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ARTICLE

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# Fatty acid biomarkers reveal landscape influences on linkages between aquatic and terrestrial food webs

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## Abstract

Stream and riparian habitats are meta-ecosystems that can be strongly connected via the emergence of aquatic insects, which form an important prey subsidy for terrestrial consumers. Anthropogenic perturbations that impact these habitats may indirectly propagate across traditional ecosystem boundaries, thus weakening aquatic-terrestrial food web linkages. We investigated how algal production, aquatic invertebrates, and terrestrial spiders influence cross-ecosystem connectivity in temperate streams across four European catchments with varying levels of human disturbance. We used fatty acid biomarkers to measure putative aquatic linkages to riparian spiders. Variation-partitioning analysis indicated that aquatic insect dispersal traits explained a relatively large proportion of variability in the fatty acid profile of spiders. Trophic connectivity, as measured by the proportion of the polyunsaturated fatty acid eicosapentaenoic acid (EPA) and the ratio of EPA to its chemical precursor, alpha-linolenic acid (ALA), was positively associated with abundances of "aerial

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active" dispersing aquatic insects. However, this positive influence was also associated with changes in environmental context and arachnid beta diversity. Structural equation modeling disentangled how aquatic insect communities influence trophic connectivity with riparian predators after accounting for biological and environmental contingencies. Our results show how subsidies of stream insects are a putative source of essential fatty acids for adjacent terrestrial food webs. Catchment-wide impacts indirectly propagated to the local scale through impacts on aquatic invertebrate communities, thus affecting stream-riparian food webs. Increased riparian tree cover enhanced stream insect subsidies via dispersal traits despite reducing aquatic primary production through shading. Consequently, ecosystem properties such as woody riparian buffers that increase aquatic-terrestrial trophic connectivity have the potential to affect a wide range of consumers in modified landscapes.

**KEYWORDS**
aquatic insects, fatty acids, food webs, land use, meta-ecosystems, riparian vegetation, spiders, trophic connectivity

## INTRODUCTION

Reciprocal flows of resource subsidies from one habitat to another can strongly influence the structure and dynamics of food webs in a wide range of ecosystems (Nakano & Murakami, 2001; Polis et al., 1997). Food web theory suggests that productivity gradients in both recipient and donor habitats can drive the magnitude of subsidy influences across habitats (Polis et al., 1997). The strength of this influence may also depend on the trophic level at which the subsidy is received, with resource quantity effects generally greater on detritivores than on higher trophic levels (Marczak et al., 2007). However, resource quality should also be considered in combination with the magnitude of subsidy fluxes between ecosystems because many consumers preferentially favor low-flux, high-quality resources (Marcarelli et al., 2011). For instance, certain taxa of aquatic microalgae synthesize large amounts of long-chain polyunsaturated fatty acids (LC-PUFAs ≥20 carbon atoms), whereas these LC-PUFAs are absent in vascular terrestrial plants (Twining, Brenna, Hairston, & Flecker, 2016). Primary producers in aquatic ecosystems are the principal source of LC-PUFAs for most animals (Hixson et al., 2015), providing essential organic compounds that affect a wide range of physiological processes, from immune function to vision and brain development (Twining, Brenna, Hairston, & Flecker, 2016). In contrast to terrestrial insect prey deficient in omega-3 LC-PUFAs, adult aquatic insects are an important vector of these fatty acids (FA) and can disproportionately affect terrestrial consumers, as seen in their importance for the breeding success of insectivorous birds (Twining, Shipley, & Winkler, 2018). Thus, the quality and quantity of aquatic-derived prey subsidies should influence communities of terrestrial consumers, but their importance in heterogeneous landscapes characterized by a diversity of aquatic and terrestrial habitats remains uncertain owing to challenges in quantifying these food web linkages.

Riparian zones prominently form the interface between aquatic and terrestrial ecosystems. They are disproportionately important in terms of land area because riparian zones strongly influence the material and organism fluxes connecting terrestrial and aquatic habitats into larger meta-ecosystems (Leroux & Loreau, 2008; Naiman & Decamps, 1997). In particular, freshwater and terrestrial food webs are typically highly connected via reciprocal resource subsidies of organic matter and prey that vary in time and space (Marcarelli et al., 2020). Inputs of terrestrial detritus and prey can sustain aquatic food webs, and the emergence of adult aquatic insects forms an important reciprocal prey subsidy that transfers aquatic-derived PUFAs to a wide range of riparian consumers that include spiders, lizards, birds, and bats (Baxter et al., 2005; Twining, Brenna, Hairston, & Flecker, 2016). The aquatic source of omega-3 LC-PUFAs makes these organic compounds useful for tracing fluxes of aquatically derived food sources to terrestrial food webs (Gladyshev et al., 2009), and they may be indicators of impaired meta-ecosystem functioning (Shipley et al., 2024).

