Stream degradation affects aquatic resource subsidies to riparian ground-dwelling spiders

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HIGHLIGHTS

- We compared emergent insect biomass/ EPA export between degraded and natural stream.
- Similar total insect biomass and EPA export from degraded and near natural stream
- Shift in contribution of insect groups to export; less stoneflies in degraded stream
- Lower EPA in ground spiders at sites with few stoneflies using crawling emergence
- Functional traits as well as nutritional quality should be considered in bioassessment.

GRAPHICAL ABSTRACT
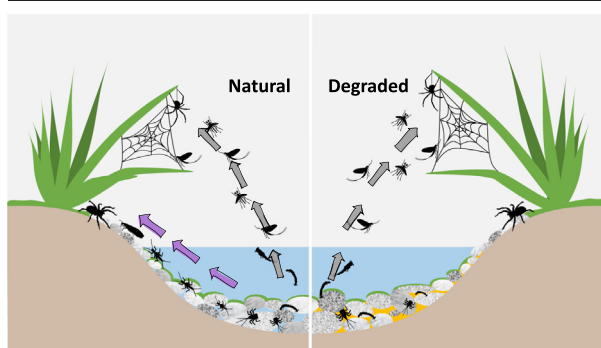
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ABSTRACT

Freshwater systems have undergone drastic alterations during the last century, potentially affecting cross-boundary resource transfers between aquatic and terrestrial ecosystems. One important connection is the export of biomass by emergent aquatic insects containing omega-3 polyunsaturated fatty acids (PUFAs), especially eicosapentaenoic acid (EPA), that is scarce in terrestrial systems. Because of taxon-specific differences in PUFA content and functional traits, the contribution of different insect groups should be considered, in addition to total biomass export. In this context, one important trait is the emergence mode. Stoneflies, in contrast to other aquatic insects, crawl to land to emerge instead of flying directly from the water surface, making them accessible to ground-dwelling predators. Because stoneflies are especially susceptible to environmental change, stream degradation might cause a mismatch of available and required nutrients, particularly for ground-dwelling predators. In this study, we estimated emergent biomass and EPA export along two streams with different levels of habitat degradation. The EPA content in aquatic insects did not differ with different degrees of habitat degradation and total biomass export in spring was with 7.9 ± 9.6 mg m^{-2} day^{-1} in the degraded and 7.3 ± 8.5 mg m^{-2} day^{-1} in the natural system, also unaffected. However, habitat degradation substantially altered the contribution of crawling emergence to the total export in spring, with no biomass export by stoneflies at the most degraded sites. The EPA content in ground-dwelling spiders was correlated with emergent stonefly biomass, making up only 16.0 ± 6.2 % of total fatty acids at sites with no stonefly emergence, but 27.3 ± 3.0 % at sites with highest stonefly emergence. Because immune function in ground-dwelling spiders has been

connected to EPA levels, reduced crawling emergence might impact spider fitness. Functional traits, like emergence mode as well as nutritional quality, should be considered when assessing the effects of stream degradation on adjacent terrestrial ecosystems.

1. Introduction

Many streams and associated floodplains have undergone severe changes over the last century (Tockner and Stanford, 2002; Verhoeven, 2014). In Europe and across the globe, humans have significantly modified almost all large rivers, resulting in drastically changed morphology and increased nutrient levels (Petts et al., 1989; Malmqvist and Rundle, 2002; Tockner et al., 2009). Although various measures were implemented under the European Water Framework Directive to improve stream health, many issues remain unresolved (Hering et al., 2010; Voulvoulis et al., 2017). One major problem is the multitude of structures, such as dams and weirs, built along river networks. In Europe, for example, at least 1.2 million barriers fragment fluvial networks (Belletti et al., 2020) and disrupt bed load transport, causing major bed load deficits and changes in stream morphology (Golz, 1994; Kondolf, 1997). Bed load deficits or so called "hungry waters" lead to bank erosion, which can cause the development of steep banks and increased fine sediment input into streams (Kondolf, 1997). Fine sediment, where deposited in large quantities, can have strong negative impacts on various instream assemblages, ranging from periphyton to macroinvertebrates and fish (see reviews by Wood and Armitage, 1997, Kemp et al., 2011, Jones et al., 2012). One negative impact of fine sediment is the clogging of interstitial pore spaces in stream beds, which typically leads to homogenization of instream habitats and reduction of accessibility for many stream organisms (e.g., Ryan, 1991; Richards and Bacon, 1994; Peralta-Maraver et al., 2019).

It is well established that both high nutrient loads and fine sediment input, singly or in combination, act as stressors on aquatic organisms (Matthaei et al., 2010; Wagenhoff et al., 2011). However, instream habitat degradation also affects adjacent terrestrial ecosystems connected in a tangled web via multiple resource pathways. For example, aquatic insects that develop in aquatic ecosystems before they emerge as adults transfer biomass to terrestrial ecosystems (Baxter et al., 2005). Human impacts, including changes in nutrient levels and stream morphology, alter aquatic insect assemblages and can disrupt lateral connectivity to riparian areas, thereby modifying cross-boundary transfers of resource subsidies (Muehlbauer et al., 2020). Riparian areas, the transitional zones linking streams and terrestrial ecosystems, are unique habitats that support many specialist species with specific resource requirements (Ramey and Richardson, 2017; Twining et al., 2018b). For instance, many riparian predators, including spiders, lizards, and birds, depend on the influx of resource subsidies from aquatic systems via emergent insects (Sabo and Power, 2002; Kato et al., 2003; Paetzold et al., 2006; Twining et al., 2018b).

Aquatic resource subsidies are important because aquatic and terrestrial resources are not nutritionally reciprocal for consumers (Twining et al., 2019). Aquatic subsidies are a rich source of omega-3 polyunsaturated fatty acids (PUFAs), especially eicosapentaenoic acid (EPA), because aquatic organisms, including emergent insects, contain on average 6 times more omega-3 PUFAs than terrestrial insects (Hixson et al., 2015; Mathieu-Resuge et al., 2021). EPA is synthesized by aquatic primary producers and accumulates in many aquatic consumers of higher trophic levels, while it is scarce in terrestrial food webs (Twining et al., 2019). EPA is essential for maintaining crucial physiological functions in animals; e.g., it is an important regulator of eicosanoid biosynthesis and therefore immune response regulation (Schlotz et al., 2016). EPA intake has been proven beneficial for different animal groups, including aquatic invertebrates (Martin-Creuzburg et al., 2018) and tree swallows, that can be considered riparian specialists (Twining et al., 2016). Biosynthesis of EPA and other long-chain PUFAs like docosahexaenoic acid (DHA) from shorter chain dietary precursor PUFAs, which are available in terrestrial systems, is often thought to be inefficient and costly (Pawlosky et al., 1997; Brenna et al., 2009; Castro et al., 2012). Therefore, riparian predators may rely

on consumption of aquatic organisms to cover their EPA demands, having not developed or lost the necessary metabolic pathways to produce EPA in adequate amounts (Twining et al., 2018a). However, it should be noted that more generalist species like blue tits (common bird) do not seem to depend on aquatic-derived EPA (Twining et al., 2021).

Human degradation of streams can affect aquatic-derived EPA availability for riparian predators through an interaction by a number of factors. First, human impacts such as enhanced nutrient loads can reduce EPA content at the base of aquatic food chains; e.g., by altering periphyton assemblages to those containing less EPA (Cashman et al., 2013). Lower EPA production at the base of the food chain is transferred to higher trophic levels (consumers), causing aquatic organisms including emergent insects to contain less EPA (Müller-Navarra et al., 2004; Taipale et al., 2016; Scharnweber et al., 2019). Second, the abundance of some stream invertebrates also can be reduced in degraded streams through negative impacts of high nutrient or fine sediment loads; e.g., aquatic invertebrates that emerge from the stream during their lifecycle seem to be particularly susceptible to environmental stressors (Manning and Sullivan, 2021). Consequently, the reduced biomass export via emerging insects will reduce EPA export to riparian zones. Third, EPA availability for riparian predators can be influenced by shifts in community composition of emergent insects possessing differing functional traits; e.g., mode of emergence. For instance, chironomids (Diptera) are typically abundant in degraded streams with high amounts of fine sediment, while other, more sensitive taxa, e.g. stoneflies (Plecoptera), may decline, (Wood and Armitage, 1997; McCaffrey, 2021). While most insects, such as chironomids, emerge directly from the water column and fly away, stoneflies crawl to the shore to emerge (Merritt and Cummins, 1996). This emergence behavior makes stoneflies easy prey for ground-dwelling predators, whereas other insects that emerge by flight are presumably less accessible. Indeed, stoneflies have been hypothesized to be a major aquatic food source for riparian ground-dwelling spiders (Paetzold et al., 2005). Consequently, lower stonefly biomass could reduce access to aquatic subsidies for ground-dwelling riparian predators such as wolf spiders. A negative effect of lower access to EPA seems likely because EPA content in ground-dwelling spiders has been linked to immune function (Fritz et al., 2017), although the impact on fitness remains unclear. While organisms can cope with limitations of certain nutrients by using specific metabolic pathways or foraging techniques, adaptation might be too slow to keep up with rapid human-caused environmental changes (Van Der Jeugd et al., 2009; Shipley et al., 2022). This asynchrony can lead to a mismatch between availability and the requirement of essential nutrients.

