Land use alters cross-ecosystem transfer of high value fatty acids by aquatic insects

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Abstract

Background Many aquatic insects emerge as adults from water bodies to complete parts of their life cycle in terrestrial ecosystems and are potential prey for riparian predators. The benefits of riparian predators from aquatic insects include higher contents of long-chain polyunsaturated fatty acids (PUFA) compared to terrestrial insects. Aquatic insects are therefore considered a high-quality food. Food containing high levels of PUFA can enhance growth and immune response of spiders. However, agricultural stressors like nutrient increase, pesticides and habitat degradation can affect the biomass of aquatic insects and in turn the diet of spiders. Studies quantifying the influence of land use on fatty acid (FA) profiles of emergent aquatic insects and riparian predators are lacking. We quantified differences in exports of FA, saturated FA, monounsaturated FA, and PUFA, FA profiles of aquatic insects and spiders between forested and agricultural sites over the primary emergence period within one year. The FA export to the riparian food web is crucial to understand energy fluxes between ecosystems. Furthermore, we monitored environmental variables to identify associations between agricultural stressors and FA profiles of aquatic insects and spiders.

Results We found differences in FA export and profiles of aquatic insects between land-use types. The quantity of total FA export via aquatic insects was lower in agricultural sites (95% CI 1147–1313 µg m^{-2}) in comparison to forested sites (95% CI 1555–1845 µg m^{-2}), while the biomass export was higher in agricultural sites. Additionally, in spring the PUFA export was significantly lower (up to 0.06 µg d^{-1} m^{-2}) in agricultural than forested sites. Agricultural stressors explained only little variation in the FA profiles of aquatic insects, e.g., 4% for caddisflies and 12% for non-biting midges. Percentage of shading and pool habitats were identified as most important variables explaining the variation in FA profiles.

Conclusion The quality of aquatic insects as food source for riparian spiders was smaller in agricultural than forested sites, which can decrease the fitness of riparian predators. To improve our capacity to predict potential adverse effects in the riparian food web, future studies should identify the mechanisms underlying a lower PUFA content.

Keywords Agriculture, Forest, Fatty acid profiles, Emergent aquatic insects, Spiders

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Background

Globally, intensive agriculture is a major land-use type [1]. In agricultural areas, stream ecosystems are threatened by enhanced nutrient inputs, pesticides and habitat degradation, which in turn jeopardizes biodiversity and human water security [2–4].

Stream ecosystems and adjacent terrestrial ecosystems are closely connected via the exchange of matter and organisms [5]. Many aquatic insects, e.g., Ephemeroptera (mayflies), Plecoptera (stoneflies), Trichoptera (caddisflies) and some Diptera (flies) emerge as adults from water bodies into terrestrial ecosystems. There, they are potential prey for riparian predators like spiders, birds and bats [6–8]. Additionally, agriculture is linked to the loss of terrestrial invertebrates [9–11]. Therefore, riparian predators can benefit from aquatic insects complementing the food source of terrestrial invertebrates [12–14].

Furthermore, aquatic insects are considered a high-quality food source, because they typically contain elevated levels of fatty acids (FA) compared to terrestrial insects [15–17]. Especially, levels of polyunsaturated FA (PUFA) of aquatic insects can be ten times higher than in terrestrial insects [15, 16]. These differences originate from the base of the food web propagating to higher trophic levels: aquatic primary producers like diatoms are capable of synthesizing long-chain PUFA [18–20], while terrestrial vascular plants cannot [21]. Additionally, many animals are not able to produce PUFA de novo and therefore depend on dietary intake of these compounds [22]. Animals like some bird and spider species that can synthesize PUFA still are constrained by high energetic costs and, thus, may only produce PUFA in the absence of other sources [22–24]. Consequently, food containing high levels of long-chain PUFA has been shown to enhance growth and immune response of spiders and birds [25, 26]. Furthermore, FA in general have been linked to the increased growth of spiders [27].

Emergence of aquatic insects is variable over time and reveals seasonal patterns [28, 29] and it has been shown that the timing of emergence can control growth rate, population biomass and maturity rate of terrestrial predators [30, 31]. Therefore, accounting for temporal dynamics is important when aiming to predict effects of total FA export via aquatic insects to terrestrial ecosystems [32].

It is known that agricultural stressors like increased nutrient concentration in stream water, pesticides and habitat degradation affect aquatic insects, e.g., by changing the composition of aquatic insect assemblages [14, 29] and increasing or decreasing their biomass, depending on the aquatic insect order [29, 33]. Furthermore, agricultural stressors can affect riparian spiders by altering the amount of aquatic insects in their diet [12], reducing their richness as well as abundance [34].

Most studies thus far have focused on PUFA profiles of aquatic insects and riparian predators without considering potential effects of agricultural stressors (e.g., [16, 17, 24, 35, 36]). One mesocosm study on Chironomidae (non-biting midges), including nutrient elevation and predation, found that FA export was highest at intermediate phosphate concentrations and that biomass of non-biting midges was the best predictor for FA export [37]. However, under laboratory conditions, with toxicant exposure (copper, pesticides, *Bacillus thuringiensis* var. israelensis) during larval stages of non-biting midges, no effect on FA profiles of adult non-biting midges and a tendency to decreased FA content in spiders was found [38]. Similarly, one field study on emergent aquatic insects in two streams included stream-bed characteristics and physicochemical variables like nutrients, but did not find an association of these variables with the FA profiles of aquatic insects [39]. In a field study, conducted in agricultural and forested streams focusing on vegetation (herbaceous and woody), the taxonomy of spiders at family level was the best predictor for FA content of spiders [40].

To our knowledge, field studies that quantified the influence of land use and associated stressors on FA profiles of emergent aquatic insects and riparian predators as well as FA export via aquatic insects are lacking. However, this would be important to estimate the effect of changing quality in terms of FA export to the riparian food web, which is crucial to understand energy fluxes between ecosystems and to predict effects on the subsidized food web [41–43]. Therefore, we aimed to quantify differences in total FA export and FA profiles of aquatic insects as well as riparian spiders between forested and agricultural sites of ten streams over the primary emergence period within one year (March–September). As spiders can prey on emergent aquatic insects, their FA profiles may be affected by changes in FA profiles of emergent aquatic insects. We collected emergent aquatic insects and riparian spiders and measured their FA profiles. In addition, we monitored a range of environmental variables to identify potential associations between agricultural stressors and the FA profiles of aquatic insects and spiders. We compared (1) total FA export via aquatic insects between both land-use types; (2) FA profiles of aquatic insects and spiders between agricultural and forested sites and (3) examined associations between agricultural stressors and the FA profiles of aquatic insects and spiders.

Methods

Study sites

To cover the primary emergence period [44], our study was conducted from 22nd March to 13th September

2018 in south-western Germany. In 10 parallel, fine substrate-dominated, mostly small, first and second order highland streams, an upstream forested site and a downstream site where agricultural land use dominated were selected (Additional file 1: Figure S1). The mean distance between the upstream and downstream sites within a stream was 5.5 (range: 1.4–14.0) km and the maximum distance between parallel streams was 50 km. All streams originated in the Palatinate Forest, a forested low mountain range. The sites were mostly free from large wastewater treatment plants and industrial facilities. Viticulture was the main agricultural land use. It has been shown that environmental variables were similar across different types of agricultural land use including viticulture, cereals and corn in this region [45]. The stream size and order of all study sites was comparable, for details see Ohler et al. [29].