Cross-habitat connectivity may be disrupted by human activities such as deforestation, agriculture, and urbanization that drive landscape impacts at multiple scales (Allan, 2004) with negative effects on aquatic and terrestrial communities (Burdon, 2020; Burdon, McIntosh, & Harding, 2020).

Rivers and streams are often highly productive ecosystems, driving fluxes of winged adult aquatic insects that can match or exceed terrestrial production per unit area (Gratton & Zanden, 2009) and disproportionately support terrestrial consumers (Bartels et al., 2012). Thus, the productivity and emergence rates of adult aquatic insects can influence the biomass, spatial distributions, and growth rates of different riparian consumers, including arachnids (Baxter et al., 2005; Marczak & Richardson, 2007). This transfer of aquatic-derived energy to riparian food webs may be further influenced by insect traits relating to life histories, body size, and dispersal (Greenwood & Booker, 2016; Kopp & Allen, 2020; McKie et al., 2018) and the dietary quality of basal resources (Twining et al., 2017; Twining, Brenna, Lawrence, et al., 2016). Recipient community structure can mediate responses to subsidies (Cottingham & Narayan, 2013), and riparian habitat properties may modulate terrestrial predator communities (Burdon, 2020; McCary et al., 2021) and their ability to consume aquatic prey via direct and indirect effects (Laeser et al., 2005), such as when land clearance impacts riparian habitats and recipient community composition. The landscape-level impacts that affect terrestrial consumers via aquatic pathways remain underappreciated; however, since these create an additive stressor routed through cross-ecosystem food web linkages. For instance, nutrient enrichment may increase stream productivity and the magnitude (but not necessarily quality) of the subsidy (Davis et al., 2011), whereas pollutants can diminish cross-ecosystem prey inputs, resulting in negative numerical responses in terrestrial consumers (Paetzold et al., 2011).

Previous studies have quantified land-use effects on stream insect emergence (e.g., Carlson et al., 2016; Goss et al., 2020; Raitif et al., 2018), but little is known about how human land uses simultaneously impact aquatic and terrestrial food webs and if these interactions contribute to altered meta-ecosystem functioning (Burdon, 2020; Larsen et al., 2016). Our study investigated factors affecting aquatic-terrestrial trophic interactions in modified landscapes. We used the FA composition of riparian spiders to estimate the realized trophic connectivity between stream and riparian habitats since (1) insects dominate spider prey biomass (Nyffeler & Birkhofer, 2017) and (2) PUFAs are effective biomarkers for tracking aquatic subsidies in terrestrial arachnids (Chari et al., 2020; Sushchik et al., 2021). We used functional traits of aquatic invertebrates (i.e., dispersal) and spiders (i.e., body size) to test hypotheses about donor and recipient communities. The incorporation of aquatic-derived energy into terrestrial food webs may be mediated by the dispersal ability of aquatic insects (e.g., Briers et al., 2005), which can influence the spatial extent of aquatic prey in adjacent ecosystems (Muehlbauer et al., 2014). Conversely, predator traits such as hunting mode and size may affect how aquatic insect prey are captured and assimilated into receiving food webs (Akamatsu et al., 2007; Nash et al., 2023). Using trait-based ecology promises greater conceptual and data synthesis by focusing on how organisms' functional attributes (traits) interact mechanistically with abiotic and biotic factors in different contexts (Wong et al., 2019). Traits help put biogeographically diverse communities into a common currency, thus enabling the consideration of their functional similarities across different ecoregions (Dolédec et al., 2011). We also considered functional syndromes (FS) in our trait analyses as the association between correlated suites of traits (Raffard et al., 2017). Traits that we predicted to be important might not be mutually exclusive (Mouillot et al., 2021), and dispersal syndromes are believed to strongly affect eco-evolutionary and ecosystem processes (Cote et al., 2022).

Our hypotheses below (see also Figure 1 and Appendix S1: Section S1: Table S1) concerned four nonexclusive factors that potentially contribute to the strength of the connection between aquatic and terrestrial food webs:

1. *Algae productivity*: We evaluated two alternative hypotheses related to algal productivity. (1) Algal production is positively correlated with trophic connectivity since algae synthesize omega-3 LC-PUFAs (Twining, Brenna, Hairston, & Flecker, 2016) and the flux of emergent adult stream insects is positively correlated with periphyton biomass (Terui et al., 2018), or (2) there is a trade-off between algal quantity and quality (sensu a subsidy–stress response), whereby ecosystem functioning is enhanced at low levels of stressors but depressed as the stressors intensify (Odum et al., 1979). Adverse environmental conditions (e.g., increased light, nutrients, and fine sediment) typical of agricultural and urban streams can reduce the nutritional quality of periphyton (Cashman et al., 2013; Yan et al., 2024) and degrade benthic resources (Burdon et al., 2013).
2. *Aquatic invertebrate communities*: We hypothesized that univoltine, medium-sized, and actively dispersing stream insects are strong contributors to the prey subsidies used by terrestrial consumers. We expected these traits to be important because they represent

