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RESEARCH ARTICLE

Land use changes biomass and temporal patterns of insect cross-ecosystem flows

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Abstract

Emergent aquatic insects constitute an important food source for higher trophic levels, linking aquatic to terrestrial ecosystems. Little is known about how land use affects the biomass or composition of insect emergence. Previous studies are limited to individual time points or seasons, hampering understanding of annual biomass export patterns and detection of phenological changes. Over 1 year's primary emergence period, we continuously determined the biomass, abundance, and identity of >45,000 aquatic insects and recorded land-use-related environmental variables in 20 stream sites using a paired design with upstream forested sites and downstream agricultural sites. Total insect biomass and abundance were 2–7 mg day^{-1} m^{-2} and 7–36 ind day^{-1} m^{-2} higher in agricultural than forested sites. However, we found turnover of families between forested and agricultural sites, with more insects with shorter generation time in agriculture, indicating lower sensitivity to land-use-related stress because of higher recovery potential. Except for stoneflies, biomass and abundance of major orders were higher in agriculture, but their phenology differed. For different orders, emergence peaked 30 days earlier to 51 days later in agriculture than forest, whereas total abundance and biomass both peaked earlier in agriculture: 3–5 and 3–19 days, respectively. The most important land-use-related drivers were pesticide toxicity and electrical conductivity, which were differentially associated with different aquatic insect order abundances and biomass. Overall, we found that land use was related to changes in composition and phenology of aquatic insect emergence, which is likely to affect food-web dynamics in a cross-ecosystem context.

KEYWORDS
abundance, aquatic insects, biomass, land use, phenology, turnover

1 | INTRODUCTION

Intensive agriculture is a globally dominant land use (Václavík et al., 2013). The intensification of agriculture is accompanied by increased pesticide and nutrient use, as well as habitat degradation (Fischer et al., 2012; Stoate et al., 2001). Stream ecosystems in agricultural areas are affected by toxicants, excessive nutrient inputs, and habitat degradation, for example the loss of riparian vegetation and channelization, which threatens biodiversity and human water security (Collen et al., 2014; Dudgeon et al., 2006; Vörösmarty et al., 2010).

Stream ecosystems and their adjacent terrestrial ecosystems are tightly linked via the flux of matter and organisms (Baxter et al., 2005). Aquatic insects like Diptera (flies), Ephemeroptera (mayflies), Plecoptera (stoneflies), and Trichoptera (caddisflies) emerge from water bodies to live as adults in terrestrial ecosystems, where they serve as prey for riparian predators, such as spiders, bats, and birds (Gray, 1993; Kato et al., 2004; Sullivan et al., 1993). Only <1%–3% of these insects return to streams (Gray, 1989; Jackson & Fisher, 1986). Especially in agricultural regions, riparian predators consuming a broad range of prey including terrestrial insects can benefit from aquatic insects (Graf et al., 2020; Krell et al., 2015; Murakami & Nakano, 2002; Nakano & Murakami, 2001; Stenroth et al., 2015) because agriculture is associated with the loss of terrestrial insects (Ewald et al., 2015; Hallmann et al., 2017; Seibold et al., 2019; Shortall et al., 2009). Insect decline can adversely affect ecosystems and their services because insects play an important role in food webs and provide ecosystem services like pollination and pest control (Kawahara et al., 2021; Raitif et al., 2019; Wagner, 2020).

Riparian predators are dependent on the nutritional quality, biomass, and composition of aquatic insects. Aquatic insects constitute a high-quality food because they contain up to 10 times higher levels of long-chain polyunsaturated fatty acids (PUFA) than terrestrial insects (Hixson et al., 2015), which promote growth and immune function (Fritz et al., 2017; Twining et al., 2016). The choice of prey depends amongst others on taxon-specific traits, including aquatic insect species size (Davis et al., 2011; Stenroth et al., 2015). Typically, predators consume prey of one to four orders of magnitude smaller than themselves (Brown et al., 2004; Cohen et al., 2003; Jonsson et al., 2005; Woodward & Hildrew, 2002). Thus, the biomass of major insect orders indicates which predators may benefit most from their emergence.

Emergence of different aquatic insect species varies over time and exhibits seasonal patterns (Nakano & Murakami, 2001), which affects population dynamics in the linked terrestrial system. The timing of emergence controls the growth rate (Sato et al., 2016; Uno, 2016), population biomass, and maturity rate of predators (Sato et al., 2016). In turn, emergence timing depends on the composition of aquatic insects because individual species exhibit differences in phenology. Complementary phenology between species contributes to temporal stability of emergence (Uno & Pneh, 2020), improving foraging opportunities for predators (Armstrong et al., 2016).

Furthermore, the trait distribution in insect assemblages can indicate responses to land use (Berger et al., 2018; Mondy et al., 2012). For instance, a short generation time translates to faster recovery and, therefore, insect assemblages with a high fraction of taxa with a short generation time may be associated with recent stress events in a habitat patch (Sherratt et al., 1999; Stark et al., 2004) also in agricultural streams (Liess & von der Ohe, 2005). Better understanding the links between land use, such as intensive agriculture, and distributions of functional traits in aquatic insect assemblages may improve mechanistic understanding of species–environment relationships (Kearney & Porter, 2009).

Studies investigating how agriculture influences the phenology, composition, and biomass of emergent aquatic insects are scarce. The major orders of emergent aquatic insects, mayflies, stoneflies, and caddisflies (EPT), are among the least studied taxa, whereas flies, mostly mosquitos, have been studied more often (InsectGapMap, 2020). Limited research, however, has shown changes in aquatic insect assemblages linked to agriculture. A recent meta-analysis suggested an increasing trend in total biomass and abundance of aquatic insects over the last decades, particularly in agricultural regions (van Klink et al., 2020), though contrasting temporal trends have been reported for several aquatic insect orders (Baranov et al., 2020; Outhwaite et al., 2020; Stepanian et al., 2020), and total abundance and biomass are poor indicators of compositional changes (Desquilbet et al., 2020; Jähnig et al., 2021). However, agriculture can alter aquatic insect assemblage composition, for instance, by favouring small-bodied insects like flies (Carlson et al., 2016; Krell et al., 2015; Stenroth et al., 2015) and shorter life cycle because their high reproduction rate can make them less prone to agricultural stress (Larsen & Ormerod, 2010; Liess & von der Ohe, 2005). In addition, agricultural pesticide use has been associated with the loss of up to 42% of aquatic invertebrate richness (including insects; Beketov et al., 2013).

Notwithstanding, agriculture can increase the biomass of aquatic insects because it is associated with elevated nutrient concentrations and reduced shading. Both can increase primary production and, in turn, food sources for aquatic insects in agricultural streams (Carlson et al., 2016; Griffiths et al., 2013; Stenroth et al., 2015; Terui et al., 2018). Furthermore, channelization typically results in increased proportion of pool habitats (Petersen Jr, 1992), where the total abundance of aquatic insects can be lower than in riffle habitats, while the abundance of single insect orders can respond differently (Carlson et al., 2013; McKie et al., 2018). Recent studies on the effects of land use on aquatic insects were limited to few weeks (Graf et al., 2020; Krell et al., 2015; Stenroth et al., 2015) and random snap-shot samples in different seasons (Carlson et al., 2016; Raitif et al., 2018). Given the high temporal variability in emergence, this limited data hampered the estimation of complete balances of biomass transfer to riparian ecosystems.