Agricultural stressors associated with FA profiles

We recorded physicochemical variables every three weeks and hydromorphological structure in March, July, and August to determine land-use-related variables associated with FA profiles of aquatic insects and riparian spiders. For instance: electrical conductivity (EC), nitrate concentration, air and water temperature, oxygen saturation, the percentage of pool habitats and the percentage of shading (Additional file 1: Table S1). Furthermore, in-stream pesticide concentrations were determined from 49 event-driven samples taken during heavy rainfall events and 85 grab samples taken every three weeks. Glass bottle samplers [46] and automated samplers (MAXX TP5, Rangendingen, Germany) took event-driven samples whenever the water level increased more than 5 cm. The samples were filtered (either automatically on site or manually in the lab) to retain particles, which were then analyzed for pesticides bound on particles. More information on pesticide sampling, analysis and exposure are described in Halbach et al. [47] and Liess et al. [48, 49].

The pesticide class of pyrethroids typically enters streams bound on particles [50] and has a high relative toxicity for aquatic insects [51, 52]. Therefore, the concentration of pesticides bound on particles in event samples was used to estimate the bioavailable concentration in water c_d following Schäfer et al. [53] and Toro et al. [54] with the equation:

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

where f_{oc} is the fraction of organic carbon in the sample, c_{tot} is the total concentration on the suspended particles, and k_{oc} is the soil organic carbon–water partitioning coefficient, which was extracted from the Pesticide Property Data Base (PPDB, [55]) and PubChem [56] database (Additional file 1: Table S2).

The logarithmic sum of toxic units (sumTU) was calculated to estimate the toxicity of the pesticide mixture [57]:

$$\text{sumTU} = \log \sum_{i=1}^{n} \frac{c_i}{\text{EC}_{50i}},$$
(2)

where c_i is the concentration of the single pesticide, EC_{50i} the acute effect concentration of the pesticide towards the most sensitive freshwater invertebrate species, and n is the number of pesticides. The R package Standartox (version 0.0.1, Scharmüller et al. [58]) was used to compile the EC_{50} values from the ECOTOX database [59]. If the EC_{50} values were missing in Standartox, the values were complemented from the PPDB [55] or Malaj et al. [60] (Additional file 1: Table S3). The maximum pesticide toxicity (maximum sumTU of all samplings per site and season; hereafter pesticide toxicity) was used in the analysis, because it may be responsible for the strongest ecological response.

Spider and aquatic insect sampling

We chose *Tetragnatha* sp. to determine effects of FA in aquatic–terrestrial food webs, as these spiders frequently colonize riparian areas and prey on aquatic insects [7] with orb webs spanning over streams [61]. Whenever feasible only female and adult spiders of the species *T. montana* were collected to minimize variation in feeding, because feeding differs between and within spider species [62]. In the subsequent FA analysis 73% of the spiders were adult female *T. montana*, for more details see Ohler et al. [63]. Up to ten spiders were gathered with a maximum distance of 1 m from the stream by hand in spring (14th–16th May 2018), summer (16th–19th, 23rd, 26th July 2018) and autumn (10th–13th September 2018).

Emergence traps with a basal area of 0.25 m² and a bottle trap without any solution [64] were used to sample aquatic insects continuously. Two traps were installed at every site covering pool and riffle habitats. This sampling method likely underestimated the fraction of stoneflies that emerge by walking on the banks. As previous studies estimated only < 1% to 3% [65, 66] of aquatic emergent insects returning to water bodies, we assume that most sampled aquatic insects would have reached the riparian area. Twice a week the traps were emptied by replacing the bottle trap.

The spiders as well as aquatic insects were transported on ice until they were euthanized in liquid nitrogen and identified in the laboratory on ice. Under a stereo microscope, spiders were identified to species level using the key by Roberts [67] and aquatic insects to family level

with the following keys Bährmann and Müller [68], Nilsson [69, 70], Schäfer and Brohmer [71]. Subsequently, spiders and aquatic insects were lyophilized to complete dryness and weighed to the nearest 0.1 µg.

FA analysis

For FA analysis the major orders of aquatic insects, i.e., mayflies, stoneflies, caddisflies and flies, were chosen. In total 21 FA with 18 or more carbon atoms were included in the analysis. Since non-biting midges (Chironomidae) dominated the emergence of flies (Diptera) [29], only their FA profiles were analyzed. The samples of aquatic insects collected over approximately two weeks (Additional file 1: Table S4) were pooled on order level prior to analysis, which is commonly done in FA analysis (e.g., [35, 39]). An analysis on family level would have exceeded financial and labor capacities, though FA profiles may differ across families [37]. Hence, the FA analysis at order level will reflect the FA profiles of the families present in one site.

After the addition of an internal standard (C17:0 200 µg mL^{-1}; C23:0 250 µg mL^{-1}, Sigma-Aldrich) the FA of all samples were extracted following Folch et al. [72] with chloroform/methanol (GC-grade, 5 mL, v:v; 2:1) at -20 °C over night. Then the samples were filtered with a syringe filter (PTFE, 13 mm, 0.45 µm, BGB), evaporated until dryness at 40 °C under nitrogen and redissolved in methanol. The volume of methanol depended on the weight of the sample (maximum ratio of weight to volume: 3:10), for details see Ohler et al. [73]. All samples were stored under nitrogen at -20 °C until derivatization. Methanolic trimethylsulfonium hydroxide (TMSH, 0.2 M, 10 µL, Macherey–Nagel) was used to derivatize FA to fatty acid methyl esters (FAME) in the sample (20 µL) at room temperature for 60 min. A gas chromatograph with a flame ionization detector (Varian CP-3800, Varian Inc) equipped with a DB-225 capillary column (30 m × 0.25 mm × 0.25 µm, Agilent J&W) was used to analyze FAME. The FAME were identified and quantified with external standards (Supelco 37 component FAME mix, 18:1n-7 FAME, ALA FAME, Sigma-Aldrich). OpenChrom [74] was used for identification and R (version 4.2.0 [75]) for quantification. Further details are given in Ohler et al. [73].

Data analysis

Comparing FA export between agricultural and forested sites

The export of FA, saturated fatty acids (SFA), monounsaturated fatty acids (MUFA) and PUFA via aquatic insects was assessed with hierarchical generalized additive models (HGAM) following Pedersen et al. [76]. This gives information about the amount of these compounds available for riparian predators. HGAM allow to identify seasonal patterns of FA, SFA, MUFA and PUFA export as well as differences between land-use types in the amount exported. The sum of all FA, SFA, MUFA and PUFA of aquatic insects in total as well as on order level were used in the HGAM. The export of FA, SFA, MUFA and PUFA was normalized for the sampling area and duration. Group-level smoothers without a global smoother for land use and land use crossed with order were applied. That means each group could differ in its shape without restriction. HGAM including one smoothing parameter for all group levels (model S, same wiggliness) yielded lower Bayesian Information Criterion (BIC, Additional file 1: Table S5) than HGAM fitted with one smoothing parameter for every group level (model I, different wiggliness). Additionally, stream was incorporated as random effect smoother. The HGAM were fitted with the R-package mgvc (version 1.8–36 [77]). The effect of land use was quantified with the 95% confidence interval (CI) of the difference between the mean fit (mean per time point) for forest and agriculture. At $a = 0.05$ non-overlapping CI were considered statistically significant. Furthermore, the mean export of FA, SFA, MUFA and PUFA per area over the whole sampling period was estimated by using the mean fits of the HGAM in forest as well as agriculture. The temporal resolution of agricultural stressors was too low to include them in model selection in HGAM.