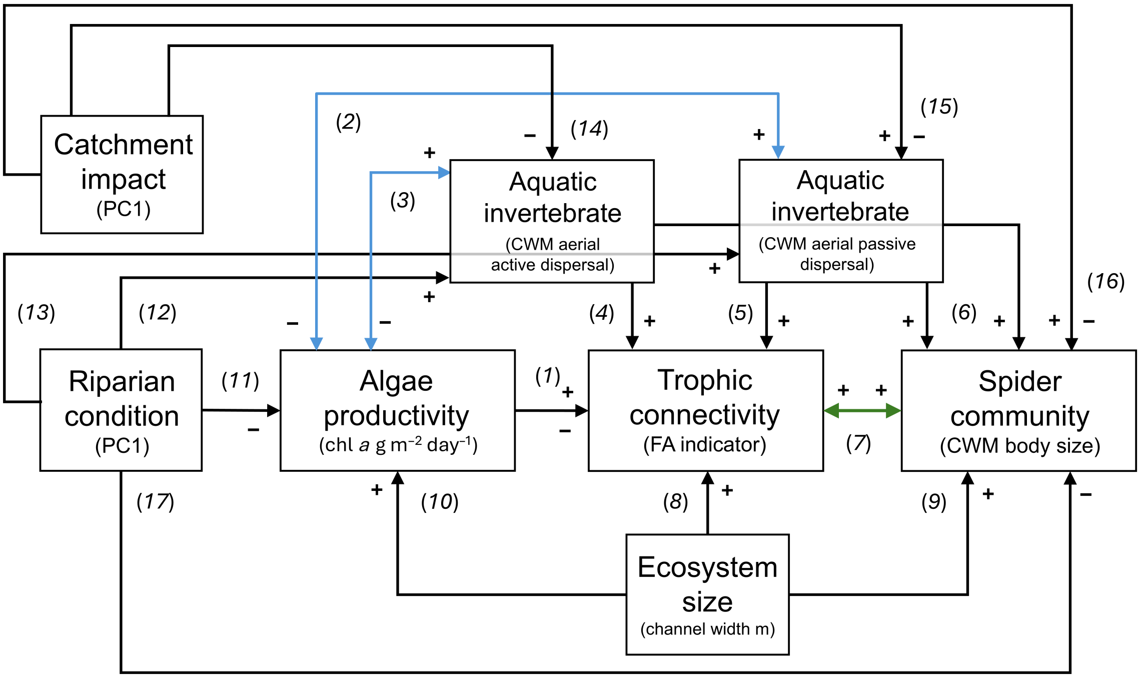

**FIGURE 1** A conceptual diagram highlighting our key hypotheses regarding the role of algal production, aquatic invertebrates, terrestrial spiders, and environmental context on stream-riparian linkages. This diagram also describes the hypothesized paths tested in the global structural equation model (SEM). The basis for the hypothesized paths and positive (+) or negative (−) influence are explained in Appendix S1: Section S1: Table S1. Blue arrows indicate paths which were considered in both directions between endogenous variables. The green arrow indicates a path that was causally unspecific (i.e., fitted as a correlated error term in the SEM), since trophic connectivity could influence spider community composition, but spider community composition also influences trophic connectivity by determining the spiders available for sampling and analysis (Appendix S1: Section S1: Table S1). chl *a*, chlorophyll *a*; CWM, community-weighted mean; FA, fatty acid.

different aspects of the prey subsidy: emergence timing (Raitif et al., 2018), abundances and biomass for optimal foraging by predators (Brose et al., 2008), and consistency and distance of flight dispersal (Kopp & Allen, 2020).

3. *Terrestrial predator communities*: We hypothesized that smaller-bodied, web-building spiders are strong contributors to the realized connectivity between aquatic and terrestrial food webs. Web-building spiders typically rely more on allochthonous diet contributions from aquatic systems than ground-hunting arthropods (Allen et al., 2024); although aquatic insect prey can have an important contribution to the diets of riparian ground-hunting spiders (Collier et al., 2002; Krell et al., 2015; Sanzone et al., 2003).
4. *Environmental context*: We hypothesized that the relative strength of the interaction between stream ecosystems and the adjacent riparian zone is decoupled with increasing stream size. Ecosystem size could be an important determinant of connectivity because stream-riparian attributes vary with (1) network position (Vannote et al., 1980) and (2) differing levels of anthropogenic impacts at local and catchment scales (Allan, 2004; Burdon et al., 2023). This meant that there could be indirect effects of these abiotic drivers on trophic connectivity mediated through the three factors mentioned above.