In this study, we therefore continuously collected data over the primary emergence period within 1 year (from March until September 2018; Corbet, 1964) to assess differences in the biomass, abundance, and composition of aquatic insects between paired forested and agricultural sites, as well as phenological patterns in each of these factors. In addition, we monitored the hydromorphological structure and water quality to assess the associations of specific environmental variables with aquatic insect assemblages.

With these data, we (i) compared total biomass (ia) and abundance (ib), as well as aquatic insect phenology, between agricultural and forested sites, (ii) studied the taxonomic and trait composition of aquatic insect assemblages, as well as their turnover, associated with land-use types, and (iii) identified land-use-related drivers associated with biomass, abundance, and composition of assemblages.

2 | MATERIALS AND METHODS

2.1 | Study sites

We studied 20 sites in 10 parallel streams, which were a maximum of 50 km apart, in southwestern Germany from March to September 2018. The study period covered the primary emergence period of 1 year (Corbet, 1964). We used a paired design, where each stream had an upstream forested site and a downstream site where agricultural land use dominated (Figure S1). The mean (range) distance between sites within a stream was 6.8 (1.6–27.0) km. Sites were preselected with GIS analysis to ensure similar catchment size, discharge, and proportion of agriculture at downstream sites. Moreover, all sites were selected to be largely free from the influence of point-source pollution from wastewater treatment plants and industrial facilities. The preselected sites were then surveyed in person to ensure that all sampling devices could be deployed in the streams.

Although agricultural land use mainly consisted of viticulture, a previous study in this region showed that environmental parameters and ecosystem function (i.e., organic matter decomposition) were similar between viticultural sites and sites with other agricultural crops (e.g. corn, wheat; Voß et al., 2015).

All study sites were similar in stream size. The mean (range) depth and maximum width of the streams in forested sites were 0.11 (0.03–0.26) and 1.83 (0.68–4.00) m, respectively. In agricultural sites, the mean depth was 0.20 (0.04–0.49) m and the maximum mean width was 1.98 (0.60–4.50) m. All streams were mostly small and fine substrate-dominated siliceous highland streams originating in the Palatinate Forest Nature Park, a forested low mountain range. Therefore, climate and geology were similar across streams. Forested streams exhibited fewer pool habitats (27 [10–80]%) than agricultural streams (44 [10–100]%) and more shading (73 [30–100]%) than streams in agriculture (62 [5–95]%).

2.2 | Land-use-related drivers of aquatic insects

TABLE 1 Mean and range of land-use-related drivers of aquatic insects used in the data analysis. All drivers recorded during the experiment are reported in Table S12

Land-use-related driver (unit)	Forest: mean (range)	Agriculture: mean (range)
Electrical conductivity (μS cm^{-1})[a]	191.8 (92.6–381)	462.2 (178.8–1899)
Nitrate (mg L^{-1})[b]	1.8 (0.5–5.1)	2.1 (1–5.3)
Oxygen saturation (%)[a]	96.6 (65.6–126.8)	91.9 (63.9–108.5)
Pesticide toxicity (maximum sumTU)[c]	−5.4 (−7.0–[−0.5])	−1.1 (−3.4–0.6)
Phosphate (mg L^{-1})[b]	0.7 (0.2–1.8)	0.7 (0.2–1.5)
Water temperature (°C)[a]	12.6 (9.4–16.6)	14.6 (11.4–18.2)
Pools (%)	27 (10–80)	44.2 (10–100)
Shading (%)	73 (30–100)	61.8 (5–95)

[a] Multi 340i, WTW Germany, was used for measurement.

[b] Compact-photometer PF-12 with visocolor, Macherey–Nagel, was used for measurement.

[c] Maximum of logarithmic sum of toxic unit for the most sensitive freshwater invertebrate species.

To identify land-use-related drivers associated with total abundance, total biomass, as well as abundance and biomass of major orders of emergent aquatic insects and for the number of EPT families, we recorded physicochemical variables as single measurements every 3 weeks over the entire study period (22 March–13 September 2018). These variables included water temperature, electrical conductivity (EC), oxygen saturation, phosphate, and nitrate concentration (Table 1). We recorded the hydromorphological structure, including the percentage of shading and percentage of pool habitat, in March, July, and August to capture changes throughout the study period (Table 1). These variables were chosen a priori because they are known to affect aquatic insect biomass and abundance (Graf et al., 2020; Raitif et al., 2018; Stenroth et al., 2015).

We also collected data on pesticide toxicity. In streams, pesticides were sampled every 3 weeks (grab samples) and during heavy rainfall events (event samples). Event samples were taken by automated samplers (MAXX TP5) and glass bottle samplers (Liess & von der Ohe, 2005) when the water level rose more than 5 cm. Further details on pesticide sampling, analytics, and exposure are provided in Halbach et al. (2021) and Liess et al. (2021). Additionally, the pesticide concentration on suspended particles was analyzed in event samples because pyrethroids regularly enter streams bound on particles (Gan et al., 2005). Furthermore, pyrethroids exhibit high relative toxicity for aquatic insects (Rico & den Brink, 2015; Rubach et al., 2010).

The particle-associated concentration was converted into an estimate of the bioavailable concentration in water c_d following Schäfer et al. (2011) and Toro et al. (1991) using the following equation:

$$c_d = \frac{c_{\text{tot}}}{f_{\text{oc}} \cdot k_{\text{oc}} + 1}, \tag{1}$$

where c_{tot} is the total concentration on the suspended particles, f_{oc} the fraction of organic carbon in the sample, and k_{oc} the soil organic carbon-water partitioning coefficient. The k_{oc} values were taken from the Pesticide Property DataBase (PPDB; Lewis et al., 2016) or the PubChem database (National Center for Biotechnology Information, 2021) (Table S1).

The toxicity of single pesticides at different concentrations was calculated using toxic units (*TU*):

$$TU = \frac{c_i}{EC_{50i}}, \tag{2}$$

where c_i is the concentration of the single pesticide, and EC_{50i} the acute effect concentration of the single pesticide towards the most sensitive freshwater invertebrate species. The toxicity of the detected pesticide mixtures was estimated using the logarithmic sum of the TU (*sumTU*) (Schäfer et al., 2013):

$$sumTU = \log \sum_{i=1}^{n} TU_i, \tag{3}$$

where *n* is the number of pesticides and TU_i the *TU* of the single pesticide. This measure has proven successful in linking toxicity and community response (Schäfer et al., 2013). The EC_{50} values were compiled from the ECOTOX database (US EPA, 2021) using the R package Standartox (version 0.0.1, Scharmüller et al., 2020). In case of missing EC_{50} values in Standartox, the values were retrieved from the PPDB (Lewis et al., 2016) or Malaj et al. (2014) (Table S2). To estimate the maximum pesticide pollution, which may be responsible for the strongest ecological response, we used the maximum *sumTU* (hereafter, pesticide toxicity) of all samplings per site and season in the analysis. *MaximumTU*, which is the *TU* of the most toxic substance in a pesticide mixture, was similar to maximum *sumTU* (Figure S2).