Emergent aquatic insects clearly transfer important resources to riparian areas, but the question remains if degraded streams provide subsidies in adequate quantity and quality to terrestrial systems. Here, we quantified the biomass export via emergent insects along two stream networks in Switzerland and compared the emerging insect assemblage. While one stream had near-natural conditions, the other suffered from morphological alterations. Further, instream conditions along each stream differed, with higher nutrient loads and fine sediment content at some sites, particularly in the degraded system. We examined if there were differences in the quantity (biomass) and quality (PUFA content) of emergent insects between and along the two stream networks in relation to differences in nutrients and streambed condition. Considering accessibility of different emergent insect groups for riparian predators, we compared export via different emergence pathways and investigated the connection between the biomass of "crawling" emergence and EPA content in a ground-dwelling predator (wolf spider). We hypothesized that: 1) the biomass export from the more degraded system (particularly at sites with greater degradation) will be lower than from the near-natural system; 2) emergent insect composition at more degraded sites will differ from near-natural sites with more insensitive (e.g., chironomids)

and less sensitive groups (e.g., stoneflies), thereby reducing "crawling" emergence in particular; 3) EPA content will be lower in emergent insects from the degraded than the near-natural system; and 4) EPA content in riparian ground-dwelling spiders is connected to the biomass of emerging stoneflies due to their crawling emergence mode.

2. Material and methods

2.1. Site description

We sampled along two adjacent 6th order streams (Necker and Glatt) in the Thur catchment in northeast Switzerland (Fig. 1). The Necker is a system with a natural flow and sediment regime that mostly runs through rural and forested areas. The Necker has a long-term annual mean discharge of 3.3 m³/s (hydrograph station Achsäge) and a basin draining 126 km² that ranges in elevation from 550 to 1550 m asl. Elevation of sampling sites ($n = 6$) ranged from 550 to 740 m asl. The Glatt has undergone many anthropogenic changes, including construction of multiple barriers that prevent bed load transport, leading to a strong bed load deficit (50–80 %) and major morphological impairment in downstream sections. The Glatt mostly flows through an agricultural landscape with mixed forested and urban areas. Mean annual discharge is 2.7 m³/s (hydrograph station Oberbühren) and the drainage area of the Glatt basin is 90 km², ranging in elevation from 480 to 950 m asl. Elevation of Glatt sampling sites ($n = 6$) ranged between 500 and 620 m asl.

2.2. Field sampling

2.2.1. Physico-chemical parameters

At each site, we recorded electrical conductivity (µS cm⁻¹ at 20 °C) (WTW LF340, Wielheim, Germany) and collected a water sample in a 0.5-l plastic bottle (rinsed 3 times, no headspace). Samples were brought back to the laboratory for chemistry analysis of pH, alkalinity, nitrate, nitrite, total nitrogen (TN), ortho-phosphate (OP), total phosphorus (TP), dissolved organic carbon (DOC), total organic carbon (TOC) and total inorganic carbon (TIC) as detailed in Tockner et al. (1997).

2.2.2. Stream bed characteristics

Stream bed characteristics were assessed using three different methods at each site: (1) Wolman pebble counts, (2) visual estimates of the degree of clogging, and (3) quantitative assessment of the surface fine sediment content. We conducted Wolman substrate counts (200 particles) to assess the grain size distribution of the river bed for each site (Wolman, 1954; Bunte and Abt, 2001). We blindly selected a grain each step along longitudinal transects and measured the b-axis via a gravelometer. At each site, the proportion of fine sediment (defined here as particles <2 mm) and degree of clogging was assessed using a visual estimate following the protocol of Schälchli et al. (2002). The surface substrates of exposed gravel bars were removed by hand at three points to enable access to the interstitial pore space below. The fine sediment content and clogging of the interstitial space was subsequently assessed through comparison with reference photographs in the field, classifying them into 5 categories as described in Mathers et al. (2021a): 1 – coarse grained, little sand, no cohesive deposits and coarse open pore space; 2 – mix of size classes with some sand present, no cohesive deposits and fine open pore space; 3 – slightly solidified substrate, fine pore space infilled with cohesive particles accounting for approximately 25 % of surface area, majority of other pore space infilled with sand; 4 – strongly solidified substrate, fine pore space infilled with cohesive particles accounting for approximately 50 % of surface area, remaining pore space infilled with sand; and 5 – strongly solidified substrate, fine pore space infilled with cohesive particles accounting for approximately 100 % of surface area. An average of the assessment (category 1–5) of the
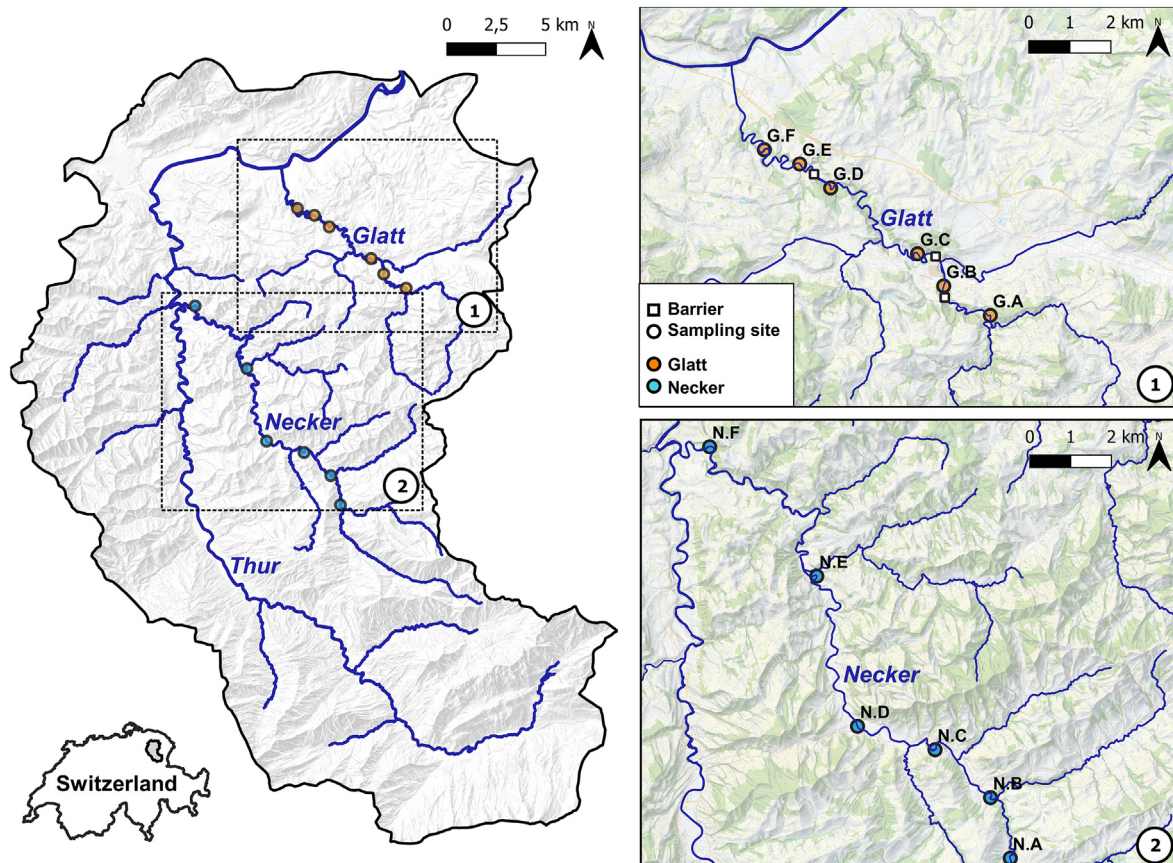

Fig. 1. Map of the Thur catchment (northeast Switzerland) with sampling sites on the Necker (N) and Glatt (G). Circles represent sampling sites; squares represent major barriers blocking bed load transport.

three points was used as an estimate for the reach. In addition, we used a quantitative resuspension technique, as described by Duerdoth et al. (2015), to quantify fine sediment deposits. In short, an open-ended cylinder was inserted into the riverbed at four locations at the site (two erosional and two depositional) and the water within the cylinder vigorously agitated for ca. 60 s to suspend surface fine sediment into the water column before a 50 ml water sample was taken. Samples were routinely processed in the laboratory for mineral content and converted to mass per m^2 using water depths in the stilling well (Mathers et al., 2021b). For each site, the geometric mean of the four samples was taken as the surface fine sediment content measure.