Comparing FA profiles between agricultural and forested sites

To identify differences in the FA profiles between land-use types, in every season, FA profiles (FA ≥ 18 carbon atoms) of aquatic insects, i.e., mayflies, stoneflies, caddisflies, non-biting midges, and spiders between forested and agricultural sites were compared with analysis of similarity (ANOSIM; 999 permutations, Euclidean distance, R-package vegan version 2.5–7 [78]). For this purpose, the content of a single FA was calculated as the proportion of the total FA content (proportion of FA) to assess potential effects of land use on the FA profiles. In autumn, a comparison of FA profiles of stoneflies between land-use types was not possible, because no stoneflies were caught in agricultural sites during autumn. The *p*-values were adjusted with the Benjamini–Hochberg method [79] to decrease the false discovery rate in multiple testing. Similarity percentage (SIMPER) analyses with the R-package vegan version 2.5–7 [78] were conducted whenever ANOSIM resulted in significant differences between land-use types to identify the specific FA contributing to the differences.

Agricultural stressors associated with FA profiles

Redundancy analysis (RDA) was conducted to identify agricultural stressors associated with changes in FA

profiles of aquatic insects and spiders. For this purpose, the mean of each FA (expressed as proportion of total FA) and environmental variables per season was calculated for spiders and aquatic insects in total. The proportion of single FA was used to determine, if agricultural stressors were in general associated with FA profiles. Furthermore, the mean of each FA per season was calculated for single orders mayflies, stoneflies, caddisflies and non-biting midges. The latter was done, because data aggregation may hamper the identification and evaluation of associations with stressors [29, 80]. We chose pesticide toxicity, percentage of shading, EC, oxygen saturation, percentage of pool habitats, phosphate and nitrate concentration as well as air and water temperature as variables potentially expressing agricultural influence based on the results of previous studies in the region [45, 81, 82]. Additionally, we included the variables stream and season. Water temperature and EC were only included in RDA for aquatic insects and air temperature only in RDA for spiders. Furthermore, the biomass of aquatic insects was included in RDA for spiders only. The variables were chosen a priori. Temperature is known to affect FA profiles of organisms, because, for example with rising temperature, organisms can modify their PUFA content to decrease fluidity of cell membranes [83, 84]. Shading, phosphate and nitrate concentration can affect primary producers and in turn the trophic transfer of FA by altering the food availability for aquatic insects [14, 85–87]. Furthermore, the variables considered in this study can affect the biomass, abundance, and assemblage composition of aquatic insects [12, 14, 29, 33] and the diet, abundance, as well as assemblage composition of spiders [12, 34]. The biomass of aquatic insects determines the potential amount of prey with aquatic origin for spiders [12]. Before the analysis the environmental variables were checked for collinearity. No collinearity was present (highest $r = 0.5$) and all environmental variables were independent from each other. Additionally, the variables were standardized, which includes mean centering and standardization to unit variance. Variable selection for the agricultural stressors was conducted with automatic forward stepwise model selection using the maximization adjusted R^2 (ordiR2step, R-package vegan version 2.5–7 [78]). Stream and season were included in the starting model. After model selection a partial RDA with stream and season as covariates was conducted to identify the variation in FA profiles originating only from the agricultural stressors. All data analysis was conducted with R [75] and figures were generated with the R-package ggplot2 version 3.4.1 [88]. The R code and data are available [63].

Results

Comparing FA export between agricultural and forested sites

Overall, 1555–1845 µg m^{-2} (95% CI) FA, 425–516 µg m^{-2} SFA, 178–204 µg m^{-2} MUFA, and 942–1114 µg m^{-2} PUFA were exported in forested and 1147–1313 µg m^{-2} FA, 329–403 µg m^{-2} SFA, 135–151 µg m^{-2} MUFA, and 670–744 µg m^{-2} PUFA in agricultural sites over the study period (Additional file 1: Table S6). Differences between land-use types in FA, SFA, and MUFA export were not significant (i.e., non-overlapping 95% CI at alpha = 0.05) over the whole study period for individual time points (Fig. 1a–c). However, during spring the PUFA export was significantly higher (up to 0.06 µg d^{-1} m^{-2}) in forested than agricultural sites (Fig. 1d). The FA, SFA, MUFA and PUFA export was highest in spring and decreased until autumn in both land-use types and the seasonal patterns of these compounds were similar within land-use types (Fig. 1a–d).

In autumn, the FA, SFA, MUFA, and PUFA export at single time points of mayflies was significantly higher in forested than agricultural sites (Fig. 2a, e, i, m), the latter approximately 0.01 µg d^{-1} m^{-2}. The FA, SFA, MUFA as well as PUFA export of mayflies peaked during spring in both land-use types (Fig. 2a, e, i, m), but individual time points were not significantly different.

In contrast, the FA, SFA, MUFA, and PUFA export via non-biting midges was significantly higher in forested than agricultural sites during spring and the beginning of summer (Fig. 2b, f, j, n). The FA export ranged from 0.04 (± 0.02) to 0.08 (± 0.04) µg d^{-1} m^{-2} (mean fit HGAM ± 2 standard errors) and from 0.02 (± 0.01) to 0.03 (± 0.02) µg d^{-1} m^{-2}, respectively. In both land-use types FA, SFA, MUFA, and PUFA export via non-biting midges reached its minimum in summer.

The export of FA, MUFA, and PUFA via caddisflies was significantly higher in agricultural than forested sites during autumn, but no significant differences at individual time points were observed for SFA export via caddisflies (Fig. 2c, g, k, o). In agricultural sites the FA export of caddisflies ranged from 0.05 (± 0.02) to 0.007 (± 0.03) µg d^{-1} m^{-2}, and the PUFA export from 0.04 (± 0.01) to 0.05 (± 0.02), whereas the FA export of caddisflies ranged from 0.02 (± 0.02) to 0.03 (± 0.01) µg d^{-1} m^{-2}, and the PUFA export was approximately 0.02 µg d^{-1} m^{-2} in forested sites. Additionally, in summer the FA export of caddisflies peaked at 0.07 (± 0.03) µg d^{-1} m^{-2} in agricultural sites, while in forested sites a plateau around 0.05 µg d^{-1} m^{-2} was observed in summer (Fig. 2c).