2.3 | Insect sampling

Aquatic insects were sampled continuously with emergence traps (basal area 0.25 m^2) as described in Cadmus et al. (Cadmus et al., 2016). At every site, two traps, each with a bottle trap without any solution, were installed in the middle of the stream, covering riffle and pool habitats. The traps were emptied twice per week by exchanging the bottle trap, which was transported on ice until the insects were euthanized in liquid nitrogen and identified in the laboratory. Insects were identified to at least the family level under a stereo microscope using the following keys: Bährmann and Müller (2015), Nilsson (1996a, 1996b); Schäfer and Brohmer (2010). Then, they were lyophilized to complete dryness and weighed to the nearest 0.1 µg. Heavy rainfall events and vandalism led to 51 traps lost in forest and 112 traps lost in agriculture (Table S3). On the whole, 45,831 specimens were identified from 1847 samples collected, 943 in forested sites, and 904 in agricultural sites, which corresponds to a difference of 4%. The loss of traps resulted in unequal numbers of samples per site and sampling date. Furthermore, the number of collection days differed occasionally between samples. Thus, the abundance and biomass of every sample were standardized per area of the trap and the number of collection days.

2.4 | Data analysis

To identify seasonal patterns of biomass and abundance of aquatic insects, hierarchical generalized additive models (HGAMs) were used following the approach of Pedersen et al. (2019). The data per sample were used for total biomass as well as abundance as response, the data per sample and order were used for the biomass and abundance at order level as response and the data per sample and family were used for the biomass and abundance at family level as response. If samples were missing, the mean per month and site was used to correct for missing samples. Briefly, the data were modelled with group-level smoothers for land use, land use crossed with order, as well as land use crossed with family, but without a global smoother (i.e. each group can be differently shaped without restriction). HGAMs fitted with group-level smoothers having the same wiggliness (model S) yielded lower Bayesian Information Criterion (BIC, Table S4) than HGAMs with different wiggliness for each group-level (model I). The latter incorporated one smoothing parameter for every group level, whereas model S included one smoothing parameter for all group levels. Stream was included as a random effect smoother. The R-package mgcv (version 1.8-36, Wood, 2011) was used to fit HGAMs. To quantify the effect of land use, the difference between the mean fit (mean at one time point) for agriculture and forest was calculated, along with the 95% confidence interval. Non-overlapping confidence intervals were considered statistically significant at alpha = 0.05. The average export per area in both land-use types of total biomass and abundance over the whole sampling period was estimated from the mean fits of total abundance and total biomass HGAMs.

To identify the environmental variables that explained the most variation between land-use types in the biomass and abundance of aquatic insects in total and per order, and for the number of EPT families, (generalized) linear mixed-effects models ((G)LMM) were used. LMMs were used for the biomass as well as abundance data, while a GLMM with Poisson distribution was applied for the number of EPT families. EPT families are sensitive towards land-use-related drivers (Raitif et al., 2018; Stenroth et al., 2015); therefore, the number of EPT families was used as an indicator of ecological quality. Given that environmental variables had lower temporal resolution than aquatic insect data, the sample size was too low to fit HGAMs. To account for the mismatch in temporal resolution, the mean per season and site was calculated for abundance, biomass, and potential land-use-related drivers. Additionally, biomass and abundance data were log-transformed to improve normality, which was checked visually using *Q*–*Q* plots, by (ln [*x* +a]), where *a* represents the minimum value >0 detectable for this variable. The number of EPT families was summed per site and season. Stream and season were incorporated as random effects. The land-use-related drivers toxicity, pools, EC, shading, oxygen saturation, and concentrations of nitrate and phosphate were standardized and used as fixed factors in the GLMMs. Variable selection was performed using the L1-penalty to identify the best-fit model with the R-package GLMMLASSO (version 1.5.1; Groll & Tutz, 2014). The L1-penalty conducts variable selection and shrinkage concurrently. This method is appropriate for our data because environmental variables were not collinear and the shrinkage reduces variance in predictions. The variance explained by the fixed factors (R^2_{marginal}), the complete model ($R^2_{\text{conditional}}$), and the random factors (adjusted intra-class correlation; ICC stream and season) were estimated (Nakagawa & Schielzeth, 2013; Nakagawa et al., 2017). To compare the number of all families and EPT families between forested and agricultural sites, a GLMM using land-use type as a fixed factor and stream and season as random factors was fitted with the R-package GLMMTMB (version 1.1.2.3; Brooks et al., 2017).

To estimate the turnover of aquatic insects, we used the Jaccard index (JI) on the presence-absence data of families per site, which is commonly used to assess compositional similarities of assemblages (Chao et al., 2005). JI calculates the proportion of taxa two sites share:

$$\mathrm{JI} = \frac{j}{a + b - j}, \tag{3}$$

where j is the number of taxa found in both sites A and B, and a and b the total number of taxa in site A and B, respectively. If both sites do not share any taxon, JI = 0, and if both sites share identical taxa, JI = 1. The differences in JI between forested and agricultural sites were analyzed with analysis of similarity (ANOSIM; 999 of permutations), which is a fully non-parametric test and robust regarding paired samples (Clarke, 1993). The results of the ANOSIM were visualized with non-metric multidimensional scaling (JI, four dimensions which resulted in optimal stress values).

Finally, the traits generation time and size of aquatic insects were compared between forested and agricultural sites with a paired *t*-test. The normal distribution of differences between paired samples was checked visually with *Q*–*Q* plots and for outliers with violin plots. Families of aquatic insects with a generation time ≥0.5 year^{-1} were classified as sensitive because of their slow recovery potential (Sherratt et al., 1999; Stark et al., 2004). Generation time was extracted from the Indicate trait database (Department System Ecotoxicology—Helmholtz Centre for Environmental Research UFZ, 2021). The size of aquatic insects, retrieved from Tachet et al. (2010), is an indicator of which predators may benefit most from aquatic insects present for additional food source because of their preference for prey of up to three magnitudes smaller than themselves (Cohen et al., 2003). Families were assigned to three size classes: small (0.25 cm < size ≤1.0 cm), medium (1.0 cm < size ≤2.0 cm) and large (2.0 cm < size ≤8.0 cm). For both traits, the ratio of biomass per size or generation time was calculated because biomass is important to understand energy flow, productivity, and food-web dynamics (Brown et al., 2004). All statistical analyses were performed with the statistical software R (version 4.0.2; R Core Team, 2020) and the code and all data are available on a Github repository: https://doi.org/10.5281/zenodo.7123465 (Ohler et al., 2022).