2.2.3. Sampling of emergent aquatic insects

Emergent aquatic insects were captured alive using floating emergence traps with a base area of 0.25 m^2 and mesh size of 100 μm between April and October 2019 to assess emergent aquatic insect biomass and community composition. Emergence traps were deployed weekly (2–3 days per week) from beginning of April to mid-May and afterwards monthly (2 × 2–3 days per month) until end of October. Overall, emergence traps were deployed for 17 sampling periods: 7 periods in spring (April/May), 6 in summer (June/July/August), and 4 in autumn (September/October). No sampling was conducted during winter (November to March) as water temperatures were low and minimal emergence was expected. Three traps were deployed per site, each covering a different habitat type (fast flowing, slow flowing and shallow habitats near the shoreline) to be able to estimate overall biomass export by insects with differing habitat preferences and emergence modes. Collected insects were returned to the laboratory, identified to the family level and frozen ($-20\,°C$ or $-80\,°C$ depending on storage time) until further analysis.

2.2.4. Spider sampling

Riparian ground-dwelling spiders were collected in spring (April/May) 0–2 m from the shoreline using a mouth aspirator. A minimum of 3 individuals were collected per site, returned to the laboratory, and kept alive in containers overnight to allow gut clearance. Afterwards, they were frozen until further analysis. All collected individuals belonged to the family of wolf spiders (Lycosidae) from the genera *Pardosa* or *Pirata/Piratula*.

2.3. Laboratory procedures

2.3.1. Fatty acid analysis

We analyzed fatty acids of 233 emergent insect samples (85 Diptera, 75 Ephemeroptera, 73 Plecoptera) and 24 ground-dwelling spiders collected from 8 sites (4 per stream) (see Kowarik et al., 2021). We found only a few single individuals of Trichoptera, which were therefore not included in the analysis. In addition, we analyzed 12 ground-dwelling spider samples collected in spring from a further 4 sites used in this study. Emergent insect and spider samples were freeze-dried and weighed using an ultrafine balance to estimate biomass export. We extracted weighed samples in dichloromethane/methanol (2:1 *v*/v) over night and added internal standard for analysis. We left samples for 5 min in an ultrasound bath and removed particles by centrifugation (3500 *g*, 5 min). We evaporated samples under nitrogen to dryness and resuspended in 4 ml methanolic HCl. We incubated samples solved in methanolic HCl for 20 min at 60 °C to obtain fatty acid methyl esters (FAMEs). Hexane was added after samples had cooled down, each sample was thoroughly mixed, and the upper hexane phase was transferred to a new vial. We reiterated this process two more times and pooled the hexane fractions into a composite sample, which was evaporated under nitrogen to dryness. We resuspended each sample in 20 to 200 μl hexane, depending on initial sample dry mass. We analyzed samples for FAME content using gas chromatography (7890B gas chromatograph, Agilent Technologies, Waldbronn, Germany); see configuration details in Martin-Creuzburg et al. (2010). We identified fatty acids based on their retention time and mass spectra, and quantified amounts by comparison to internal standards using multipoint calibration curves of known concentration (for details see Martin-Creuzburg et al. (2017)).

2.4. Data analysis

2.4.1. Environmental variables

All analyses were conducted in R 3.6.2 (R Core Team, 2019). To characterize substrate conditions at each site, we used the Wolman pebble counts to calculate grain size percentiles and the statistical parameters of median, percentiles, sorting, skewness and kurtosis (Bunte and Abt, 2001). In addition, we estimated substrate diversity by calculating Shannon's diversity index ("diverse", package "vegan"; Oksanen et al. (2019)), an ecologically meaningful spatial heterogeneity index, based on the grain size distribution (Mathers et al., 2021a). The index has been used in different fields as a measure of habitat heterogeneity (Yarnell et al., 2006; Turley et al., 2017). Differences in stream-bed characteristics and physico-chemical parameters between the two rivers were tested using one-way ANOVA after log transformation of data to ensure normal distribution. Correlations among variables were checked (supplement A, Fig. 1) and one variable for each cluster of correlated variables was used for principal component analysis (PCA) (package "FactoMineR"; (Lê et al., 2008)). Two separate PCAs were conducted from the variables, one describing stream bed characteristics and the other physico-chemical variables. We used adonis2 (package "vegan", (Oksanen et al., 2019)) to perform a non-parametric multivariate analysis of variance (PERMANOVA) on Bray-Curtis similarity matrices to check if stream identity (Necker, Glatt) explained variance among sites. Separation among groups (stream identity) was considered significant at $p < 0.05$. Larger pseudo F-ratios (F) indicate a more pronounced separation among groups. PERMANOVA is a robust method without explicit assumptions about data distribution, as it takes only ranks of dissimilarities into account (Anderson, 2001).

2.4.2. Biomass export via emergent aquatic insects

Biomass export was calculated by normalizing measurements from each site and sampling date to dry mass export per standard stream square meter per day. To achieve this, the mean dry mass captured over one sampling period in the three traps (covering different habitats) at each site was calculated and divided by trap area and number of deployment days. Those values were then used to calculate average and standard deviation of dry mass export per month (from all sampling dates in the respective month) and per season. Insect biomass export was split into "crawling" (stonefly) and "flying" (other groups) emergence. We tested if there was a significant difference in total, crawling and flying dry mass export between rivers using a mixed model with square root transformed biomass data and date fitted as a random effect. Tests were run separately for each season. For spring, where aquatic subsidies are believed to be most important (Nakano and Murakami, 2001), we did a multivariate comparison of insect families contributing to biomass export using PERMANOVA. We tested how much of the variance was explained by stream identity. In addition, we tested if environmental principal components (chem_PC1, chem_PC2, sed_PC1, sed_PC2) were significant explanatory variables ($p < 0.05$) using PERMANOVA. To investigate which insect families contributed most to observed dissimilarities, we used a similarity percentages routine (SIMPER). We visualized the differences in groups contributing to biomass export using a non-metric multidimensional scaling (nMDS) (package "vegan").

2.4.3. PUFA content in emergent aquatic insects

We examined the content of five individual PUFAs, three omega-3 PUFAs (alpha-linolenic acid - ALA, stearidonic acid - SDA and eicosapentaenoic acid – EPA) and two omega-6 PUFAs (linolenic acid - LIN, arachidonic acid – ARA) in emergent aquatic insects. DHA was only detectable in trace amounts in a few samples and excluded from analysis. Although insects were identified to family level, PUFA contents were compared at the order level similar to other studies considering PUFA export by emergent insects (Martin-Creuzburg et al., 2017; Shipley et al., 2022). We further compared PUFA content (% and mg) among seasons and between the two streams using factorial ANOVA (type III) (Anova, package "car"; (Fox and Weisberg, 2019)). We ran post-hoc tests separately for each pair of combinations when interaction effects were significant ($p < 0.05$). We

tested the significant main effects when interaction effects were not significant ($p > 0.05$). As post-hoc tests, we performed multiple pairwise comparisons of estimated marginal means (EMMs) with Tukey corrections (package "emmeans"; (Lenth, 2021)). We tested data for assumptions for homogeneity of variance and normality, and transformed data where required. For percent data, we used the arcsine square-root transformation (Sokal and Rohlf, 1995). We report all values as untransformed means. For spring, we ran a multivariate comparison of PUFA content (% of total fatty acids) using PERMANOVA to assess the proportion of variance explained by insect order, season and stream. In addition, we tested if environmental PCs explained the variance. To investigate which PUFAs contributed most to observed dissimilarities, we used a similarity percentages routine (SIMPER). We visualized patterns in PUFA composition using PCA.

2.4.4. EPA export via emergent aquatic insects and transfer to riparian spiders

We related emergence data to biomass specific average EPA content (mg per dry mass) observed in different insect orders per site and season to calculate daily EPA export. Average EPA content was multiplied with exported dry mass of the respective insect order per standard square meter at the respective site. All sampling dates of each season were treated as replicates to calculate EPA export (mg m^{-2} day^{-1}) for the respective season (mean ± sd). EPA export via "crawling" and "flying" emergence was calculated separately. For an estimation of total EPA export over the complete sampling period, average daily export for each month was calculated and multiplied with number of days to obtain total export for each month. The sum EPA export over all months was used as a rough estimate of total EPA export over the sampling season, which should be close to export per year as winter months have low export (Nakano and Murakami, 2001).

To investigate if EPA content in ground-dwelling spiders was connected to biomass export via crawling emergence, the average exported crawling biomass for each site and EPA content in spiders in spring were correlated. Arsine square-root transformed values of EPA content (% of total fatty acids) were used, while average biomass export was square-root transformed. We used a mixed model, first separately for each stream and then with sites from both streams combined, with stream as a fixed effect and site as a random effect. Analysis was done for spring only, as aquatic

subsidies are believed to be most important for riparian predators in spring (Nakano and Murakami, 2001).

