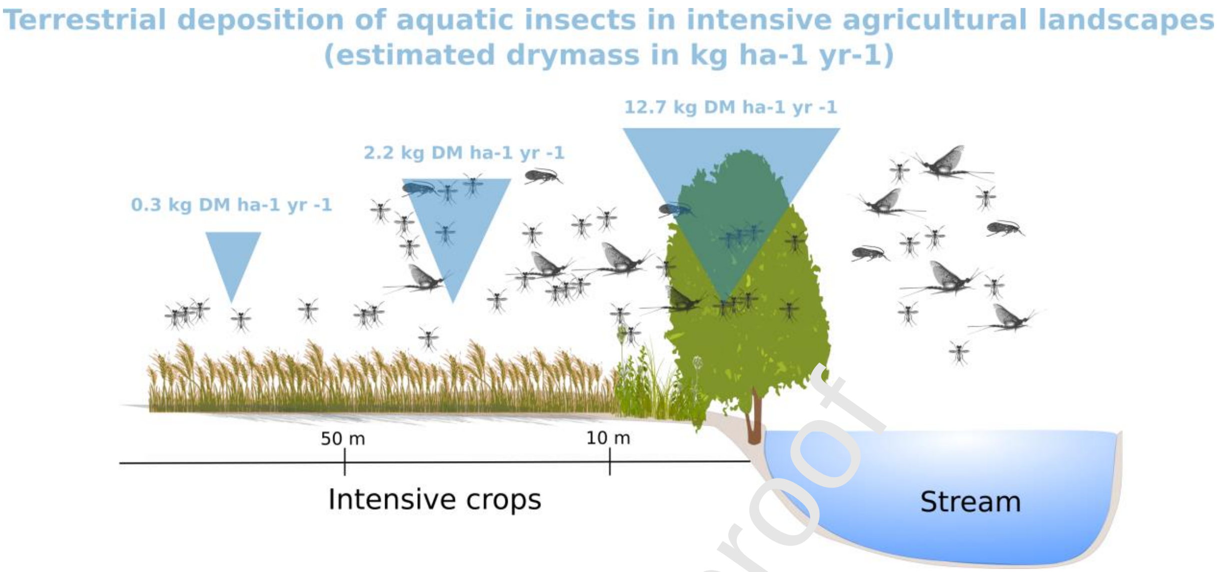
JMR, MP, JR conceived the study. JR conducted fieldwork and laboratory analysis. JR analysed data with contributions from MO and MP. JR wrote the manuscript with input and revision of all contributing authors.

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Graphical abstract



Highlights

- We show that aquatic insects dispersed farther in agricultural than forest streams
- 12.5 kg ha^{-1} yr^{-1} of winged aquatic insect drymass fell at 0-10 m from stream
- Ephemeroptera and Trichoptera are dominant at the stream vicinity
- 50% of emerging Chironomidae dispersed farther than 25 m inland
- Such aquatic insect deposition on land could influence the terrestrial food web