# METHODS

## Study design

As described in Burdon, Ramberg, et al. (2020), study sites (Figure 2) were distributed across Europe in four catchments with varying levels of human development: Norway (Oslo Fjord), Sweden (Lake Mälaren), Belgium (Zwalm River), and Romania (Argeș River). Nested within these catchments were 10–12 streams flowing through an impacted landscape (agricultural, urban or mixed agricultural and urban land uses), each with a site pair: an upstream site with no forested riparian buffer (hereafter *Unbuffered* sites), and a downstream site with a forested riparian buffer (*Buffered*). We included 5–6 pristine or least impacted reference sites (*Forest*) on

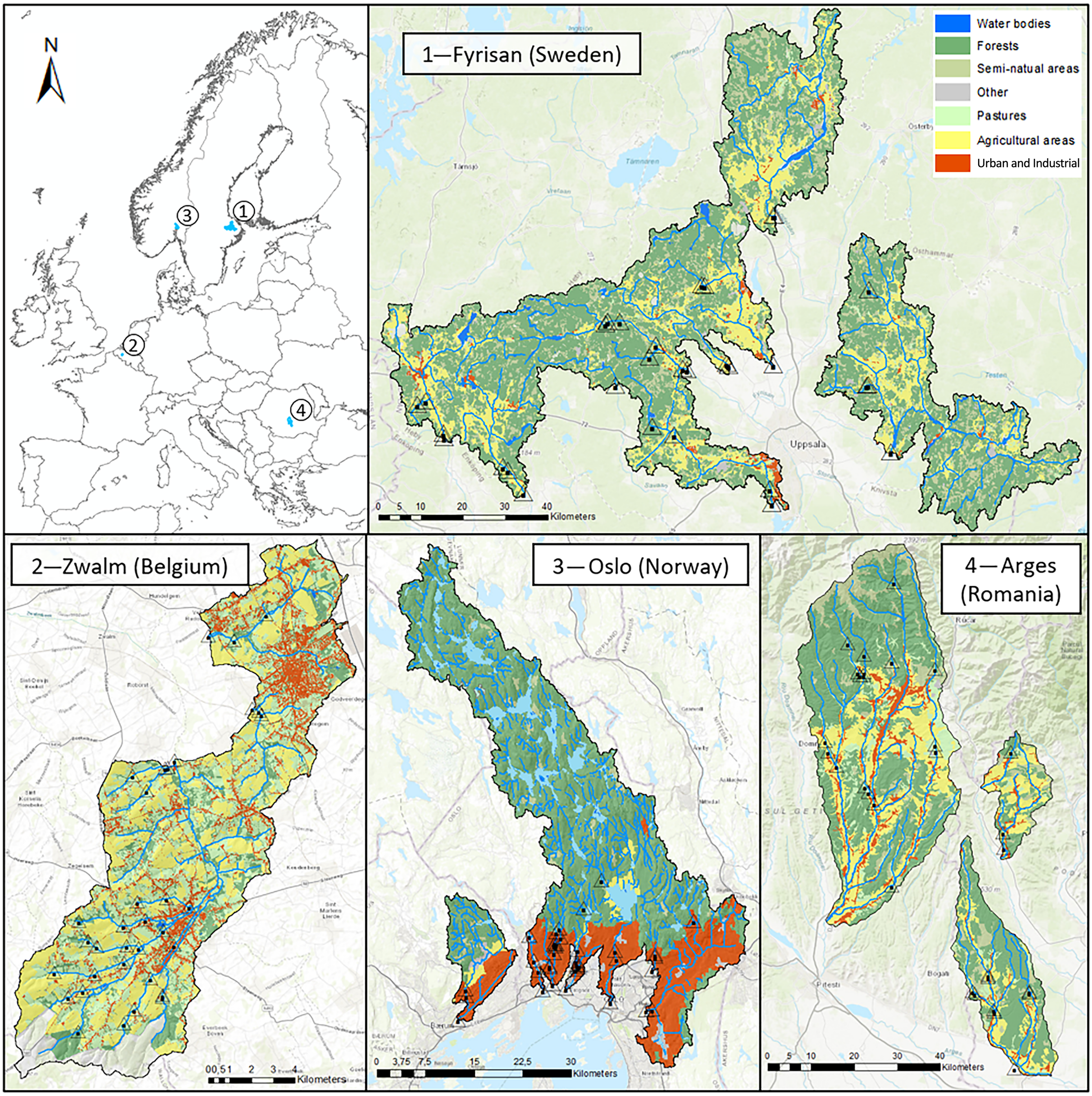

**FIGURE 2** The four catchments across Europe: (1) Sweden (stream reaches in the Lake Mälaren basin), (2) Belgium (stream reaches in the Zwalm river basin), (3) Norway (stream reaches in the Oslo Fjord basin), and (4) Romania (stream reaches in the Argeş river basin). Each basin had multiple sub-catchments dominated by forest, agriculture and urban land uses. Streams were sampled in the sub-catchments including forested-unforested site pairs. Site locations are indicated by the open triangles filled with a black dot.

additional streams in each country to help characterize the range of ecosystem responses to cumulative impacts of catchment land uses and extend our gradient of riparian habitat conditions (Burdon, Ramberg, et al., 2020).