3. Results

3.1. Differences in environmental variables between streams

3.1.1. Physico-chemical parameters

Nutrient levels (N and P) differed significantly between streams. At the Necker, nutrients were low (TN: 1.2 ± 0.7 mg l^{-1}, TP: 12 ± 7 mg l^{-1}) (mean ± standard deviation), slightly increasing downstream (supplement A, Fig. 2A). Conductivity was 341 ± 24 µS cm^{-1} and relatively low. In contrast, the Glatt had significantly higher TN (3.7 ± 1.6 mg l^{-1}) and TP (61 ± 24 µg l^{-1}) levels, and significantly higher conductivity (582 ± 74 µS cm^{-1}) than the Necker ($p < 0.001$). Carbon constituents and pH did not significantly differ between the two streams but some sites, especially G.A, had a higher pH and the Glatt displayed variable carbon levels. In the Glatt, there was an increase in TN ($p < 0.01$) and TP ($p < 0.001$) between the 3 upstream and 3 downstream sites (supplement A, Fig. 2A). All N and P constituents were highly correlated. In a PCA using TP, TN, DOC and pH as parameters, the two streams had distinct clusters, and stream identity explained 77 % of the variance (PERMANOVA: F = 33.9, $p = 0.004$) (Fig. 2A). Chem_PC1 represented a gradient of increasing nutrient (N, P) levels. The division between the upstream and downstream sites on the Glatt was also visible in the multivariate comparison.

3.1.2. Stream-bed characteristics

None of the bed load metrics such as Shannon's grain diversity and median grain size differed significantly between systems ($p > 0.05$), but surface fine sediment and clogging was generally higher at the Glatt than the Necker ($p < 0.05$) (supplement A, Fig. 2B). For some parameters, especially those connected to fine sediment input, we found strong differences between streams but also among sites, especially along the Glatt; i.e., lower degree of clogging at sites G.A and G.C than the other sites. In the stream-bed PCA, these two sites clustered with the Necker sites along sed_PC2, which was mainly explained by clogging (Fig. 2B). Stream identity did not explain variance among sites (PERMANOVA: F = 1.5, $p = 0.28$).
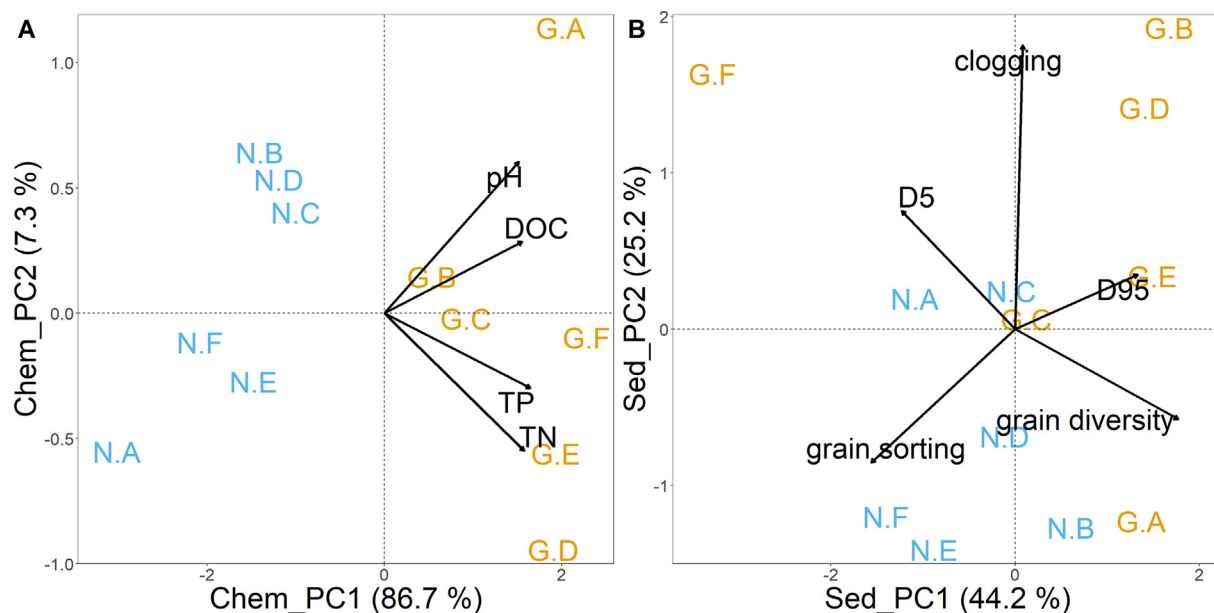

Fig. 2. A) Principal component analysis of physico-chemical parameters for the different sampling sites along the Glatt (orange) and Necker (blue). DOC – dissolved organic carbon, TP – total phosphorus, TP – total nitrogen. B) Principal component analysis of stream-bed characteristics. Clogging – degree of stream bed clogging by fine sediment, D5 – grain size percentile D5, D95 – grain size percentile D95, grain diversity – Shannon grain diversity.

3.2. Biomass export via emergent insects

3.2.1. Patterns of biomass export

Biomass export via emergent insects showed strong site and season specific variation, ranging from 1.0 to 80 mg m^{-2} day^{-1}. Highest biomass export occurred in summer with highest peaks in July for almost all sites in both streams (Fig. 3A). Total biomass export did not differ significantly between streams in spring (Glatt: 7.9 ± 9.6 mg m^{-2} day^{-1}; Necker: 7.3 ±

8.5 mg m^{-2} day^{-1}; $p > 0.05$) or summer (Glatt: 17.7 ± 15.2 mg m^{-2} day^{-1}; Necker: 14.2 ± 18.2 mg m^{-2} day^{-1}; p > 0.05), but there was a statistically higher total export from the Glatt than the Necker in autumn (Glatt: 7.9 ± 5.7 mg m^{-2} day^{-1}; Necker: 4.6 ± 5.7 mg m^{-2} day^{-1}; $p < 0.001$) (Fig. 3B).

The high biomass export in summer was mainly driven by flying emergence, whereas crawling emergence peaked in spring and autumn. Biomass export via crawling emergence was generally lower than via flying
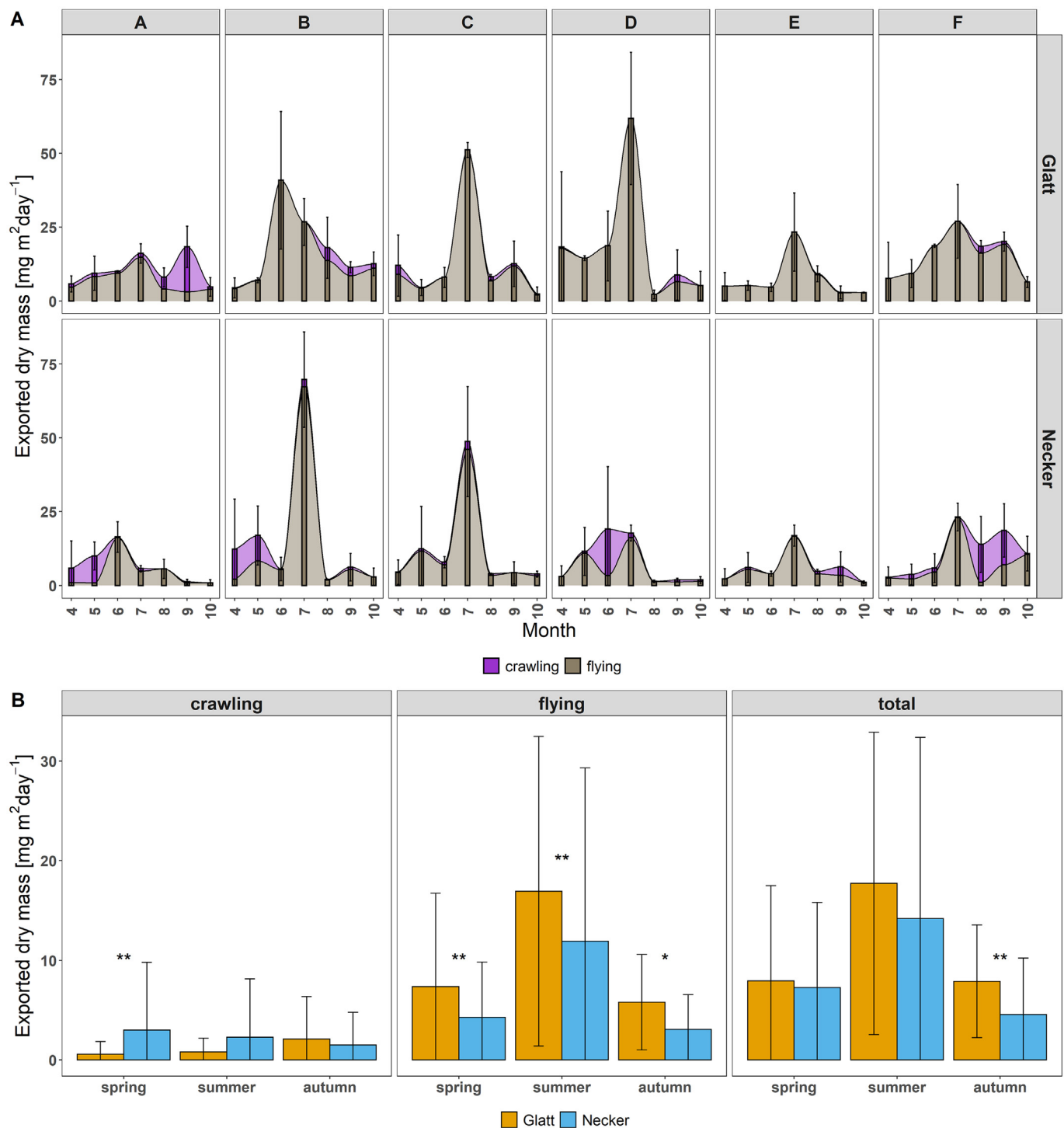