Starting at the second half of spring at single time points, the FA, SFA, MUFA, and PUFA export via stoneflies was significantly higher in agricultural
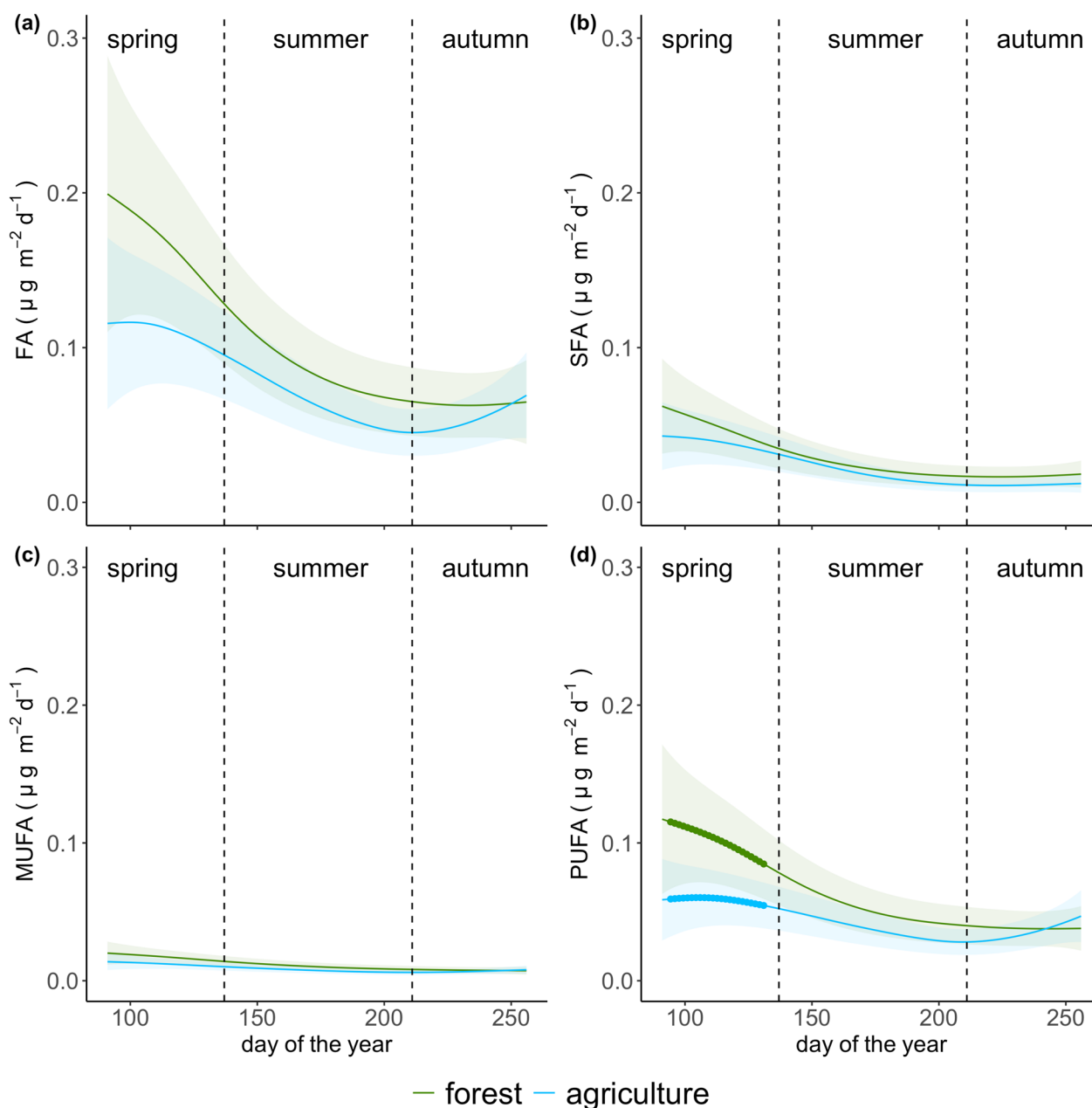
Fig. 1 Modeled seasonal patterns of fatty acid (FA), saturated fatty acid (SFA), monounsaturated fatty acid (MUFA) and polyunsaturated fatty acid (PUFA) export from streams of the total emergence including non-biting midges, mayflies, stoneflies, and caddisflies. The values were derived with hierarchical generalized additive models (HGAM) fitted with 354 observations. Solid lines represent the predicted mean fit values of the HGAM, and the ribbon shows ± 2 standard errors around the mean fit. Dots indicate significant differences (non-overlapping 95% confidence intervals at alpha = 0.05) between agricultural and forested sites. Blue shows the seasonal patterns in agriculture and green in forest for **a** FA export, **b** SFA export, **c** MUFA export, and **d** PUFA export. Seasons: spring: 18th March–16th May, summer: 17th May–26th July, autumn: 27th July–13th September

than forested sites, though in forested sites the maximum FA export 0.02 (± 0.01) µg d^{-1} m^{-2} (beginning of spring) was the same as the maximum FA export 0.02 (± 0.01) µg d^{-1} m^{-2} (end of spring) in agricultural sites (Fig. 2d, h, l, p).

Comparing FA profiles between agricultural and forested sites

We did not find differences in FA profiles of spiders and stoneflies between agricultural and forested sites (Table 1, Additional file 1: Figure S2). FA profiles of
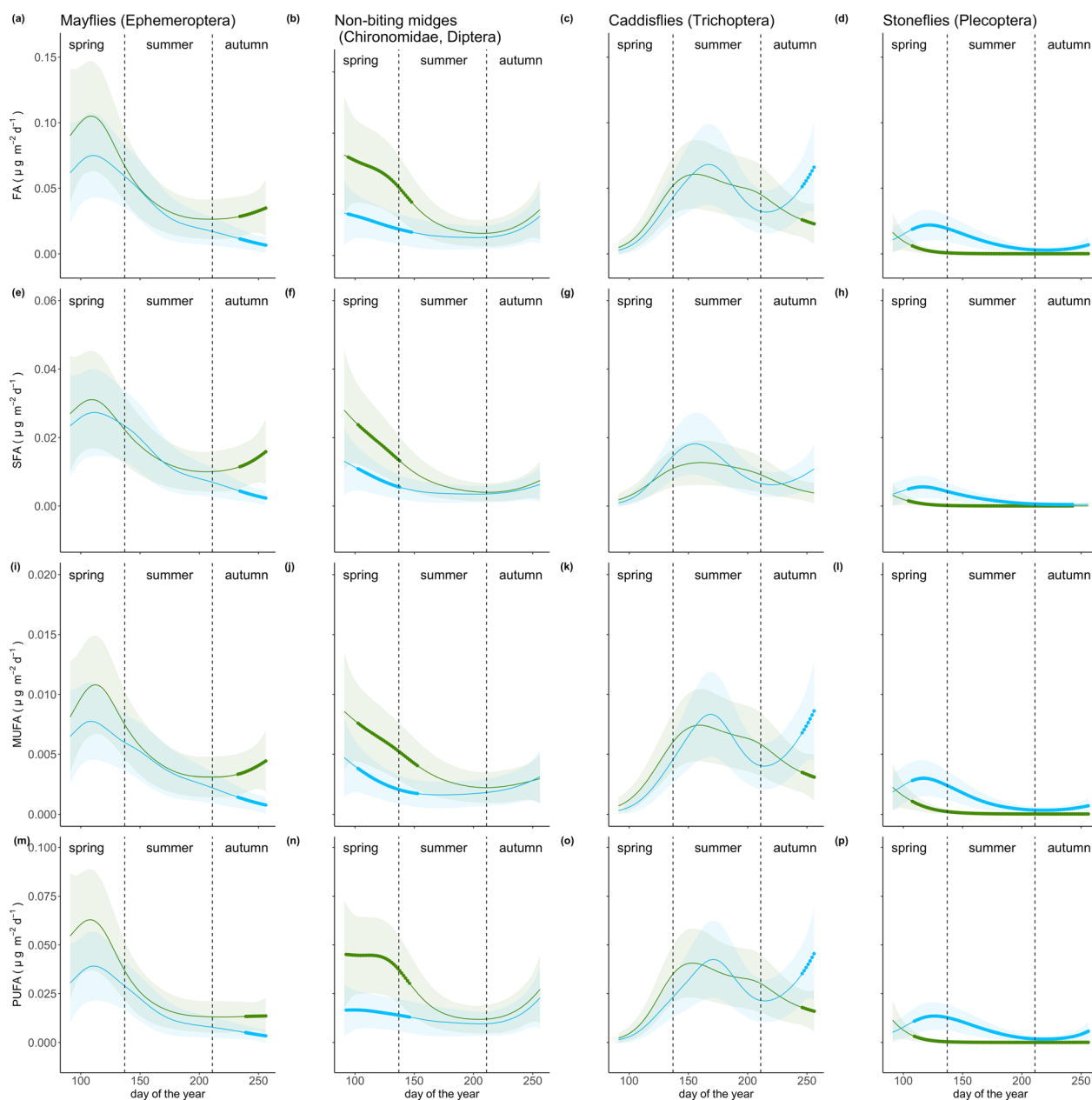
Fig. 2 Modeled seasonal patterns of fatty acid (FA), saturated fatty acid (SFA), monounsaturated fatty acid (MUFA) and polyunsaturated fatty acid (PUFA) export from streams of aquatic insect orders. The values were derived with hierarchical generalized additive models (HGAM) fitted with 998 observations. Solid lines represent the predicted mean fit values of the HGAM, and the ribbon shows ± 2 standard errors around the mean fit. Dots indicate significant differences (non-overlapping 95% confidence intervals at alpha = 0.05) between agricultural and forested sites. Blue shows the seasonal patterns in agriculture and green in forest for **a, e, i, m** mayflies, **b, f, j, n** non-biting midges, **c, g, k, o** caddisflies, and **d, h, l, p** stoneflies. Seasons: spring: 18th March–16th May, summer: 17th May–26th July, autumn: 27th July–13th September. Beware that the *y*-axis scale varies