3 | RESULTS

3.1 | (ia) Higher total biomass in agriculture than forest

During our study period, more biomass was exported per area in agricultural sites than in forest sites (95% confidence interval: 0.106–0.124 and 0.066–0.074 kg m^{-2}, respectively). The temporal pattern in total emerging biomass also differed between agricultural and forest sites (hierarchical generalized additive model: HGAM, Tables S4 and S5). For example, the highest biomass in summer (17 May–26 July) was reached 20 days earlier in agriculture than in forest. At the beginning of spring (22 March–16 May), total biomass in agricultural sites was 1 $\text{mg day}^{-1}\ \text{m}^{-2}$ higher than in the forest sites (Figure 1a and Figure S3a,b). This difference was significant (i.e. non-overlapping 95% confidence intervals at alpha = 0.05) and increased to 7 $\text{mg day}^{-1}\ \text{m}^{-2}$ until mid-spring where the maximum in both land-use types occurred: 13 (±6) mg $\text{day}^{-1}\ \text{m}^{-2}$ in agricultural sites (mean fit HGAM ±2 standard errors) and 6 (±3) $\text{mg day}^{-1}\ \text{m}^{-2}$ in forest sites. Total biomass was similar at the beginning of summer (~5 $\text{mg day}^{-1}\ \text{m}^{-2}$) and in autumn (27 July–13 September, ~3 mg $\text{day}^{-1}\ \text{m}^{-2}$), with a period in between where at agricultural sites biomass was significantly higher (difference from 3 to 4 mg $\text{day}^{-1}\ \text{m}^{-2}$).

3.2 | (ib) Higher total abundance in agriculture than forest

Nearly twice as many individuals emerged in agricultural than in forest sites (95% confidence interval: 431,383–510,017 and 241,499–274,701 ind m^{-2}, respectively). The temporal patterns of total abundance differed between land-use types (HGAM, Tables S4 and S5, Figure 1b and Figure S3c,d), but were more similar than for total biomass. The mean fit of total abundance was significantly different between agriculture and forest from spring to the end of summer (range of difference: 7–36 $\text{ind day}^{-1}\ \text{m}^{-2}$) and, as with total biomass, converged to a similar pattern in autumn. During spring, the peak in forest total abundance was more pronounced than in forest total biomass, but at 24 (±9) ind $\text{day}^{-1}\ \text{m}^{-2}$, it was only approximately one third as high as in agriculture (59 [±21] ind $\text{day}^{-1}\ \text{m}^{-2}$). During summer, the difference between agriculture and forest was smaller, ranging from 9 to 17 ind $\text{day}^{-1}\ \text{m}^{-2}$.

3.3 | (ii) Turnover and temporal patterns in composition

The number of all families (generalized linear mixed-effects models; GLMM, $p = 0.12$) and EPT families (GLMM, $p = 0.14$) were similar between forested and agricultural sites (Table S6, Figure S4), but a turnover in the composition of insect families from forest to agriculture was found (analysis of similarity: ANOSIM, $R = 0.31$, $p = 0.001$, Figure S5). A moderate increase close to statistical significance of families with a shorter generation time (paired *t*-test, $p = 0.08$, Cohen's $d = 0.62$, Table S7, Figure S6) was observed in agricultural sites, but there were no size differences observed between land-use types (Table S7, Figure S7).

The biomass and abundance of all major orders of emergent aquatic insects, that is, flies, mayflies, stoneflies, and caddisflies, exhibited significant differences between land-use types in spring and summer. Stonefly and mayfly biomass and abundance, as well

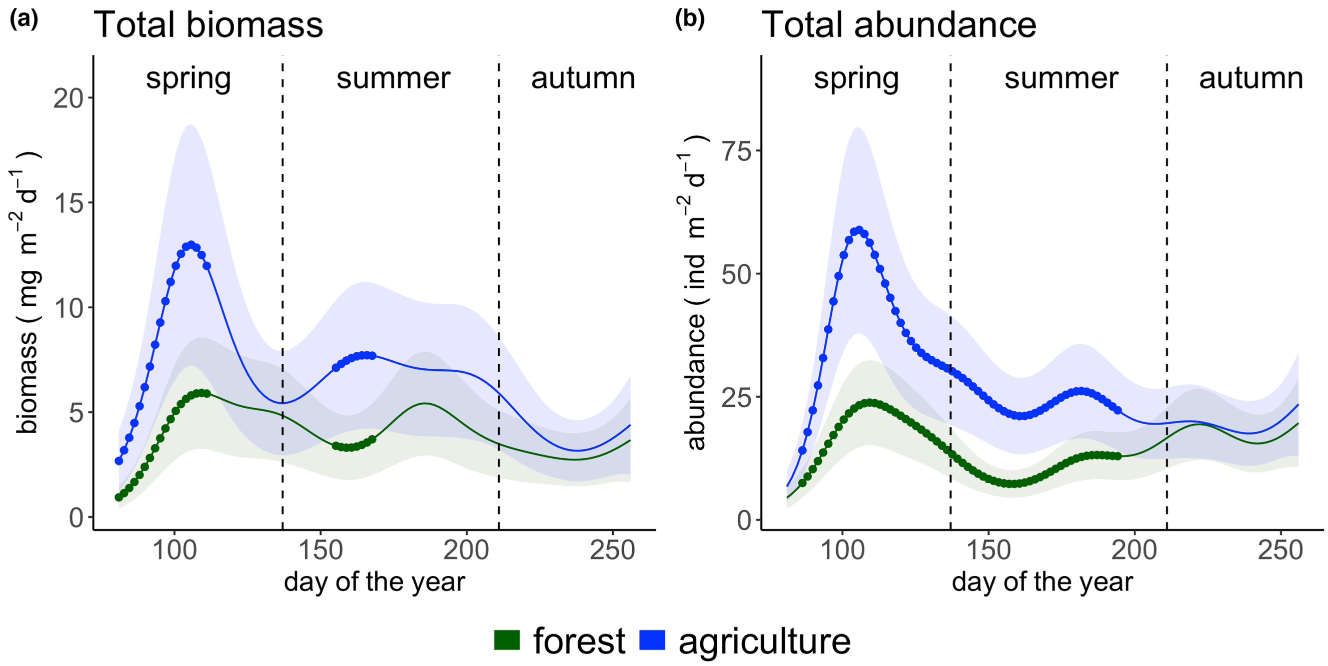

FIGURE 1 Predicted seasonal patterns (spring: 22 March–16 May, summer: 17 May–26 July, autumn: 27 July–13 September) of aquatic insects derived with hierarchical generalized additive models (HGAMs) fitted with 1911 observations. The solid line shows the predicted mean fit values of the HGAM, and the ribbon indicates ±2 standard errors around the mean fit. Dots mark significant differences with non-overlapping 95% confidence intervals at alpha = 0.05 between agriculture and forest. Green represents the pattern in forest and blue in agriculture for (a) total biomass and (b) total abundance

as caddisfly abundance, also differed between land-use types in autumn (Figures 2 and 3), though the difference for stoneflies was much smaller than for the other orders. Except for stoneflies, biomass and abundance were both higher in agricultural sites.

The temporal patterns of fly abundance were similar in both land-use types (Figure 3a) but differed for biomass (Figure 2a). Fly biomass peaked during spring at 8 (±2) mg day^{-1} m^{-2} in agriculture before declining drastically for the remainder of the study, whereas biomass reached a maximum at 2 (±1) mg day^{-1} m^{-2} in forest sites, then declined slightly until mid-summer. During summer, fly biomass peaked 30 days earlier in agriculture than in forest (Table S8). Over the whole sampling period, the same number of fly families was found in forested and agricultural sites, but their phenology differed between land-use types (Figures S8, S9; Table S9). For instance, the biomass maximum of drain flies (Psychodidae) occurred 76 days earlier in agriculture than in forest (Table S9).