Fig. 3. A) Dry mass export by emerging aquatic insects through two different emergence modes "flying" (grey) and "crawling" (purple) for the Glatt (upper row) and Necker (lower row). Bars represent monthly means and error bars are standard deviation. Curves represent estimation of dry mass export based on a local smoother function. B) Comparison of biomass export via emergent aquatic insects in spring, summer and autumn in the two streams. Bars represent mean export per season, error bars are standard deviation, and asterisks show significant differences.

emergence, and only at some sites in spring (N.A, N·B) and autumn (G.A, N·F) were levels similar between emergence modes. Flying emergence export was highest at the Glatt during all seasons ($p < 0.05$). We found significantly higher crawling emergence export at the Necker (3.0 ± 6.8 mg m^{-2} day^{-1}) than the Glatt (0.6 ± 1.3 mg m^{-2} day^{-1}; $p < 0.01$) in spring, especially at sites N.A (6.7 ± 6.4 mg m^{-2} day^{-1}) and N·B (9.5 ± 12.6 mg m^{-2} day^{-1}). At the Glatt, sites G.A (1.1 ± 0.7 mg m^{-2} day^{-1}) and G.C (1.8 ± 2.5 mg m^{-2} day^{-1}) had highest crawling emergence export in spring, while crawling emergence export was close to zero (< 0.3 mg m^{-2} day^{-1}) at the other sites. We found no significant patterns present in both streams when comparing crawling, flying and total biomass export along environmental gradients (chem_PC1, chem_PC2, sed_PC1, sed_PC2) within each stream (supplement B).

3.2.2. Community composition in spring

In spring, 4 % of the variation in emergent aquatic insect composition was explained by stream identity (PERMANOVA: F = 4.0, $p = 0.003$). The three main taxa contributing to the separation were Chironomidae, Baetidae and Taeniopterygidae (SIMPER: 78 %). Comparing sites, G.A with the most natural stream-bed characteristics in the Glatt, clustered with the Necker sites in the nMDS (Fig. 4). Site G.A also clustered with the Necker sites in the PCA comparing stream-bed characteristics among sites. When we considered environmental PC scores as factors explaining community composition, all terms together explained 10 % of the variance (PERMANOVA: F = 2.2, $p = 0.002$), but no single term had a significant effect (PERMANOVA, $p > 0.05$). However, the gradient of clogging by fine sediment (sed_PC2) matched the distribution of sites in the nMDS in which crawling taxa (purple in plot) at low fine sediment sites and flying taxa (grey in plot) at higher fine sediment sites drove community separation (Fig. 4).

3.3. PUFA content in emergent insects

3.3.1. Individual PUFAs

3.3.1.1. Differences among orders. In all emergent aquatic insect orders investigated here, EPA made up the largest proportion of all PUFAs (18.8 ± 6.3 % of total fatty acids), with no significant differences found among insect orders ($p > 0.05$) (Fig. 5A). EPA content calculated per dry mass was

significantly higher in Ephemeroptera than in other insect orders ($p < 0.001$), while patterns for the other PUFAs were similar when calculated as percentage or per dry mass (for per dry mass see supplement C). ALA was the second most abundant omega-3 PUFA. ALA content was higher in Plecoptera (13.0 ± 5.7 %) than in the other orders (Ephemeroptera: 5.1 ± 2.4 %, $p < 0.001$; Diptera: 6.4 ± 2.8 %, p < 0.001) in spring, whereas no difference was found among orders during the other seasons (p > 0.05). SDA was only present in relatively low quantities (< 10 % of total fatty acids) and content did not differ among insect orders in spring (p > 0.05) but was significantly higher in Ephemeroptera than Plecoptera and Diptera in summer and autumn ($p < 0.001$). LIN was the most abundant omega-6 PUFA and LIN content was significantly higher in Diptera (17.7 ± 7.8 %) and Plecoptera (13.2 ± 6.2 %) than Ephemeroptera (3.5 ± 1.6 % $p < 0.001$) in all seasons. ARA was only present in relatively low quantities (< 10 % of total fatty acids) and, except in spring, ARA content was also significantly higher in Diptera (summer: 5.1 ± 2.1 %; autumn: 3.5 ± 2.1 %) and Plecoptera (summer: 7.2 ± 2.2 %; autumn: 6.1 ± 1.6 %) than Ephemeroptera (summer: 1.3 ± 0.8 %; autumn: 0.8 ± 0.6 %, p < 0.001). Therefore, with both higher LIN and ARA content Diptera and Plecoptera contained, in general, more omega-6 PUFAs than Ephemeroptera. For details about seasonal differences in PUFA content see supplement D.

3.3.1.2. Stream specific differences. SDA content in all insect groups in spring was significantly higher at the Necker (Diptera: 5.9 ± 3.7 %, p < 0.001; Plecoptera: 7.5 ± 4.4 %, p < 0.001; Ephemeroptera: 6.1 ± 2.9 %, $p < 0.05$) than the Glatt (Diptera: 2.6 ± 2.9 %, Plecoptera: 1.1 ± 1.5 %, Ephemeroptera: 2.9 ± 1.6 %). We found no other significant differences in PUFA content of emergent insects between the two streams (Fig. 5A).

3.3.2. Multivariate comparison

Insect order explained 27 % (PERMANOVA: F = 53.9, $p = 0.001$) of the differences in PUFA profiles followed by season at 10 % (PERMONOVA: F = 19.4, p = 0.001). Stream identity only explained 1.5 % (PERMAONVA: F = 6.0, p = 0.001) of the variation in PUFA profiles. The interaction terms of "order:season" and "season:river" were also significant. The PCA revealed a separation between grazing Ephemeroptera (Baetidae, Heptageindae) and other emerging insects (Diptera: Chironomidae, Plecoptera), especially in summer and autumn (Fig. 5B) (separation among insect orders: PERMANOVA: spring: F = 13.8, p = 0.001, R2 = 0.25; summer: F =
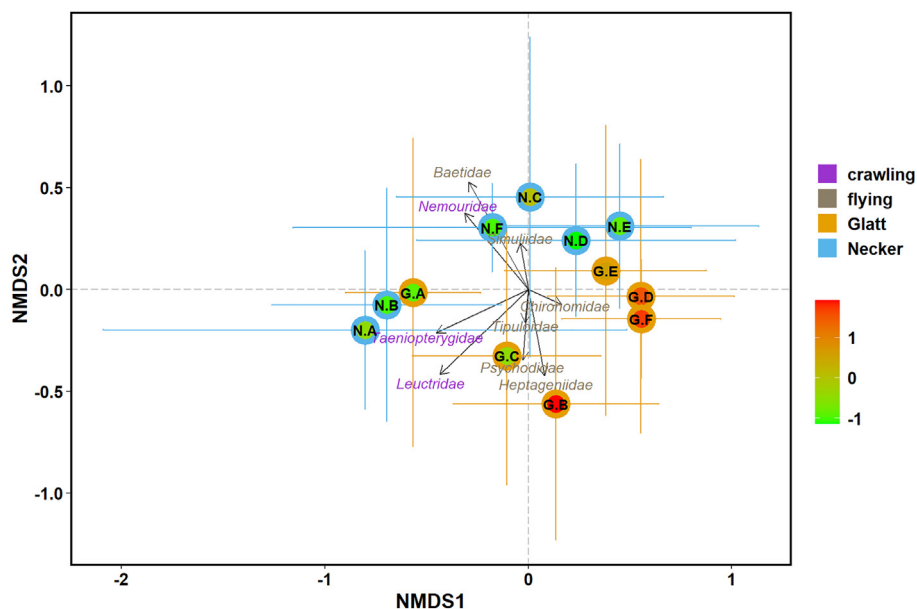