Streams used were wadeable, 1st–3rd order (i.e., approximately 2–5 m wide), with a stable streambed (i.e., infrequent hydrodynamic disturbance) dominated by gravels and cobbles. For site categorization, we focused on the presence and extent of woody riparian vegetation. Forest reference sites typically had intact forest extending to the upstream catchment boundaries. Both buffered and unbuffered sites were in modified landscapes (impacted by mixed agricultural and urban land uses). Key criteria applied for selecting buffered sites included minimum buffer length (i.e., >50 m moving upstream), width (>2–3 × wetted stream width), extent (buffer on both banks of the stream segment), and composition (dominated by small and large trees). Unbuffered sites typically only had a few isolated riparian trees (Burdon, Ramberg, et al., 2020).

## Stream and riparian environment

Water samples were collected for water quality analyses (i.e., total nitrogen, ammonium, nitrite- and nitrate-nitrogen, total phosphorus, dissolved reactive phosphorus, specific conductivity, and pH) during three different seasons (autumn 2017, spring and summer 2018). We collected water samples 10 cm below the water's surface in the channel thalweg at the downstream end of each site. Site pairs were sampled on the same day. Water samples were stored on ice and refrigerated upon return to the laboratory, whereby they were analyzed within 24 h of collection following standard methods (Fölster et al., 2014). We recorded wetted channel widths at 5–6 transects distributed in a stratified random approach over a 50-m habitat assessment reach (HAR) at the time of sampling in two seasons (summer and autumn). Riparian habitat characteristics within the HAR were surveyed at each site following Burdon, Ramberg, et al. (2020). Surveys targeted both banks and were carried out in summer 2018 with complete leaf-out for all woody plant species. Six 50-$m^2$ rectangular plots (10 × 5 m) were used to describe vegetation characteristics. Canopy cover (in percentage) was measured using the smartphone app "CanopyApp" (University of New Hampshire, Durham, NH, USA). We estimated the pooled cover (% area) of nine vegetation/habitat categories (managed grasses, unmanaged grasses, herbs, mosses and lichens, small trees and shrubs, rocks and bedrock, bare ground, leaf litter, manmade features) within each plot (Burdon, Ramberg, et al., 2020). We also identified, enumerated, and measured the size of all trees with a dbh ≥5 cm in each riparian plot to estimate tree density (in number of trees per square meter). Upstream catchment land-cover (in percentage) estimates for eight categories (water bodies, wetlands, forests, seminatural areas, other, pastures, agricultural areas, urban and industrial) were obtained from the CORINE Land Cover inventory (CLC, 2018).

## Algae and terrestrial organic matter

To quantify algal biomass accrual, we evenly placed four unglazed tiles (16 $cm^2$) within a 30-m effective sampling reach (ESR), which was nested within the larger HAR (Burdon, Ramberg, et al., 2020). Habitat conditions were comparable among ESRs (i.e., moderate-fast flowing reaches with rocky substrate). Tiles were deployed for ≈30 days during spring–summer, after which algal biomass accrual (—in milligrams of chlorophyll *a* per square meter per day) was assessed using one of two complementary methods for thin (<2 mm) biofilms (Echenique-Subiabre et al., 2016; Harris & Graham, 2015; Kahlert & McKie, 2014). The first method involved in situ measurements using a portable fluorometer (Benthotorch, BBE Moldaenke, Schwentinental, Schleswig-Holstein, Germany) which quantifies the fluorescence of chlorophyll *a* (chl *a*) and converts this information to chlorophyll biomass (Kahlert & McKie, 2014). The second method involved pigment extraction and spectrophotometry in the laboratory (Biggs & Kilroy, 2000). Coarse particulate organic matter (CPOM) was recorded from Belgian and Swedish benthic invertebrate samples (see below). CPOM expressed as grams of dry mass per square meter was sorted, washed, sieved, and oven-dried at 60°C for 48 h before weighing.

## Aquatic invertebrates

We sampled macroinvertebrates once within the ESR at each site during the summer months (May–August) following Burdon, Ramberg, et al. (2020). The ESR had flowing water (i.e., run-riffle sequence) with hard-bottomed sections (e.g., cobble, gravels). We standardized sampling effort (Hauer & Resh, 2007) using 500-μm mesh netting and area per unit sampled (≈0.0625 $m^2$) using a Surber sampler. Six replicate subsamples were collected (three erosional/riffle-run habitats, three depositional/pool-run habitats), pooled together, sieved to remove water, then preserved (96% ethanol) for later sorting. Macroinvertebrates were identified to the lowest practicable taxonomic level (e.g., species or genus) using standard identification guides (see literature cited in Burdon, Ramberg, et al., 2020). Benthic insect production is strongly correlated with adult aquatic insect emergence in streams (Statzner & Resh, 1993), justifying our use of trait abundances from benthic invertebrates as surrogate predictors for the potential prey flux to recipient riparian predators (Burdon & Harding, 2008). We used the DISPERSE database (de Figueroa et al., 2020) to assign dispersal trait modalities to aquatic invertebrates and calculate abundance-weighted trait frequencies. The DISPERSE database compiles information on multiple dispersal-related biological traits of European aquatic macroinvertebrates (Sarremejane et al., 2020). DISPERSE includes nine dispersal-related traits subdivided into 39 trait categories for 480 taxa, including Annelida, Mollusca, Platyhelminthes, and Arthropoda such as Crustacea and Insecta, generally at the genus level. Trait modalities in the DISPERSE database are fuzzy coded (0–3) following the approach used by Usseglio-Polatera et al. (2000). We selected 10 traits (Table 1) based on previous studies (e.g., Kopp & Allen, 2020; McKie et al., 2018), preliminary analysis, and considered opinion that we thought best described the attributes (e.g., univoltine, medium-sized, and actively dispersing stream insects) that we hypothesized to be important for aquatic-terrestrial trophic connectivity. Reducing the number of traits used also helped to combat correlations among traits (cf. trait syndromes).