The biomass of mayflies peaked in spring at the same time between land uses, with 5 (±2) and 2 (±1) mg day^{-1} m^{-2} in agriculture and forest, respectively (Figure 2b). A second peak of mayfly biomass occurred 20 days after the first peak in forest (Table S8), whereas mayfly biomass in agriculture declined over the rest of the study period. In contrast, mayfly abundance showed a maximum plateau at 1 (±1) ind day^{-1} m^{-2} from spring to early summer in forest, whereas in agriculture biomass and abundance patterns were similar (Figure 3b). Flatheaded mayflies (Arthropleidae) and primitive minnow mayflies (Siphlonuridae) were absent from agricultural sites. The phenology of mayfly families between land-use types was otherwise similar except for the biomass of spiny crawler mayflies (Ephemerellidae; Figures S10 and S11).

Stonefly biomass and abundance peaked during spring in forest, whereas nearly no stoneflies emerged in agriculture (Figures 2c and 3c). All stonefly families peaked in spring. Needle flies (Leuctridae) and green stoneflies (Chloroperlidae) were absent from agricultural sites (Figures S12 and S13).

The biomass pattern of caddisflies was similar over time in both land-use types (Figure 2d). The caddisfly biomass reached a maximum of 6 (±2) mg day^{-1} m^{-2} in agriculture and peaked 10 days later at 4 (±2) mg day^{-1} m^{-2} in the forest (Table S8). By contrast, caddisfly abundance peaks exhibited a greater temporal shift with earlier emergence in forest. During summer, forest abundance peaked at 1 (±1) ind day^{-1} m^{-2} and peaked 51 days later in agriculture at 1 (±1) ind day^{-1} m^{-2} (Figure 3d, Table S8). In forested sites no lepidostomatid case makers (Lepidostomatidae) were sampled, whereas in agricultural sites five caddisfly families were lacking (Figures S14 and S15). Abundance patterns were similar for caddisfly families between land-use types, although biomass patterns differed. For example, net-spinning caddisflies' (Hydropsychidae) biomass peaked during summer in the forest, whereas they exhibited three overlapping peaks in agriculture (Figure S14a, Tables S4 and S9). More information on families can be found in the Supplementary text: Results family biomass and abundance.

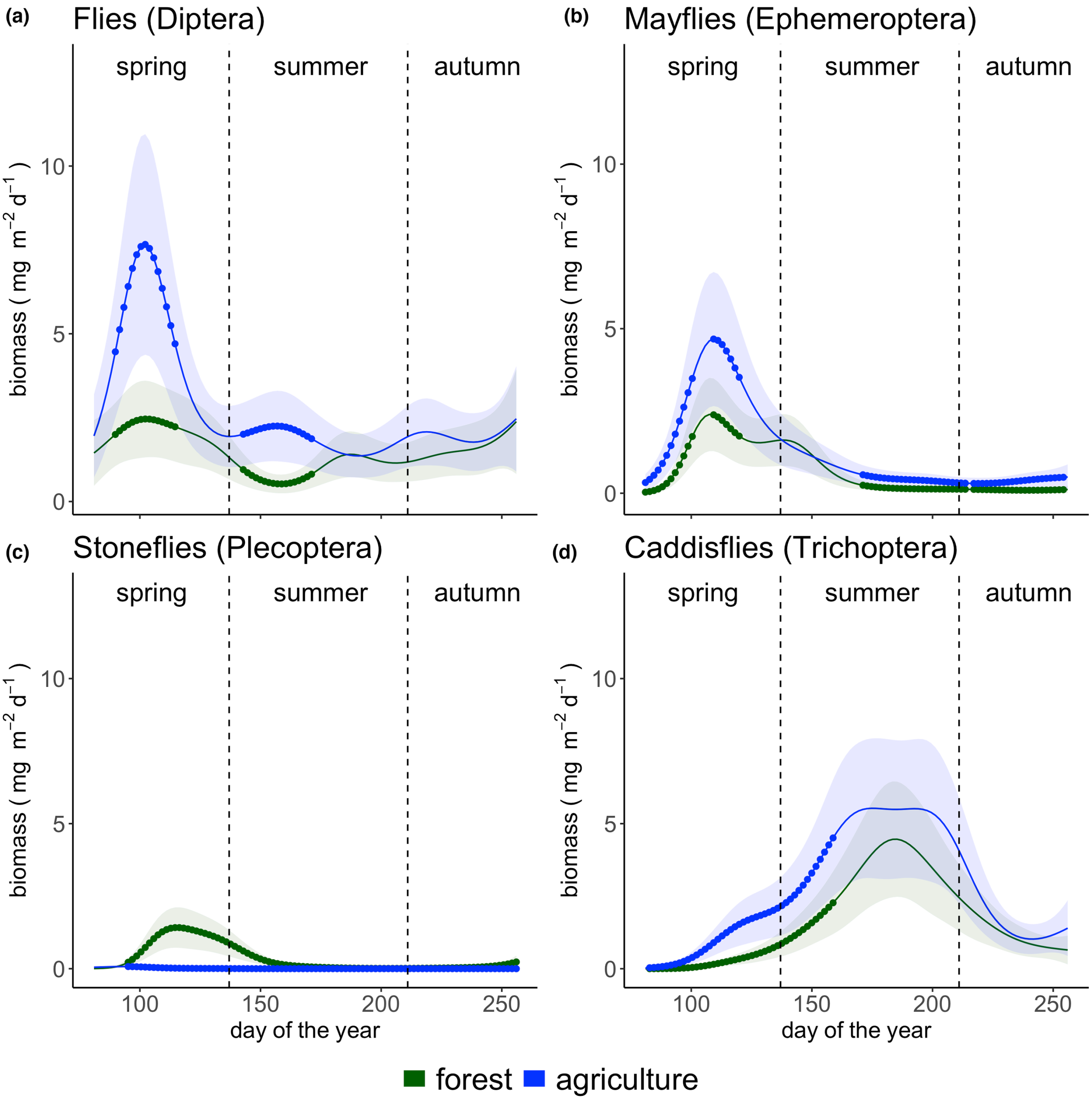

FIGURE 2 Predicted seasonal patterns (spring: 22 March–16 May, summer: 17 May–26 July, autumn: 27 July–13 September) of aquatic insect order biomass derived with hierarchical generalized additive models (HGAMs) fitted with 7644 observations. The solid line shows the predicted mean fit values of the HGAM, and the ribbon indicates ±2 standard errors around the mean fit. Dots mark significant differences with non-overlapping 95% confidence intervals at alpha = 0.05 between agriculture and forest. Green represents the biomass pattern in forest and blue in agriculture for (a) flies, (b) mayflies, (c) stoneflies, and (d) caddisflies

3.4 | (iii) Land-use-related drivers of aquatic insect emergence

Pesticide toxicity and electrical conductivity (EC) exhibited the most pronounced differences among the selected land-use-related drivers between forested and agricultural sites, and both variables were higher in agriculture. On average, shading was higher in forested than agricultural sites, and temperature, pool habitats, and nitrate and phosphate concentrations were higher in agricultural sites (Figure S16, Table 1). Oxygen saturation was higher in agriculture in spring but higher in forest in summer and autumn.