Fig. 4. Non-metric multidimensional scaling (nMDS) of dry mass export for different insect families at the two study streams in spring (stress level = 0.21). Color of symbol border is stream identity, and color of symbol indicates degree of clogging by fine sediment (sed_PC2 score) at the respective site. Text color represents emergence mode of respective insect group. Points represent mean and error bars are standard deviation.
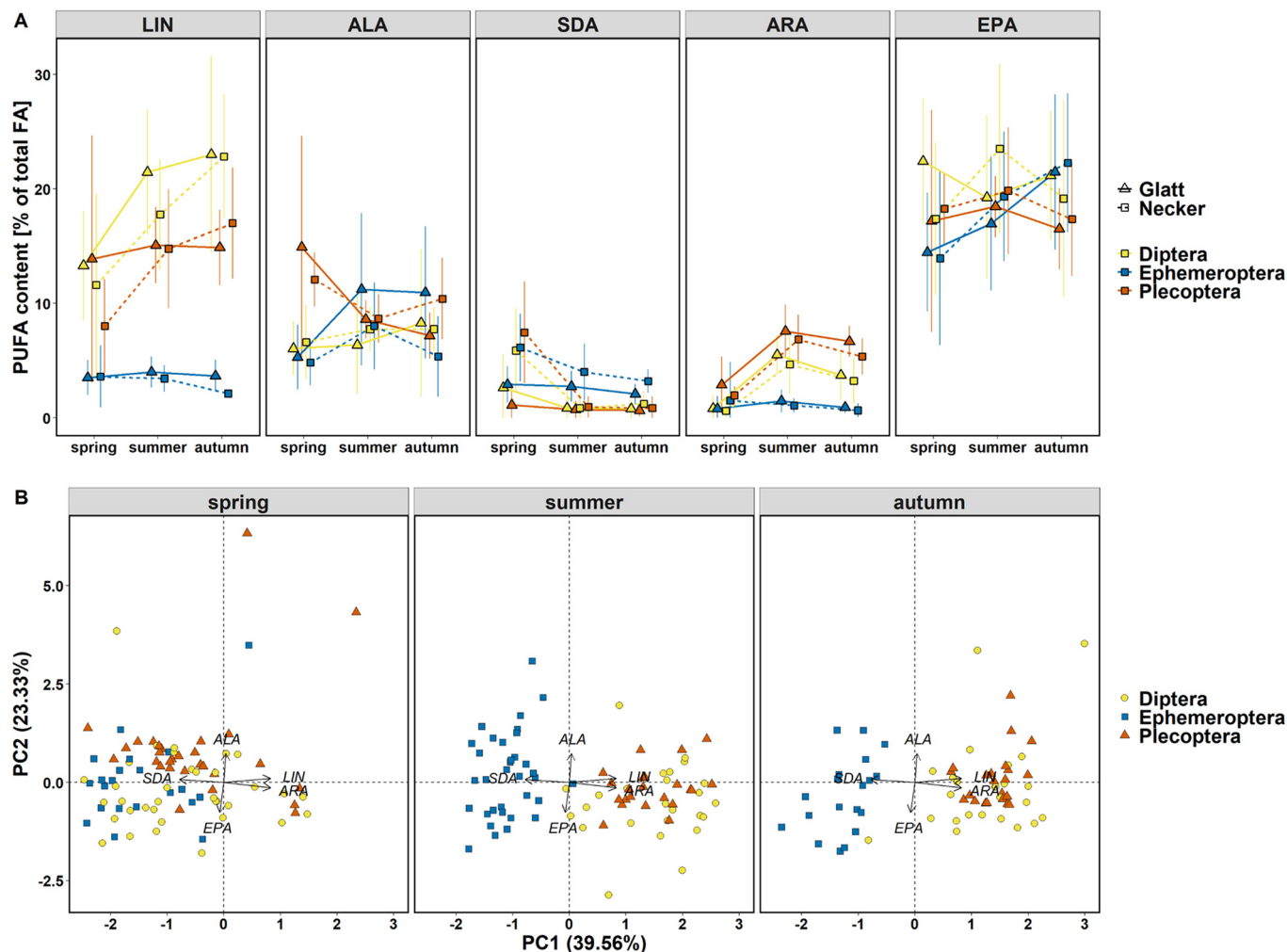
Fig. 5. A) Individual PUFA content (as % of total fatty acids) in Diptera, Ephemeroptera and Plecoptera by stream (Glatt, Necker) and season. Points represent mean content and error bars are standard deviation. B) Principal component analysis of PUFA profiles of emergent aquatic insects, highlighting differences among orders. *LIN* - linolenic acid, *ALA* - alpha-linolenic acid, *SDA* - stearidonic acid, *ARA* - arachidonic acid, *EPA* - eicosapentaenoic acid.

38.5, p = 0.001, R2 = 0.50; autumn: F = 19.7, p = 0.001, R2 = 0.38). While season explained only 11 % of the differences in Ephemeroptera (PERMANOVA: F = 4.2, p = 0.001), season explained 26 % of the differences in Diptera (PERMANOVA: F = 14.5, p = 0.001) and 28 % in Plecoptera (PERMANOVA: F = 13.8, p = 0.001) (supplement D, Fig. 1).

We found no significant differences in PUFA content between streams in summer and autumn, but in spring 9 % of variation in PUFA content in Diptera (PERMANOVA: F = 3.6, *p* = 0.005) and 18 % in Plecoptera (PERMANOVA: F = 6.0, *p* = 0.002) was explained by stream. LIN and EPA contributed mainly to the differences between streams (SIMPER: Diptera: 48 %; Plecoptera: 63 %). However, site G.A again clustered with the Necker sites in spring for Diptera (Fig. 6). Environmental PCs did not explain the variance in PUFA profiles.

3.4. Estimation of EPA export via emergent insects

Total EPA export followed a similar temporal pattern as biomass export, as EPA content in emergent insects did not significantly differ among seasons (Supplement E). In spring, estimated average export was 0.13 ± 0.18 mg m^{-2} day^{-1} at the Glatt and 0.09 ± 0.12 mg m^{-2} day^{-1} at the Necker. Highest EPA export occurred in summer with up to ~1 mg m^{-2} day^{-1} on some sampling dates. Sites G.D (0.44 ± 0.55 mg m^{-2} day^{-1}) and N.B (0.40 ± 0.53 mg m^{-2} day^{-1}) were sites with the highest average EPA export (Supplement D). On average, 0.27 ± 0.30 mg m^{-2} day^{-1} EPA was exported from the Glatt and 0.23 ± 0.30 mg m^{-2} day^{-1} from the

Necker in summer. In autumn, average EPA export was 0.14 ± 0.09 mg m^{-2} day^{-1} at the Glatt and 0.07 ± 0.09 mg m^{-2} day^{-1} at the Necker. EPA export via crawling emergence was very low at the Glatt and especially in spring (no crawling export at sites G.D, G.E, G.F). In contrast, crawling emergence export was high at some sites at the Necker, especially N.B (0.13 ± 0.01 mg m^{-2} day^{-1}). Total EPA export was estimated to be 41 ± 15 mg m^{-2} y^{-1} at the Glatt and 32 ± 15 mg m^{-2} y^{-1} at the Necker (study period: April–October).

3.5. EPA transfer to ground dwelling spiders

Dry mass export via crawling emergence was one of the main differences among sites in spring, with highest exports at sites N.A and N.B (Fig. 7A). We also found differences in EPA content in ground-dwelling spiders among sites in spring (Fig. 7B). There was a relationship between biomass exported via crawling emergence (stoneflies) and EPA content in ground-dwelling spiders with EPA making up only 16.0 ± 6.2 % of total fatty acids in spiders at sites with no stonefly emergence, but 27.3 ± 3.0 % at sites with highest stonefly emergence in spring. The correlation between EPA content in ground-dwelling spiders and stonefly biomass was significant at the Necker (F = 8.24, p = 0.012) but not at the Glatt (F = 2.41, p = 0.14). Combining data from both streams we found a significant effect of stonefly biomass on EPA content in ground-dwelling spiders (*p* = 0.002, F = 11.87), while stream had no significant effect (F = 0.93, p = 0.34) (Fig. 7C).
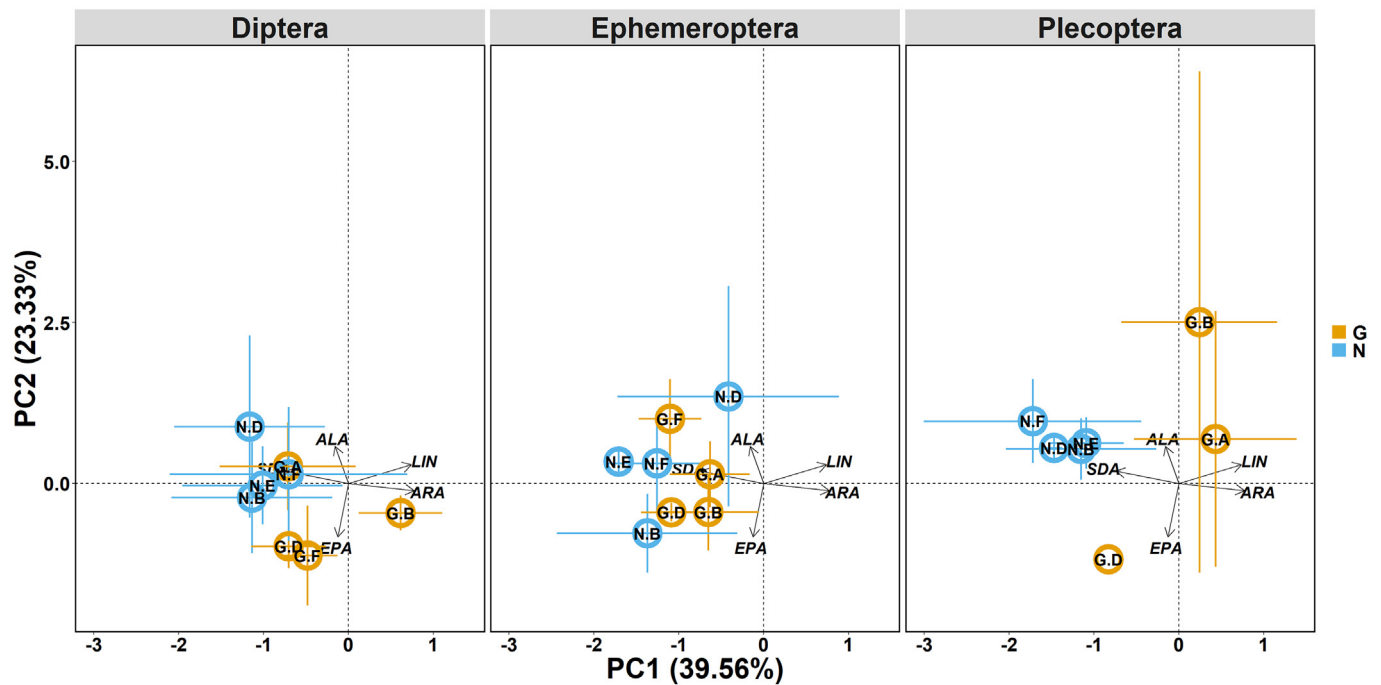
Fig. 6. Principal component analysis of PUFA profiles of emergent aquatic insects, highlighting differences among sites in spring. Symbol color indicates stream identity (Glatt and Necker). Points represent means and error bars are standard deviation. *LIN* – linolenic acid, *ALA* – alpha-linolenic acid, *SDA* – stearidonic acid, *ARA* – arachidonic acid, *EPA* – eicosapentaenoic acid.