## Riparian invertebrates

We surveyed and collected predatory riparian invertebrates in summer 2018 using daytime surveys. We targeted web-building spiders (Araneae) and ground-living arachnids (Araneae and Opiliones). Semiquantitative sampling provided abundance data and material for analyses (Burdon, Ramberg, et al., 2020). Two observers surveyed both banks over the HAR using the same 50-$m^2$ plots described above. The exact time taken for the search was recorded (target 10 min) per plot using two people. We sampled ≥4 plots, but where necessary we sampled all six to get enough spiders for biomarker analyses (e.g., ≥20 individuals). We calculated the "catch per unit effort" (CPUE) to make abundances between sites comparable (Equation 1):

$$\mathrm{CPUE} = \frac{N}{(A/2T)} \tag{1}$$

**TABLE 1** Ten aquatic invertebrate dispersal traits from Sarremejane et al. (2020) hypothesized to be important for aquatic-terrestrial trophic connectivity in temperate streams.

| Trait | Modality | Code |
|---|---|---|
| Maximum body size (cm) | ≥0.5–1 | s3 |
| Life cycle duration | ≤1 year | cd1 |
| Potential no. reproductive cycles per year | One | cy2 |
| Dispersal strategy | Aerial passive | dis3 |
| | Aerial active | dis4 |
| Adult life span | <1 week | life1 |
| | ≥1 week–1 month | life2 |
| Wing-pair type | 1 pair + halters | wnb2 |
| | 1 pair + 1 pair of small hind wings | wnb3 |
| | 2 similar-sized pairs | wnb5 |

where the total sampling duration (2*T*, in hours), area sampled (*A*, in square meters), and the total number of invertebrates collected (*N*) were used to calculate the CPUE; the time taken (*T*) was multiplied by two to calculate total sampling duration. Sampling techniques used for collection included visual searching and collection by hand (the preferred method for most habitat types) and sweep-netting in long grasses. The samples were kept on ice in the field to prevent FA denaturation due to high temperatures, and frozen immediately upon return to the laboratory at −20°C prior to identification and preparation for biomarker analyses. Riparian invertebrates were identified using guides described in Burdon, Ramberg, et al. (2020). Spiders (Araneae) were identified to Family level whereas Opiliones were left at Order (although most individuals were from the suborder Palpatores). We used the databases of Entling et al. (2007) and Gossner et al. (2015) to describe traits of terrestrial arachnids, supplemented with information from Blandenier (2009) and Macías-Hernández et al. (2020). These traits included body size and mode of hunting, and were used to calculate abundance-weighted trait frequencies.

## Fatty acid analysis

Following taxonomic identification, our targeted web-building spiders (Agelenidae, Araneidae, Linyphiidae, Tetragnathidae), ground-hunting spiders (Lycosidae, Pisauridae), and arachnids (Opiliones) were prepared for FA analysis. Invertebrates belonging to the same group at each site were pooled together to reduce individual variations in FA content and reach analysis mass requirements (≈5-mg DM). Samples were freeze-dried (LyoDry compact, Mechatech systems LTD, Bristol, UK) and homogenized (i.e., grinding with a mortar and pestle); the mass recorded, then stored at −20°C. We analyzed the samples for 38 FAs (Appendix S1: Section S2: Table S2) at the Swedish Metabolomics Centre, Umeå, Sweden, following methods based on Grieve and Lau (2018) as described in Ramberg et al. (2020). The processing involved three main steps: lipid extraction, methylation, and gas chromatography–mass spectrometry (GC–MS); full methods are described in Appendix S1: Section S2.

## Community-weighted mean traits

Community-weighted mean (CWM) trait abundances were calculated using the "FD" R package (Laliberté & Legendre, 2010). The CWM is defined as the mean of values present in the community weighted by the relative abundance of taxa bearing each value (Lavorel et al., 2008). CWM trait values are sensitive to environmental gradients (Carreño-Rocabado et al., 2012; Vandewalle et al., 2010), making them useful for assessing community dynamics and ecosystem properties (Frainer et al., 2018; Lavorel et al., 2008). Community analyses (F. J. Burdon, unpublished data) and published research (Popescu et al., 2021; Ramberg et al., 2020) identified spider body size (mean body length in millimeters for males and females) as a key trait describing differences between arachnid communities dominated by small, web-building spiders (e.g., Linyphiidae, Tetragnathidae) and those typified by large, ground-living spiders (e.g., Lycosidae, Pisauridae).