We fit 11 GLMMs to identify the main drivers of total biomass and total abundance of aquatic insects, as well as biomass and abundance of the major emergent aquatic insect orders. One GLMM was fit for every response variable, for example total biomass, biomass of caddisflies and number of EPT families. Only in seven best-fit models

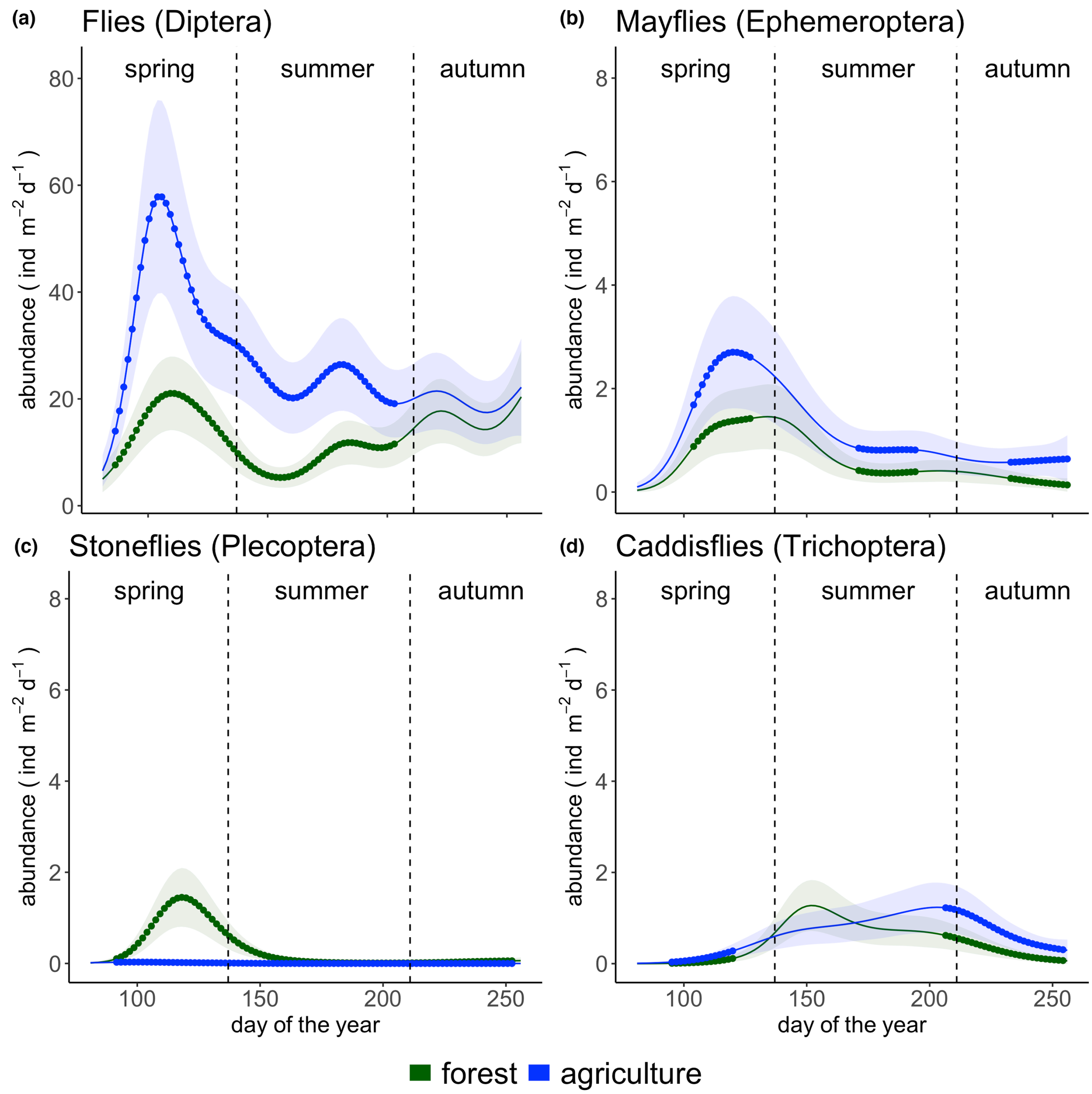

FIGURE 3 Predicted seasonal patterns (spring: 22 March–16 May, summer: 17 May–26 July, autumn: 27 July–13 September) of aquatic insect order abundances derived with hierarchical generalized additive models (HGAMs) fitted with 7644 observations. The solid line shows the predicted mean fit values of the HGAM, and the ribbon indicates ±2 standard errors around the mean fit. Dots mark significant differences with non-overlapping 95% confidence intervals at alpha = 0.05 between agriculture and forest. Green represents the abundance pattern in forest and blue in agriculture for (a) flies, (b) mayflies, (c) stoneflies, and (d) caddisflies. Note that the *y*-axis scales vary by a factor of 10: (a) 0–80 ind day^{-1} m^{-2}, (b)–(d) 0–8 ind day^{-1} m^{-2}

were explanatory variables selected to explain changes in biomass and abundance of single orders. The other four best-fit models, including the models for total biomass and abundance, did not contain explanatory variables, but only random effects and the intercept. The explained variance of these models ($R^2_{\text{conditional}}$) ranged between 33% for total abundance and 57% for mayfly abundance. The variance explained by stream (random factor) varied between 28% for total abundance and 40% for total biomass and mayfly abundance, and variance explained by season (random factor) ranged from 8% for total and fly abundance to 40% for mayfly abundance (GLMM, Table 2).

The models containing explanatory variables explained between 30% and 83% of variance, when considering random effects ($R^2_{\text{conditional}}$, GLMM, Table 2). Specifically, pesticide toxicity (Equation 2, see Section

2) and EC were included in four models, water temperature, shading, and phosphate concentration in two models, and the percentage of pool habitats in one model (Table 2). Pesticide toxicity was negatively associated with the number of EPT families and with stonefly biomass and abundance, but it was positively associated with mayfly biomass. By contrast, EC showed a positive association with caddisfly abundance and biomass but negative associations with stonefly and mayfly abundances. Water temperature exhibited a positive relationship with mayfly biomass but a negative one with stonefly biomass. Phosphate concentration was positively associated with the number of EPT families and stonefly biomass. Shading was negatively associated with fly biomass but positively associated with stonefly biomass. Finally, mayfly biomass decreased with the percentage of pool habitats.

4 | DISCUSSION

In this study, we assessed the association between land use and the export of aquatic insects to terrestrial ecosystems by continuously monitoring insects and physicochemical variables over the primary emergence period in paired agricultural and forested stream sites. An overview of the results is given in Table S10. We (i) compared total biomass as well as abundance between agricultural and forested sites and found that total aquatic insect biomass and abundance were higher in agricultural than forested sites.