4. Discussion

4.1. Stream differences in physico-chemical and stream-bed characteristics

The two study streams differed in nutrient levels, most likely due to clear differences in land use (Omernik, 1976). Sites along each stream also displayed differences in environmental conditions. For instance, we saw a slight increase in nutrients in the Necker further downstream, albeit nutrients were at low levels, whereas we found a significant difference between the three upper sites and lower sites at the Glatt. Here, a wastewater

treatment plant between the sites G.C and G.D likely explains the increase in nutrient levels at the three downstream sites. In addition, although stream-bed characteristics was more similar than expected, we found a higher surface fine sediment content and degree of clogging in the Glatt than Necker, especially at sites below barriers. For instance, site G.A, which was upstream of all major barriers, had low levels of clogging and fine sediment. Site G.C also had relatively low degree of clogging by fine sediment, despite being below a barrier. Here, and in contrast to other sites, stream banks between the barrier and the sampling site were not easily erodible and therefore little fine sediment entered the system. At other
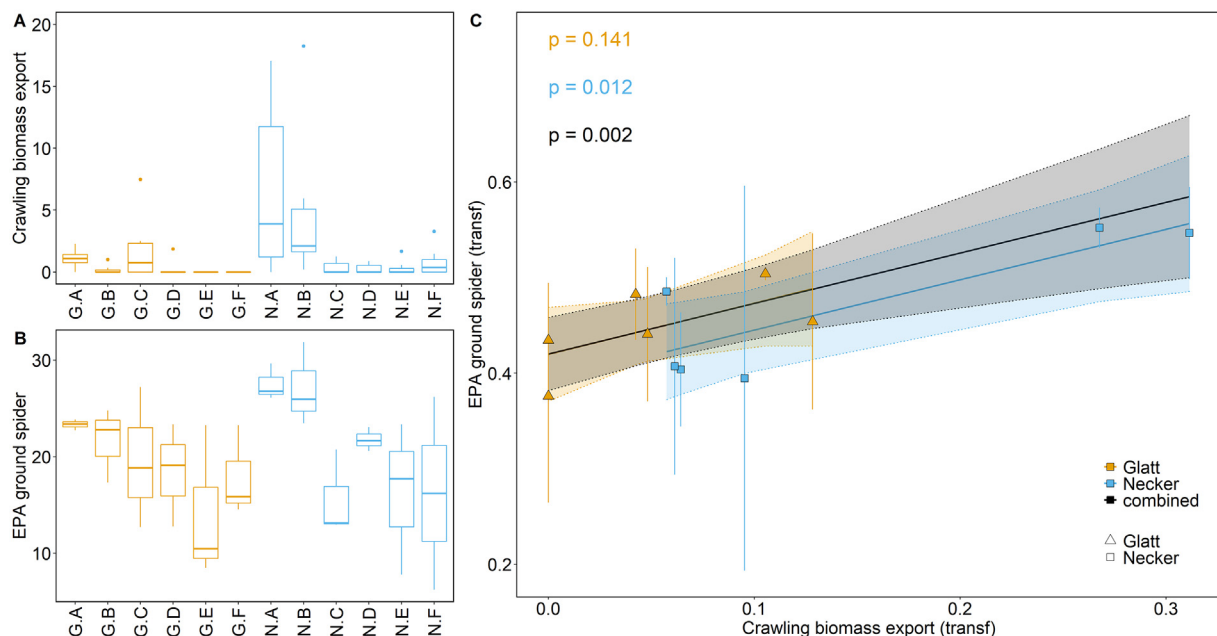

Fig. 7. A) Plecoptera dry mass export (mg m^2 day^{-1}) per site at the Glatt (orange) and Necker (blue) in spring. B) EPA content (% of total fatty acids) in ground-dwelling spiders per site in spring. C) Association between stonefly biomass and EPA content in ground-dwelling spiders at the two study streams (Glatt and Necker).

sites in the Glatt, especially G.B, strong bank erosion was visible and likely caused the high degree of clogging we observed.

4.2. Quantitative differences in biomass export of aquatic insects

Biomass export via emergent aquatic insects was strongly dependent on season and site-specific characteristics, with strong variations in emergence likely linked to organism life cycles and weather-related fluctuations in emergence. For example, Ivković et al. (2013) showed that temperature and local weather conditions (e.g. cloudiness) can have a strong influence on emergence. While we expected a major peak of aquatic emergence in spring (Corbet, 1964; Nakano and Murakami, 2001), peak export was in July at most sites and corresponded with highest water temperatures (supplement F). It is likely that we missed some of the temporal dynamics of emergence due to the non-continuous emergent aquatic insect sampling, as mass emergence can happen during relatively narrow time frames (Sweeney and Vannote, 1982; Anderson et al., 2019). For example, Anderson et al. (2019) found some emergence events lasted for only 4–8 days. However, continuous sampling was not possible due to limited resources and recurrent high flow events, during which emergent insects trap deployment was not possible. Total biomass export at both streams was at similar levels in spring and summer, and even higher at the Glatt than Necker in autumn. Complex interactions among different environmental stressors and insect families might explain the observed biomass export patterns; so-called subsidy-stress relationships. For instance, increased nutrient availability, up to a threshold, boost insect population growth via bottom-up effects, while high fine sediment loads have been shown to counteract this effect (Townsend et al., 2008; Matthaei et al., 2010). Total insect biomass export can be affected both in a positive and negative direction depending on the strength and interaction of different stressors.

Importantly, community composition changes and sensitive invertebrate groups, especially EPT (Ephemeroptera, Plecoptera, Trichoptera) taxa, typically are replaced by more generalist species with high fine sediment and nutrient loads (Wood and Armitage, 1997; Miltner et al., 1998; Niyogi et al., 2007). In particular, many stonefly taxa are sensitive to high levels of nutrients, excessive fine sediment deposits and habitat degradation (Relyea et al., 2000; Lock and Goethals, 2014). Because of the unique emergence mode of stoneflies, lower stonefly emergence equals lower crawling emergence, potentially reducing subsidy transfer to ground-dwelling predators. Our results corroborate this as we observed a reduced biomass export by stoneflies at the Glatt in spring. In summer, stonefly emergence was low in both streams, therefore observed differences were small. In autumn, we observed a stonefly emergence peak at a few Glatt sites, consisting of Leuctridae (supplement G), a stonefly family that seems to be less sensitive to environmental stress (Extence et al., 2013); thus we found no difference in crawling emergence in autumn. Sediment sensitive stonefly families (Nemouridae, Taeniopterygidae) occurred mainly in spring at the Necker and to some extent at the less impaired Glatt site (G.A). It needs to be further investigated how efficient taxa using crawling emergence were caught in comparison to flying taxa. The majority of individuals using crawling emergence were caught in the traps placed close to shore. The differences found between amounts of flying and crawling emergence might be biased by different trapping efficiencies. However, the differences in crawling emergence found between sites should not be affected by a potential sampling bias because the same method was used at all sites.