## Data analysis

Following Burdon, Ramberg, et al. (2020) we used principal components analysis (PCA) to describe catchment-wide anthropogenic influences (i.e., upstream human impacts). The PCA decomposed mean log-transformed water quality variables and logit-transformed upstream land-cover variables into Axis 1 site scores (henceforth *Catchment impact* PC1) explaining 42.3% of total variation (Appendix S1: Section S3: Table S3). We also used PCA to decompose the mean quantitative habitat attributes (% canopy cover, tree density, and habitat cover variables) recorded in the six riparian plots into Axis 1 site scores (henceforth *Riparian condition* PC1) explaining 36.7% of total variation (Appendix S1: Section S3: Table S3). Riparian condition (PC1) was correlated with the % wooded area within an upstream grid of 0.03 km$^2$ centered on the channel ($F_{1,93} = 32$, $p < 0.001$, $R_m{}^2 = 32\%$), indicating that our local spatial scale of observation was appropriate. We tested differences in catchment impact and riparian condition PC1 site scores between site types, countries, and their interaction using linear mixed models with sub-catchment as a random effect. Mean wetted channel widths were correlated with upstream catchment area ($F_{1,93} = 150$, $p < 0.001$, $R_m{}^2 = 76\%$), so we used width as an indicator of network position and ecosystem size (potentially influencing flux magnitude to riparian habitats).

Differences in arcsine square-root transformed riparian spider %FA composition between site types (Unbuffered, Buffered, and Forest) were tested using the R functions “adonis2” and “pairwise.adonis2” (for permutational multivariate ANOVA; PERMANOVA) and “betadisper” (for multivariate homogeneity of group dispersions), respectively, with a strata term for *Site Pair* and permutation testing with 999 randomizations. We included *Spider Family*, *Country*, and *Site Pair* nested in *Country* as fixed categorical predictors (blocks) in our PERMANOVA models; additional models tested the influence of spider *Mode of Hunting* (i.e., ground-living vs. web-building) and *Body size*. Post hoc differences in the betadisper models were tested using the “TukeyHSD” function. We used Similarity Percentage analysis (SIMPER) with the “simper” R function to identify FAs contributing to differences between site types and modes of hunting.

We tested the influence of environmental and biotic predictors on Hellinger transformed riparian spider %FA composition using redundancy analysis (RDA) and variation partitioning. We considered three environmental predictors representing network position (wetted channel width) and human impacts at the local (riparian condition PC1) and catchment scales (catchment impact PC1). We considered biotic predictors at three different trophic levels that were hypothesized to contribute to trophic connectivity: algal productivity, CWM aquatic invertebrate dispersal traits (Table 1), and CWM spider body size. We considered CWM spider body size as an indicator of predator functional composition since this was independent of taxonomic identity, but we also considered mean spider body size in additional models. We log-transformed data to help improve normality and homoscedasticity. All data was standardized (i.e., centered on column means and scaled by unit variance) using the “decostand” R function.

To select model predictors and avoid overfitting models, we removed highly collinear ($r > 0.8$) predictors (i.e., Maximum body size (≥0.5–1 cm) ~ Life cycle duration (≤1 year), Adult life span (<1 week) ~ Life cycle duration (≤1 year), Wing-pair type (1 pair + halters) ~ Dispersal strategy: Aerial passive). We then used a forward-selection procedure to select a subset of explanatory variables following Blanchet et al. (2008) using the “forward.sel” function in the “packfor” R package (Dray et al., 2016). We used the “vif.cca” R function to obtain variance inflation factors (VIF). Predictor variables (i.e., dis4, cy2) were excluded from RDA models when they had VIF scores ≥4 (Hair et al., 2010). The final RDA model was fitted using the “rda” R function and visualized using “ggord” (Beck, 2024).

We used four variation-partitioning models to test different hypotheses related to FA composition in riparian spiders:

1. The first model ($\mathrm{VP}_{\mathrm{connect}}$) grouped predictors selected for the RDA model to test our main hypotheses regarding the relative contributions of stream productivity gradients (algae productivity), aquatic insect dispersal traits (CWM wnb5, wnb3, life2, dis3), and spider body size (mean body size and CWM body size

as a descriptor of community functional composition) to aquatic–terrestrial food web connectivity. We included the environmental predictors selected (catchment impact PC1, riparian condition PC1) to assess abiotic contingencies in responses.