mayflies (ANOSIM: $R = 0.13$, *p*-value = 0.014) exhibited significant differences (i.e., *p*-value < 0.05) between land-use types in spring (Table 1). The FA eicosapentaenoic acid (20:5n-3, EPA), alpha-linolenic acid (18:3n-3, ALA), linoleic acid (18:2n-6c, LIN), elaidic acid (18:1n-9t, ELA),

octadecanoic acid (18:0, ODA) and eicosanoic acid (20:0, EA) contributed most to these differences (Table 2). All of these FA, except EPA, tended to have higher proportions in mayflies in forested than agricultural sites (Table 2, Additional file 1: Figure S2). Additionally, these

Table 1 Results of the analysis of similarities (ANOSIM) for the fatty acid (FA) profiles

Organism group	Season	*R*	*p*-value	Sample size
Spiders	Spring	− 0.02	0.858	91
	Summer	− 0.02	0.858	52
	Autumn	0.02	0.858	87
Mayflies	Spring	0.13	**0.014**	58
	Summer	0.08	0.06	69
	Autumn	0.07	0.858	32
Stoneflies	Spring	− 0.16	0.858	20
	Summer	0.14	0.858	14
Caddisflies	Spring	0.15	0.504	16
	Summer	0.1	**0.026**	69
	Autumn	0.05	0.858	39
Non-biting midges	Spring	0.12	**0.036**	65
	Summer	0.1	0.06	76
	Autumn	− 0.01	0.858	55

Spiders and aquatic insects per order were compared within the same season between forested and agricultural sites. The Benjamini–Hochberg method was used to adjust the *p*-values. Since stoneflies were not caught in agriculture in autumn, no ANOSIM could be conducted. Differences between forested and agricultural sites were indicated by *R* values: $R < 0.25$ barely separated, $R < 0.5$ clearly separated with some overlap, $R > 0.75$ well separated [89]. $R < 0$ greater dissimilarity within than between groups [90]. Bold values indicate significant *p*-values (i.e., *p*-values < 0.05)

FA explained between 22% (EPA) and 6% (ELA, LIN) of the differences.

The FA profiles of non-biting midges differed significantly between land-use types in spring (ANOSIM: $R = 0.12$, *p*-value = 0.036, Table 1). The FA contributing most to these differences were: gamma-linolenic acid (18:3n-6, GLA), ALA, EPA, ODA and EA, of which GLA explained most of the differences (21%) and EA the least (7%, Table 2). GLA, ODA and, EA tended to reach higher proportions in non-biting midges in forested than agricultural sites, while ALA and EPA tended to have higher proportions in aquatic insects in agricultural than forested sites (Table 2, Additional file 1: Figure S2).

Furthermore, in summer caddisflies revealed significant differences in FA profiles between forested and agricultural sites (ANOSIM: $R = 0.1$, *p*-value = 0.026, Table 1). ALA, EPA, LIN, EA, ODA and GLA contributed most to these differences. The former three FA tended to have higher proportions in caddisflies in agricultural sites than forested sites and the latter three FA in forested sites (Table 2, Additional file 1: Figure S2). Overall, these FA explained between 20% (ALA) and 7% (LIN) of the differences in FA profiles of caddisflies between land-use types (Table 2).

Table 2 Results of similarity percentage (SIMPER) analyses conducted when significant differences between forested and agricultural sites in fatty acid (FA) profiles were found with analysis of similarity (ANOSIM)

Order	Season	FA	Average	Standard deviation	Ratio	Average agriculture	Average forest	Cumulative contribution	Single contribution
Mayflies	Spring	EPA	0.09	0.06	1.51	0.31	0.19	0.22	0.22
		ALA	0.05	0.05	0.99	0.09	0.12	0.35	0.13
		ODA	0.05	0.05	1.13	0.23	0.27	0.48	0.13
		EA	0.04	0.04	1.08	0.05	0.10	0.58	0.10
		ELA	0.03	0.03	0.82	0.03	0.05	0.64	0.06
		LIN	0.03	0.03	0.89	0.07	0.08	0.70	0.06
Caddisflies	Summer	ALA	0.09	0.06	1.36	0.22	0.16	0.20	0.20
		EPA	0.06	0.05	1.33	0.21	0.17	0.34	0.14
		EA	0.05	0.04	1.33	0.10	0.15	0.47	0.13
		ODA	0.05	0.05	1.13	0.11	0.16	0.59	0.12
		GLA	0.04	0.03	1.16	0.06	0.08	0.68	0.09
		LIN	0.03	0.02	1.22	0.05	0.04	0.75	0.07
Non-biting midges	Spring	ALA	0.1	0.07	1.39	0.22	0.19	0.20	0.20
		GLA	0.1	0.08	1.19	0.11	0.21	0.41	0.21
		EPA	0.08	0.05	1.40	0.18	0.06	0.57	0.16
		ODA	0.05	0.04	1.27	0.24	0.25	0.68	0.11
		EA	0.03	0.03	1.19	0.06	0.07	0.75	0.07