Additionally, we (ii) analyzed the taxonomic and trait composition of aquatic insects, as well as their turnover, associated with land-use. Except for stoneflies, biomass and abundance of major orders of aquatic insects were higher in agriculture, but their phenology differed. Differences in emergence timing among different taxa may affect the foraging opportunities of riparian predators (Armstrong et al., 2016). Furthermore, we identified turnover in the composition of insect families between forested and agricultural sites, with a tendency of families exhibiting a longer generation time in forest and shorter generation time in agriculture, which matches the results of Liess and von der Ohe (2005) for in-stream invertebrate communities in agricultural streams.

Moreover, we (iii) determined land-use-related drivers associated with biomass, abundance, and composition of aquatic insects. Pesticide toxicity and EC were the most important land-use-related drivers associated with biomass and abundance for selected aquatic insect orders, whereas the aggregated parameters of total abundance and total biomass of aquatic insects were not associated with land-use-related drivers. In the following, we discuss the differences between land-use types as well as seasons and how the land-use-related drivers may have affected the aquatic insect assemblages.

4.1 | (i) Higher total biomass and abundance in agriculture than forest

Our finding that total biomass and abundance of aquatic insects were higher in agricultural than in forested streams is in line with previous studies (e.g. Carlson et al., 2016; Krell et al., 2015; for corresponding values see Table S11). Higher total biomass and abundance in agricultural sites may be caused by elevated nutrient concentrations and reduced shading, both which have been shown to increase primary production in agricultural streams and, in turn, food availability for aquatic insects (Carlson et al., 2016; Griffiths et al., 2013; Stenroth et al., 2015; Terui et al., 2018). However, neither nutrients nor shading were selected as explanatory variables in the models for total biomass or abundance in our study, implying that other unmeasured stream-level variables may have contributed more to their differences. Furthermore, total abundance and biomass were affected differently. Total abundance was mainly constituted from small-bodied insects, whereas total biomass was frequently constituted by less abundant but large-bodied insects. Nonetheless, aquatic insects are part of the riparian food web, and changes in their total biomass and abundance can affect other trophic levels. For example, their presence can enhance predation on terrestrial herbivorous insects and, in turn, reduce herbivory (Graf et al., 2017; Henschel et al., 2001), although the underlying mechanism is unknown. Thus, increased total biomass and abundance of aquatic insects in agricultural areas have implications for both stream and terrestrial ecosystem structure and function.

4.2 | (ii) Turnover and temporal patterns in composition

We identified seasonal patterns and shifted phenology between land-use types within the primary emergence period. Raitif et al. (2018) and Yuen and Dudgeon (2016) found similar seasonal patterns for mayflies and caddisflies, but different patterns for flies, in agricultural and forested sites, respectively. The shifted phenology between land-use types may be beneficial for mobile predators, which can exploit aquatic insects as food source in the landscape and thus prolong the use of this food source. By contrast, for sessile predators a shift in phenology may be disadvantageous, if the shift leads to a mismatch of life cycles (Schindler & Smits, 2017).

In addition, we found turnover of families between forested and agricultural sites, which is in line with other studies reporting turnover of species rather than an overall decline in total insect biomass (Baranov et al., 2020; Dornelas et al., 2019; Kaelin & Altermatt, 2016). The tendency for higher occurrence of aquatic insects with shorter generation time in agriculture indicates a turnover towards assemblages with lower vulnerability to land-use-related stress because they have a higher recovery potential (Sherratt et al., 1999; Stark et al., 2004). The fact that the site position was associated with the land use effect (i.e. downstream site always affected by land use) raises the question whether position itself contributed to the observed difference (Vannote et al., 1980). The upstream and downstream sites exhibited only small distances to each other. Aquatic insect assemblages of close sites reveal spatial autocorrelation, which means closer sites show higher similarities in insect assemblages. Spatial autocorrelation of aquatic insect communities occurs

TABLE 2 Estimated regression parameters, standard errors (SE), *Z* values for the best-fit generalized linear mixed-effects models (GLMMs) obtained with L1-penalty and 60 observations. σ_{stream} is the standard deviation of the random effect stream, σ_{season} is the standard deviation of the random effect season, R^2_{marginal} is the variance explained by the fixed factors, $R^2_{\text{conditional}}$ is the variance explained by fixed and random factors, $\text{ICC}_{\text{adjusted}}$ is the variance explained by the random factors stream and season. EPT is the abbreviation for stonefly, mayfly, and caddisfly families and EC for electrical conductivity

Model	Parameter	Estimate	SE	*Z* value	σ_{stream}	σ_{season}	R^2_{marginal} (%)	$R^2_{\text{conditional}}$ (%)	$\text{ICC}_{\text{adjusted}}$ Stream (%)	$\text{ICC}_{\text{adjusted}}$ Season (%)
Total biomass	Intercept	1.45	0.30	4.86	0.56	0.35	0	48	40	21
Fly biomass	Intercept	0.45	0.21	2.12	0.27	0.25	13	30	12	10
	Shading	−0.32	0.14	−2.25						
Mayfly biomass	Intercept	−1.05	1.06	−0.98	1.06	1.73	12	83	53	75
	EC	−0.43	0.20	−2.12						
	Pools	−0.25	0.19	−1.37						
	Toxicity	0.23	0.19	1.19						
	Water temperature	0.72	0.28	2.55						
Stonefly biomass	Intercept	−4.16	0.65	−6.36	0.83	1.01	30	66	30	39
	EC	−0.24	0.19	−1.27						
	Phosphate	0.32	0.16	2.04						
	Shading	0.49	0.17	2.87						
	Toxicity	−0.41	0.19	−2.17						
	Water temperature	−0.79	0.27	−2.94						
Caddisfly biomass	Intercept	−0.65	0.81	−0.81	1.48	1.12	14	79	66	52
	EC	0.87	0.17	5.16						
Total abundance	Intercept	3.02	0.21	14.57	0.39	0.18	0	33	28	8
Fly abundance	Intercept	2.87	0.22	13.08	0.43	0.20	0	34	30	8
Mayfly abundance	Intercept	−0.75	0.51	−1.48	0.75	0.75	0	57	40	40
Stonefly abundance	Intercept	−2.96	0.39	−7.54	0.40	0.60	23	55	64	59
	Toxicity	−0.61	0.13	−4.51						
Caddisfly abundance	Intercept	−1.56	0.59	−2.63	0.96	0.85	16	80	18	33
	EC	0.64	0.16	3.90						
Number of EPT families	Intercept	1.24	0.14	8.70	0.17	0.19	14	31	9	12
	Phosphate	0.19	0.07	2.74						
	Toxicity	−0.15	0.07	−2.12						

for example, because juvenile aquatic insects drift downstream (Bailey, 1966; Elliott, 1971). Further, it was shown, that upstream forested sites reduce effects of agricultural stressors on aquatic insect assemblages in downstream agricultural sites, probably by recolonisation of aquatic insects from upstream sites (Orlinskiy et al., 2015). Therefore, the position itself is unlikely to cause the observed differences alone. Only experiments and modelling can answer this question finally, because under field conditions an upstream agricultural site would affect the downstream forested site as well. Better understanding turnover and trait composition helps to identify at-risk taxa in agricultural areas and, in turn, to inform implementation of mitigation measures preventing their loss, for example, by reducing the amount of pesticide runoff into streams.