We also observed within stream differences in emergent insect composition associated with environmental conditions. The most upstream site at the Glatt (G.A), which had, with low levels of fine sediment, stream-bed characteristics comparable to those at the Necker, demonstrated a similar composition of emergent insects as Necker sites, while other Glatt sites with altered stream-bed characteristics also differed in insect groups contributing to the biomass export. Combined environmental PCs were significant predictor variables for variance in composition, but no single environmental PC had a significant effect, likely because high variability in biomass export among sampling dates made comparison of patterns

among sites difficult. Although no single environmental PC was found to be a significant predictor variable, the gradient of clogging by fine sediment (sed_PC2) matched the distribution of sites with taxa that emerge via crawling. Those sites with high degree of clogging by fine sediment were associated primarily with taxa tolerant to fine sediment such as Chironomidae that emerge via flight, while a low degree of clogging by fine sediment was associated with those that use crawling emergence, especially the two stonefly families Nemouridae and Taeniopterygidae.

4.3. Qualitative differences in biomass export of aquatic insects

PUFA profiles differed among insect groups, with highest levels of EPA content per biomass in Ephemeroptera (mayflies) as reported previously (Martin-Creuzburg et al., 2017; Twining et al., 2021). With their high EPA content and large size, mayflies are valuable prey for riparian predators, especially those that predominantly catch flying prey (e.g., birds, web-building spiders). In contrast, mayflies may be more difficult to access for ground-dwelling predators. In this study system, mayflies were estimated to make up only a small proportion (< 10 %) of the diet of ground-dwelling spiders (Kowarik et al., 2021). EPA content per biomass in stoneflies was lower, but stoneflies are more accessible to ground-dwelling spiders and we found that stoneflies were especially abundant in early spring when aquatic subsidies are particularly important for riparian predators (Nakano and Murakami, 2001). Mayflies, on the other hand, were abundant later in the season, in particular during June and July, when other terrestrial prey items were available to spiders as well. While PUFA profiles were similar during all seasons in mayflies, we observed a shift in PUFA profiles in Diptera and Plecoptera. In Plecoptera, this shift could be largely explained by seasonal shifts in the presence of families. Taeniopterygidae and Nemouridae were only found in spring while Leuctridae were present in all seasons. However, we did also observe a small shift in Leuctridae PUFA profiles between spring and summer (supplement H), likely due to differences at the base of food chain among seasons.

Apart from seasonal differences, the position of sites in the stream network, such as altitude, might also drive differences in community composition as well as PUFA profiles (Grubaugh et al., 1996; Guo et al., 2021). In this study, longitudinal changes did not explain compositional differences among sites, as sites G.A and G.B were near each other with minimal altitudinal difference, but we saw an abrupt shift between these two sites in assemblage composition and PUFA profiles, and not gradually downstream. Here, it is likely that stream-bed characteristics (especially clogging) was an important factor because nutrient levels were comparable but the degree of clogging by fine sediment changed drastically between sites due to a large barrier disrupting the sediment continuum. Downstream of the barrier, we saw enhanced clogging/fine sediment content and altered community structure with stoneflies contributing less to biomass export at the site below the barrier.

We expected a difference in EPA content between streams due to changes at the base of the food chain (periphyton). For example, Scharnweber et al. (2019) found lower EPA in aquatic insects (Chironomidae) with increasing phosphorus concentrations in a mesocosm study. In our study, periphyton at the base of the aquatic food chain contained comparable levels of EPA in both streams (higher at some Glatt sites in spring) (supplement I). Total EPA content in emergent insects was similar at the Glatt and Necker as well. However, the lack of the differences in EPA may be associated with the levels observed in our study sites. Scharnweber et al. (2019) tested much higher phosphorus concentrations (20–1000 μg l^{-1}) than the highest values found at our sites (max P levels <100 μg l^{-1}). As such, we found no reduction in total EPA export in the range of environmental conditions we observed. It may be that stronger human degradation might lead to differences in EPA transfer into riparian systems. While EPA content was relatively similar in emergent insects in both rivers, there was a stream separation of PUFA profiles of emergent insects, especially for Diptera. Only the least degraded Glatt site (G.A) clustered with the more pristine Necker sites. Some of this variation in PUFA composition (especially SDA) between sites occurred at the base of the

food chain (supplement J), suggesting that different PUFA composition in periphyton can influence the quality of PUFA export. It remains unclear why this similarity in PUFA profiles to periphyton was not visible in the grazing Ephemeroptera, but internal processes like bioconversion and selective retention may play a role (Kühmayer et al., 2020; Steinberg, 2022).

4.4. Emergent aquatic insects as vectors of EPA export

Emergent insects exported biomass and EPA from both the natural and more degraded stream network to adjacent riparian areas. On average, estimated total EPA export per square meter was 30–40 mg over the sampling season (April to November). While aquatic insect emergence also takes place during winter (ice free), this happens only at low levels (Nakano and Murakami, 2001), therefore our estimate is comparable to yearly exports. Our values are on the low range of other studies that calculated EPA + DHA export from ~40 up to 4500 mg m^{-2} y^{-1} for different biomes (Gladyshev et al., 2019), but were similar to export from a small German lake (~33 mg m^{-2} y^{-1}) (Martin-Creuzburg et al., 2017). In contrast to other studies, export of DHA via emergent insects was close to zero and therefore not quantified here; most likely because copepods that appear able to synthesize DHA (Nanton and Castell, 1998; Nielsen et al., 2019) were not an important part of the food web. In Martin-Creuzburg et al. (2017), predacious *Chaoborus* that are known to prefer copepods as food sources (Swift and Fedorenko, 1975; Pastorok, 1980) contributed to DHA export, but they were not found in the our study.

Although total EPA export was comparable between streams, there was still a large anthropogenic impact associated with stream degradation. Specifically, less biomass and EPA export came from stonefly emergence in the degraded stream, thus likely being less accessible to ground-dwelling predators like riparian wolf spiders. While there was no connection between EPA content in aquatic insects and ground spiders, and no difference in EPA content in ground-dwelling spiders between the two streams (Kowarik et al., 2021), differences in EPA content in ground-dwelling spiders among sites were correlated with emergent stonefly biomass. Indeed, sites with low or no emergent stonefly biomass also had ground-dwelling spiders with lower EPA content in spring, indicating that ground-dwelling spiders were to some degree dependent on aquatic insects with a crawling emergence to build up EPA deposits. Most stoneflies are sensitive to habitat degradation, thus the transfer of EPA to ground-dwelling riparian predators might be strongly affected by instream habitat degradation. EPA content in ground spiders has been linked to immune function (Fritz et al., 2017). The question remains how important aquatic EPA is for riparian predators. While Hixson et al. (2015) highlight aquatic systems as the principal EPA source, the soil food web has been suggested as an alternative source of EPA (Menzel et al., 2018). However, EPA content decreases with distance from the stream edge (Chari et al., 2020), linking EPA to aquatic systems. Internal conversion from dietary precursors is another possible source of long-chain PUFAs. Recent studies suggest that some web-building spiders can convert dietary precursor PUFAs to long chain PUFAs such as EPA (Mathieu-Resuge et al., 2021; Twining et al., 2021). Further research is required to assess the ability of different predators to cover their EPA demands from metabolic processes, however taking EPA up with the diet likely improves fitness and is less costly.

The loss of stoneflies as a result of instream degradation endangers the existence of an export pathway leading to ground-dwelling predators. While we could not disentangle the effects of high nutrients and fine sediment, the stark contrast between sites G.A and G.B, which were similar in nutrients, suggests fine sediment as an important factor driving lower levels of crawling emergence. Further research is needed to assess the consequences of human impact in aquatic systems on stonefly populations and the cascading effects to riparian ecosystems.

5. Conclusion

Emergent aquatic insects from both systems transported EPA acquired during their larval stages to riparian areas. In the range of environmental conditions studied here, the EPA content in emergent aquatic insects and total biomass and EPA export by emergent aquatic insects was unaffected. Our results indicate however, that when assessing the effects of stream degradation, not just total insect biomass export but the potential modifications to assemblage composition and how those translate to specific mechanisms of PUFA export is important. We highlight, that functional traits, like mode of emergence, unique to specific taxa, must be considered because they relate to certain pathways of resource transfer between aquatic and terrestrial ecosystems. In our study, a distinct shift in insect groups contributing to the biomass export at degraded sites in spring (loss of stoneflies) impacted the functional connectivity to ground-dwelling predators. Although the total export was at similar levels, the EPA export via crawling emergence, accessible to ground-dwelling predators, was reduced. Lower EPA content in ground-dwelling spiders at sites with low stonefly emergence suggests at least a partial dependence of riparian ground-dwelling spiders on this crawling emergence pathway to acquire EPA in adequate quantities. Importantly, stonefly decline is a general result of degradation that can weaken aquatic-terrestrial linkages with potential effects for other ground-dwelling predators such as floodplain beetles, amphibians and lizards.

CRediT authorship contribution statement

Declaration of competing interest

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2022.158658.

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