Average is the contribution of FA to the average between-group dissimilarity, ratio is the average to standard deviation ratio, average agriculture is the average abundance in agricultural sites and average forest the average abundance in forested sites. FA with the closest higher cumulative contribution to 0.7 are presented.
EPA eicosapentaenoic acid (20:5n-3), *ALA* alpha-linolenic acid (18:3n-3), *GLA* gamma-linolenic acid (18:3n-6), *LIN* linoleic acid (18:2n-6c), *ELA* elaidic acid (18:1n-9t), *ODA* octadecanoic acid (18:0), *EA* eicosanoic acid (20:0)

Agricultural stressors associated with FA profiles

The partial RDA (first axis: $F = 3.7062$, p-value $= 0.025$, second axis: $F = 1.9292$, p-value $= 0.359$) of the FA profiles of all analyzed aquatic insects (non-biting midges, mayflies, stoneflies, caddisflies) included water temperature, EC, percentage of pool habitats, oxygen saturation as well as percentage of shading (Fig. 3a) and explained 5% of the variation in FA profiles (Additional file 1: Table S7). For instance, FA profiles of aquatic insects of forested sites were associated with increasing percentage of shading and FA profiles of aquatic insects of agricultural sites with increasing percentage of pool habitats.

In the final partial RDA (first axis: $F = 7.5766$, p-value $= 0.007$, second axis: $F = 3.2750$, p-value $= 0.084$), the variables oxygen saturation, phosphate as well as nitrate concentration, EC, water temperature, percentage of pool habitats and shading, explained 12% of the variation of FA profiles of non-biting midges (Fig. 3b, Additional file 1: Table S7). Increasing percentage of shading and oxygen saturation were associated with FA profiles of non-biting midges in forested sites.

No RDA axes (first axis: $F = 2.8377$, p-value $= 0.152$, second axis: $F = 1.7128$, p-value $= 0.431$) were significant for mayflies and stoneflies (first axis: $F = 1.7548$, p-value $= 0.249$, second axis: $F = 1.0624$, p-value $= 0.419$). The agricultural stressors EC, pesticide toxicity, phosphate as well as nitrate concentration were selected for the final partial RDA for mayflies and percentage of shading and phosphate concentration for stoneflies (Fig. 3c, d). The agricultural stressors explained for mayflies and stoneflies 6% of the variation in FA profiles (Additional file 1: Table S7).

For caddisflies, the final partial RDA (first axis: $F = 2.9864$, p-value $= 0.023$, second axis: $F = 0.9749$, p-value $= 0.784$) contained percentage of pool habitats, pesticide toxicity and shading (Fig. 3e), though only 4% of variation were explained by the agricultural stressors (Additional file 1: Table S7). Pesticide toxicity was associated with the FA profiles of aquatic insects in agricultural sites.

For spiders no RDA axes were significant (first axis: $F = 2.4217$, p-value $= 0.253$, second axis: $F = 2.1278$, p-value $= 0.230$) and air temperature, percentage of shading, phosphate as well as nitrate concentration explained 3% in the variation of the FA profiles in the partial RDA (Fig. 3f).

Discussion

Comparing FA export between agricultural and forested sites

The export of total FA of aquatic insects was approximately 26–29% higher in forested than agricultural sites, although the biomass of aquatic insects was 61–68% higher in agricultural than forested sites [29]. At individual time points only significant differences of the total PUFA export were observed: in spring more PUFA were exported in forested than agricultural sites. In contrast, at individual time points the biomass of aquatic insects was higher in agricultural than forested sites in spring [29]. Additionally, the biomass of non-biting midges and mayflies was higher in agricultural than forested sites [29], while the FA, SFA, MUFA and PUFA export via non-biting midges and mayflies was higher in forested than agricultural sites. This indicates that the FA, SFA, MUFA, as well as PUFA content in aquatic insects is lower in agricultural than forested sites, and in turn the quality of aquatic insects in terms of FA, SFA, MUFA and PUFA export is decreased in agricultural sites in comparison to forested sites.

The agricultural site was always downstream of the forested site. Hence, the results may partially be influenced by a location effect, where downstream sites are typically larger [91], though the distance between sites within one stream was low and a similar study found that invertebrate populations from the upstream and downstream site were connected [92]. Thus, the spatial location effect is likely negligible compared to the influence of land use. One reason for the lower FA, SFA, MUFA, and PUFA export in agricultural sites may have been energy costs due to agricultural stressors (for details of agricultural stressors see "Agricultural stressors associated with FA profiles"). Typically, in moderate stress conditions the cost for maintenance increases to meet the enhanced energy demand for protection against stressors and the repair of damages [92, 93]. This can lead to a consumption of energy reserves like lipids like neutral lipid FA [93–95]. Additionally, ingested FA, including PUFA, may be directly oxidized (β oxidation) to carbon dioxide and water to generate adenosine triphosphate (ATP) [96, 97]. The β oxidation of FA is a very efficient ATP source, which can facilitate ATP-dependent mechanisms like the elimination of toxicants, detoxification and the repair or replacement of damaged molecules [98]. Furthermore, agricultural stressors like pesticides can alter the sex ratio of emergent aquatic insects [99] and FA profiles as well as export can differ between male and female aquatic insects [37, 100, 101]. For example, female non-biting midges were associated with higher SFA levels and a higher total FA content, while male non-biting midges were associated with higher PUFA levels [101]. Future studies, including among others, the sex ratio of aquatic insects and the energy costs to cope with agricultural stressors can help to better understand the decrease in FA, SFA, MUFA, as well as, PUFA export in agricultural sites, despite the higher biomass export in comparison to forested sites.
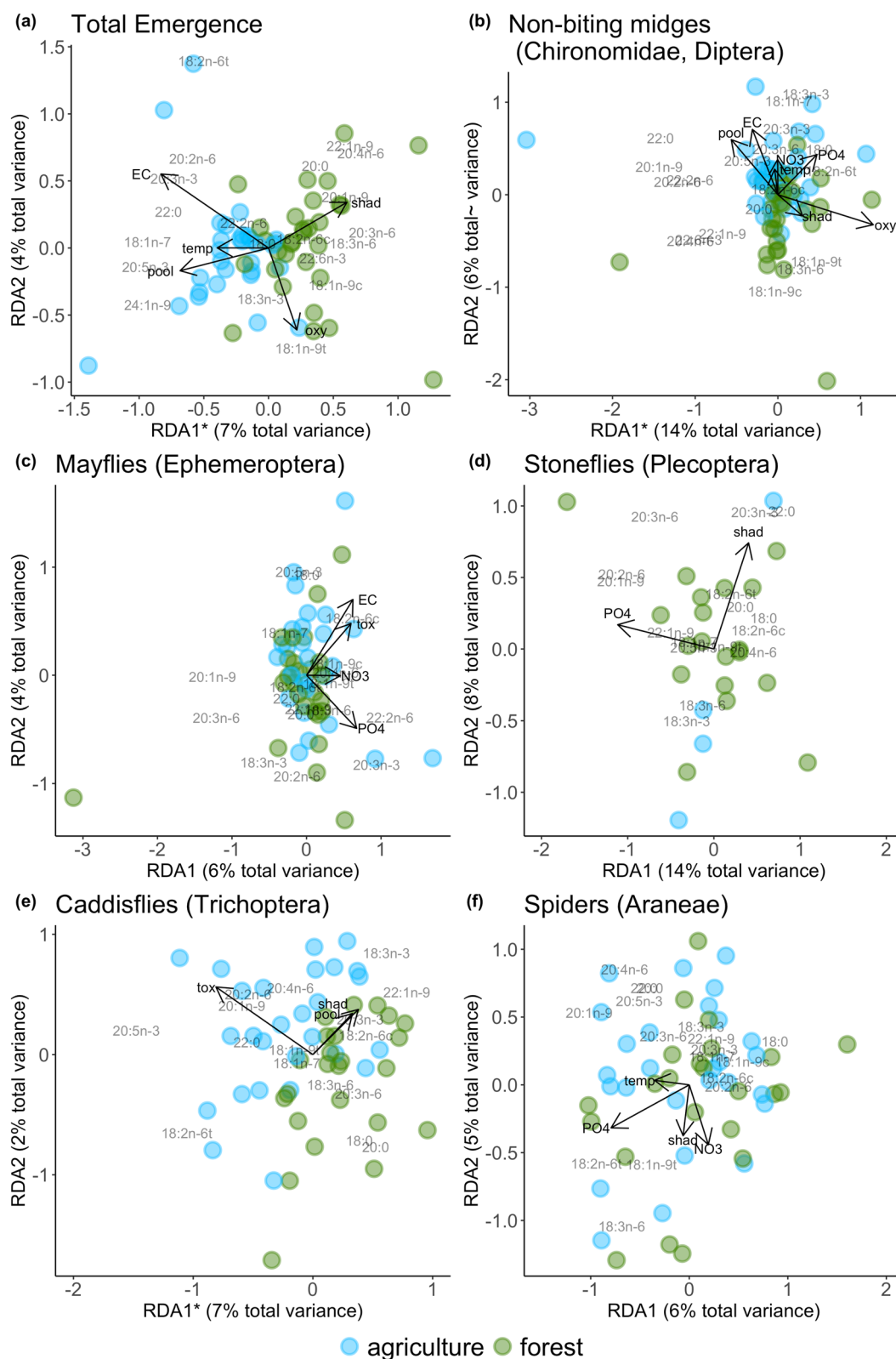
Fig. 3 Plot of the partial redundancy analysis (RDA) with stream and season as covariates. Colors indicate land-use type: blue = agriculture, green = forest. Asterisks at axes mark significance. *NO3* nitrate concentration, *PO4* phosphate concentration, *oxy* oxygen saturation, *pool* percentage pool habitats, *temp* temperature (for spiders: air temperature, for emergent aquatic insects: water temperature), *tox* pesticide toxicity, *EC* electrical conductivity, *shad* percentage of shading