Patterns in insect abundance and biomass, as well as order-specific phenology, could have cascading effects on predator growth and immune function (Fritz et al., 2017; Twining et al., 2016). We found that in both land-use types, total abundance was driven by the abundance of flies, whereas total biomass was dominated by different orders across seasons (e.g. caddisflies in summer; Figures 1–3). Other studies have shown similar results (e.g. Carlson et al., 2016; Krell et al., 2015; Raitif et al., 2018; Stenroth et al., 2015). These seasonal biomass patterns are accompanied by differences in traits like size, the export of PUFA, and, in turn, prey quality for riparian predators. For instance, of the major orders of aquatic insects, mayflies have the highest, and caddisflies the lowest, PUFA concentrations (Martin-Creuzburg et al., 2017). In our study, mayflies emerged mainly in spring and caddisflies in summer in both land use types; therefore, more PUFA may have been available during spring for riparian predators, thereby affecting predator dynamics.

Additionally, taxon-specific traits (e.g. size) determine which predators can benefit most from the presence of aquatic insects as an additional food source (Davis et al., 2011; Stenroth et al., 2015). We found a similar size distribution in forested and agricultural sites, though seasonal differences occurred. For example, in agriculture, small-bodied flies dominated biomass during spring, whereas larger-bodied caddisflies dominated biomass in summer. Thus, in spring, smaller predators like spiders may have benefited most from emerging insects, whereas larger predators like birds received a higher amount of suitable prey in summer. By contrast, during spring in forest, biomass of flies, mayflies and stoneflies was similar. So smaller as well as larger predators may have benefited equally. Overall, the changes in prey quality and phenology can have far-reaching consequences to the riparian food web by altering predator population dynamics (Sato et al., 2016) and, in turn, biomass at other trophic levels like terrestrial insects and plants (Graf et al., 2017; Henschel et al., 2001).

4.3 | (iii) Land-use-related drivers of aquatic insect emergence

Identifying the factors that influence shifts in aquatic insect assemblages and phenology is important for understanding the cascading effects of human actions on stream ecosystems. We found that pesticide toxicity and EC were associated with differences in abundance and biomass of aquatic insects. These, and additional land-use-related drivers considered in this study (i.e. oxygen saturation, percentage of pool habitat, percentage of shading, water temperature, and nitrate and phosphate concentrations), are known to determine aquatic insect habitat quality in terms of hydromorphological structure and water quality (Graf et al., 2020; Raitif et al., 2018; Stenroth et al., 2015). Land-use-related drivers associated with reduced habitat quality like pesticide toxicity were worse in agricultural than forested sites. However, none of these variables were selected in statistical models to explain total abundance or biomass of aquatic emergent insects. Total abundance and biomass represent aggregated features of the community that may amalgamate taxa with different responses to stressors, including land use (Jähnig et al., 2021). Indeed, it is well known that the major orders of aquatic insects respond differently to land-use-related drivers (Carlson et al., 2016; Raitif et al., 2018; Stenroth et al., 2015). For instance, higher water temperature and pesticide toxicity were associated with reduced biomass of stoneflies, which prefer colder streams (Illies, 1955) and are more vulnerable to pesticides than other aquatic insects (Rico & den Brink, 2015; Rubach et al., 2010). In addition, mayflies are adapted to lower levels of EC than caddisflies, stoneflies, and flies, which may explain the reduction of mayfly biomass with increasing EC in our study (Dunlop et al., 2008; Kefford et al., 2011, 2012; Szöcs et al., 2012). Overall, this questions the usefulness of aggregated community features to study insect trends and drivers of community assembly as well as for management.

Changes in water salinity, and by extension in EC (a proxy for total dissolved ions regularly used to express salinity in water) may affect taxa through osmoregulatory stress, toxic effects of ions, or both (Cañedo-Argüelles et al., 2013). In Australia, the aquatic invertebrate assemblage changed, with a constant reduction of EPT species, along a gradient from <50 to $>30{,}000\,\mu\mathrm{S\,cm}^{-1}$ (Kefford et al., 2011). A study on German streams found strong turnover of aquatic insects when the natural background EC was exceeded by $>400\,\mu\mathrm{S\,cm}^{-1}$ (Le et al., 2021). In our study region, the natural background EC is $\leq 100\,\mu\mathrm{S\ cm}^{-1}$ (Stöppel, 2005), and we found EC values in a range of 93 to $381\,\mu\mathrm{S\,cm}^{-1}$ in forested sites. In agricultural sites, however, we found EC in the range of 179 to $1899\,\mu\mathrm{S\,cm}^{-1}$, corresponding to levels that have been shown to drive community change.

Pesticides, the second major driver of adult aquatic insect assemblage in our study, are globally present in streams (Beketov et al., 2013; Malaj et al., 2014; Stehle & Schulz, 2015). A countrywide monitoring study of streams across Germany, including some of the same sites as our study, found that pesticides regularly exceeded concentrations considered harmful for aquatic insects and, similarly, were the main driver for assemblage changes of juvenile vulnerable aquatic insects during their aquatic life stage (Liess et al., 2021). In the future, aquatic insect assemblage changes due to pesticides may increase because of increasing global pesticide use (Bernhardt et al., 2017; Kattwinkel et al., 2011) and increasing pesticide toxicity towards aquatic insects (Schulz et al., 2021). These trends could lead to higher variability in emergence (Uno &

Pneh, 2020), therefore altering foraging opportunities for predators (Armstrong et al., 2016). Further, pesticide toxicity has been shown to cause earlier insect emergence (Cavallaro et al., 2018), which may affect the growth rate, population biomass, and maturity rate of predators (Sato et al., 2016) and may lead to a mismatch in predator and prey cycles.

5 | CONCLUSION

Our study, which focused on different land-use types in temperate streams, revealed differences in aquatic insect abundance, biomass, and phenology between forested and agricultural sites and identified several land-use-related drivers associated with changes in order-level assemblages. These differential effects may vary with different land-use practices within land-use categories, as well as geographically. Therefore, we suggest that future studies should consider land-use intensity over a range of ecosystem types.

The aggregated parameters total abundance and biomass of insect emergence, which have frequently been used in meta-analyses, were not associated with land use related drivers. Thus, we question their suitability to evaluate the anthropogenic influence on ecosystems and their use may result in missing complex responses to environmental change.

Overall, we were able to quantify the export of aquatic insects in the primary emergence period in different land-use types as well as seasonal patterns. These results can be included in modelling, for example, of food-web dynamics or meta-ecosystems. Further, the knowledge of important land-use-related drivers associated with aquatic insects enables to implement of specific management strategies to protect aquatic insect assemblages.

AUTHOR CONTRIBUTIONS

Katharina Ohler, Verena C. Schreiner, Matthias Liess, Ralf B. Schäfer designed the study and discussed the results; Katharina Ohler, Verena C. Schreiner, Moritz Link selected the sampling sites; Katharina Ohler, Verena C. Schreiner, Moritz Link conducted field work; Katharina Ohler identified insects; Katharina Ohler analysed data; all authors revised the manuscript.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in GitHub at https://doi.org/10.5281/zenodo.7123465, reference number (Ohler et al., 2022).

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