The smaller PUFA export in agricultural sites may have consequences for riparian predators like decreased growth and impaired immune response [25–27]. The extent of the effects on riparian predators depends on their foraging strategy [24] and riparian predators may need to invest more time and energy in foraging to meet their PUFA demand, if the PUFA content in their food sources is decreased [102–104]. This may in turn impair their fitness [102, 104, 105].

The difference in FA export via stoneflies should be interpreted with caution, because only four observations (three in spring, one in summer) were available for agricultural sites, while in forested sites 33 observations (17 in spring, 13 in summer, three in autumn) were used in the HGAM. Furthermore, our sampling method missed stoneflies emerging by crawling on land, which may have led to an underestimation of the FA, SFA, MUFA and PUFA export via certain stonefly families. Notwithstanding, previous studies in our study region found only few stoneflies in agricultural streams [82, 106, 107]. Our sampling intervals may have allowed aquatic insects to utilize FA while being trapped for maximum 2–3 days, thereby resulting in a potential underestimation of FA export. Given that the sampling intervals were similar in both land-use types, this very likely does not affect comparisons between land-use types. Furthermore, the consumption of aquatic prey by riparian predators may also occur several days after the day of their emergence. Thus, the sampling interval may provide a realistic estimation of FA available for riparian predators. However, without being trapped the FA profiles of emergent aquatic insects feeding as adults (non-biting midges, stoneflies, some caddisflies) [108–110] may also change due to the consumption of terrestrial food sources. How the feeding as adults will affect the FA profiles of emergent aquatic insects will depend, for instance, on the assimilation time of terrestrial-derived FA in the tissue of adult emergent aquatic insects and their ability to synthesize FA [111]. Additionally, we omitted the FA content of other fly families than non-biting midges in the total export of FA, which also lead to an underestimation of the total FA export, though the biomass of non-biting midges peaked at least a factor of ten higher than the biomass of other fly families [29].

In spring, the PUFA export was higher than in the other seasons in both land-use types. Therefore, during spring riparian predators may have benefited most from the nutritional quality in the sense of PUFA of aquatic insects, because PUFA can enhance growth, reproductive success and immune response in riparian predators [25–27, 104]. Especially, for riparian birds breeding in spring this is favorable, because PUFA intake via aquatic insects seems to be crucial for their reproductive success [104, 112].

Differences of FA profiles between agricultural and forested sites

We found differences in FA profiles of mayflies, caddisflies and non-biting midges between agricultural and forested sites (Table 1, 2, Additional file 1: Figure S2). In all three orders, ALA, EPA, ODA and EA contributed most to the differences in FA profiles. EPA tended to have higher proportions in agricultural than forested sites, while ODA and EA tended to reach higher proportions in forested sites (Table 2, Additional file 1: Figure S2).

The differences across FA profiles may have originated from direct effects on aquatic insects. For instance, agricultural stressors probably required aquatic insects of agricultural sites to invest more energy into maintenance and repair processes [92, 93] compared to insects of forested sites. Thereby, FA may have been used to meet the increased energy demand [96]. Specific agricultural stressors are discussed in section "Agricultural stressors associated with FA profiles".

Furthermore, the differences in FA profiles of aquatic insects may have originated from indirect effects in the aquatic food web, because FA are transferred from primary producers to higher trophic levels [19, 20]. In headwater streams, conditioned leaves may be an important food source [91, 113]. Conditioned leaves are colonized by microorganisms like aquatic fungi, which have been shown to alter the FA content of leaves [114]. The FA octadecanoic acid (18:0, ODA) is commonly found in aquatic fungi [114, 115] and tended to be higher in forested than agricultural sites. The percentage of shading tended to be smaller in agricultural than in forested sites (Additional file 1: Figure S3), which can lead to increased primary production in comparison to forested sites [86]. Therefore, the tendency of higher eicosapentaenoic acid (20:5n-3, EPA) levels of aquatic insects in agricultural sites may have originated from the relatively high EPA levels in aquatic primary producers [15, 19, 116]. EPA is an important membrane compound and serves as precursor for many bioactive molecules, e.g., eicosanoids [117, 118], this may affect the quality of emergent aquatic insects as food source for riparian predators. While the lower FA, SFA, MUFA, and PUFA content compromises the quality of emergent aquatic insects, the potential increase in single FA like EPA enhances the quality. Therefore, a higher EPA content may buffer potential negative effects of an overall lower FA content.

In addition, a turnover of aquatic insect families between forested and agricultural sites was shown [29] and may have contributed to the differences between FA profiles, driven by differences in the functional feeding groups and the trophic transfer of FA [37]. For instance, in summer four caddisfly families (Goeridae, Glossosomatidae, Phryganeidae, Philopotamidae) emerged only

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in forested sites and two caddisfly families (Lepidostomatidae, Limnephilidae) only in agricultural sites [29]. The latter two families are shredders, while the families emerging only in the forested sites belonged to the functional feeding groups grazers, shredders, collectors and predators.

Although we found differences in FA profiles of mayflies, caddisflies and non-biting midges between forested and agricultural sites, we did not find any differences in FA profiles of spiders between forested and agricultural sites. Spiders are capable of extracting nutrients selectively from their prey to avoid nutritional imbalances [119]. Moreover, spiders usually consume aquatic and terrestrial insects [12, 13], thus also terrestrial insects contribute to the spiders' FA profile. Additionally, spiders are able to synthesize EPA de novo [23], while it is unknown if they can also synthesize other FA. Therefore, the synthesis of EPA by spiders may have masked potential land-use related differences. In previous studies the EPA content in ground dwelling spiders correlated with the biomass of stoneflies [39], PUFA profiles of riparian spiders were more similar to the PUFA profiles of emerging aquatic insects than terrestrial insects [120], and riparian spiders relied more on the PUFA content of aquatic emergent insects than spiders further away from a forested lake [17].

However, it remains unclear how other riparian predators may have been affected by land use in our study, because the amount of aquatic insects in the diet of riparian predators can vary with the foraging strategy. For instance, ground-hunting and web-building spiders differ in their proportion of aquatic insects in their diet and in environmental factors affecting the amount of consumed aquatic insects [12, 13]. Additionally, birds that are aerial insectivores may consume more aquatic insects than gleaners, bark-probers, as well as ground-foragers [121] and therefore may rely more on aquatic insect consumption to meet their PUFA demand [17, 26] than gleaners [24]. Future studies including riparian predators with different foraging strategies are needed to understand the effect of land use on FA profiles in the riparian food web better.

Agricultural stressors associated with FA profiles

Generally, environmental variables associated with impaired habitat quality for aquatic insects and spiders [12, 14, 29, 33, 34] were less favorable in agricultural than forested sites, e.g., higher pesticide toxicity as well as lower percentage of pool habitats and less shading (Additional file 1: Figure S3, Table S1). Nonetheless, little variation in FA profiles of aquatic insects in total and on order level was explained by these variables.

Primary production and nutrient availability in streams depend on light availability and can decrease with the increase of shading [86]. Therefore, shading and nutrients may affect aquatic insects' FA profiles by the trophic transfer of FA from primary producers to higher trophic levels [15, 19, 73, 116]. The effect of pool habitats on FA profiles may be explained by differences at the base of the food web (algal primary production, conditioned leaves, [122, 123]) and the occurrence of different functional feeding groups in pool and riffle habitats [124], which in turn can result in different FA profiles. EC (commonly used to estimate the salinity of water) can cause osmoregulatory stress and can be associated with ions that are toxic for aquatic insects [125]. Together with pesticide toxicity, EC can increase the energy demand of aquatic insects [92, 93], followed by FA utilization to fulfill the enhanced energy demand [96], and thereby altering the FA profiles of aquatic insects. To our knowledge, it is currently not known if specific FA are utilized or FA in general. Increasing temperature, as observed in agricultural sites, can cause FA profile alterations, as organisms adapt their PUFA content to adjust membrane fluidity to higher temperatures [83, 84]. However, the land-use intensity in the studied agricultural sites was similar. Furthermore, the intensity of agriculture and potentially of agricultural stressors may increase in the future, as for instance globally more pesticides with a higher toxicity towards aquatic insects are used [126–129].

Most variation in all FA profiles was explained by stream and season (Additional file 1: Table S7). The families of aquatic insects differed across streams and seasons. For instance, the mayfly families Arthropleidae and Siphlonuridae emerged only in summer [29]. Therefore, the composition of aquatic insect assemblages may be more important for the FA profiles than agricultural stressors. This is partly in line with Kowarik et al. [39], who only found an effect of season on the FA profiles of aquatic insects, but not of environmental variables. Furthermore, the FA profiles of species of non-biting midges were shown to differ [37]. Future studies identifying underlying mechanisms of the differences between families are needed to estimate the effect of a turnover of aquatic insect assemblages between land-use types on FA profiles.

Conclusion

The quantity of PUFA export via aquatic insects was decreased in agricultural sites in comparison to forested sites. Additionally, we found differences in FA profiles of aquatic insects between land-use types. We suggest a decreased quality as food source for riparian predators relying on the dietary intake of PUFA. Future studies are needed to identify the mechanisms behind the lower

PUFA content in agricultural sites to implement strategies maintaining the PUFA content in aquatic insects. These strategies may focus on the mitigation of stressors that may affect aquatic insects, for example decreasing of pesticide exposure and reforestation to decrease temperature in agricultural streams. Furthermore, our results can be incorporated in modeling food-webs or meta-ecosystems to increase our understanding of effects of timing, food quantity as well as quality in these systems.

Abbreviations
ALA   Alpha-Linolenic acid
ATP   Adenosine triphosphate
EC   Electrical conductivity
EA   Eicosanoic acid
ELA   Elaidic acid
EPA   Eicosapentaenoic acid
FA   Fatty acids
GLA   Gamma-Linolenic acid
LIN   Linoleic acid
MUFA   Mono unsaturated fatty acids
ODA   Octadecanoic acid
PUFA   Polyunsaturated fatty acids
SFA   Saturated fatty acids

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12302-023-00831-3.

Additional file 1: Figure S1. Sampling sites in south-western Germany (European Environment Agency, 2007). **Table S1.** Mean and standard deviation (sd) of all environmental variables monitored during the field experiment in forested and agricultural sites. **Table S2.** Name, CAS-number, acute EC50 value, taxon and source of EC50 values of the pesticides used in the calculation of the logarithmic sum of the toxic unit (sumTU). **Table S3.** Name, CAS-number, *koc* (soil organic carbon–water partitioning coefficient) value of the pyrethroids used in the calculation of the particle-associated concentration of an estimate of the bioavailable concentration in water. **Table S4.** Time periods, in which samples of emergent aquatic insects were pooled on order level for fatty acid analysis. **Table S5.** Results of hierarchical generalized additive models (HGAM) to identify seasonal patterns of fatty acid export via aquatic insects. **Figure S2.** Mean proportion and standard deviation of fatty acids (FA). **Table S6.** 95% confidence intervals of the total export of all fatty acids, saturated fatty acids, monounsaturated fatty acids, and polyunsaturated fatty acids during the primary emergence period in forested and agricultural sites. **Table S7.** Results of the partial redundancy analysis (RDA) and RDA. **Figure S3.** Differences of environmental variables between forested and agricultural sites visualized with violin plots.

Author contributions
KO, VCS, MLiess, RBS designed the study; KO, VCS, MLink selected the sampling sites; KO, VCS, MLink conducted the fieldwork; KO and LR conducted the fatty acid analysis and identified the spiders; KO identified the insects, analyzed the data and drafted the manuscript. All authors revised the manuscript.

Declarations

Competing interests
The authors declare no competing interests.

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