2. The second variation-partitioning model ($\text{VP}_{\text{riparian}}$) explicitly tested how riparian vegetation structure (riparian condition PC1) influences spider FA composition, with biotic variables grouped as *Food web* predictors and the catchment impact PC1 as *Environment* predictors.
3. Our third variation-partitioning model ($\text{VP}_{\text{country}}$) investigated the influence of nonindependencies in the dataset introduced by country and spider families.
4. The fourth model ($\text{VP}_{\text{bodysize}}$) was a variant on $\text{VP}_{\text{country}}$ using mean body size in place of spider taxonomic identity.

The significance of each independent variation component was permutation-tested using 999 randomizations. Models were fitted with the "varpart" and "rda" R functions; we visualized the results of the $\text{VP}_{\text{connect}}$ model using the "venneuler" R function (Wilkinson, 2022).

Based on the RDA results and previous studies (Chari et al., 2020; Sushchik et al., 2021; Twining, Razavi, et al., 2021), we identified the omega-3 LC-PUFA eicosapentaenoic acid (EPA, 20:5n-3) as a potential indicator FA of trophic connectivity. In addition to EPA, we also tested another omega-3 LC-PUFA, docosahexaenoic acid (DHA, 22:6n-3), and their molecular precursor, the omega-3 short-chain PUFA alpha-linolenic acid (ALA, 18:3n-3). Since ALA is present in aquatic and terrestrial primary producers (Twining, Razavi, et al., 2021), we expected different responses from the omega-3 LC-PUFAs, which should be derived from aquatic subsidies only. We tested the ratio of EPA to ALA, since an aquatic subsidy influence should cause EPA to increase disproportionately to ALA (Mathieu-Resuge et al., 2022).

We tested the influence of spider mode of hunting and body size on %EPA using linear mixed-effects (LME) models. We also used LME to assess the relationship between trophic connectivity and the CWM abundances of active and passive aerial dispersing invertebrates. The fixed effects were the dispersal traits and the random effects *Spider Family* and *Site* nested in *Site Pair*. We did not include *Country* as a random or fixed effect because the high correlations ($r > 0.7$) with other predictors violated the assumption of exogeneity needed for unbiased estimation (Grilli & Rampichini, 2015; Schielzeth et al., 2020) and required that we employ a VIF threshold <4 to avoid Type II errors (Zuur et al., 2010). We fitted LME for each trait individually, and an LME including both traits to compare the slope of the relationship between trait abundances and trophic connectivity. We used variation partitioning to investigate the shared variation explained by country, spider family, and the dispersal traits. We also assessed the potential trade-off between algal quality and quantity by modeling the relationship between % EPA and algal productivity using generalized additive models (GAM). LME were fitted with the "lme4" and "blme" R packages (Bates et al., 2015; Chung et al., 2013); and GAM with the "mgcv" R package (Wood, 2017). Model VIF scores were calculated using the "check_collinearity" command in the "performance" R package (Lüdecke et al., 2021). Univariate LME models were visualized with density plots for country using the "ggMarginal" function in the "ggExtra" R package (Attali & Baker, 2023).

We used structural equation modeling (SEM) to test multiple hypotheses (Appendix S1: Section S1: Table S1) in a causal network (Figure 1). Our hypotheses focused on the influence of stream productivity gradients, aquatic insect dispersal traits, and spider community functional composition on trophic connectivity (%EPA, %ALA, EPA:ALA) and how catchment and riparian land uses might modulate these relationships in coupled stream–riparian ecosystems. The SEMs used riparian spider FA data (238 samples from 85 sites), Tetragnathidae (53 sites), and Lycosidae (60 sites) from all countries after accounting for missing values. SEMs pooling family-level data into web-building and ground-hunting spider feeding modalities are presented in Appendix S1: Section S3: Figure S8.

Data were transformed to improve normality and homoscedasticity, then standardized. Some constraints were applied a priori to model selection. We only considered the same invertebrate predictors used in the LME representing two broad trait syndromes (active and passive aerial dispersal); these two predictors were included in all model iterations. Each model component included fixed and random effects. Our main response was trophic connectivity, and we included random effects for *Spider Family* and *Site* nested in *Site Pair*. All other endogenous predictors included a random effect for *Site Pair*. We did not use random or fixed effects for *Country* due to the same issues highlighted above for the LME, except for algal biomass accrual, where *Site Pair* nested in *Country* was used as a random effect due to the different approaches used for estimating chl *a* concentrations across countries. Issues with singularity (some dimensions of the variance–covariance matrix were estimated as exactly zero) meant we removed most of the random effects from the SEMs testing tetragnathid and lycosid responses to avoid model overfitting. To achieve model parsimony, nonsignificant paths were removed where possible. We included correlated error terms where they made ecological sense and improved model fit. Shipley's test of directed separation was used to identify unspecified paths and help assess model adequacy in conjunction with Fisher's *C*. The Akaike information criterion (AIC) and corrected AIC for small sample sizes ($\text{AIC}_\text{c}$) scores were compared for all model iterations; where $\Delta\text{AIC} < 2$ we considered the models equivalent and chose the most parsimonious one. We considered SEMs using spider %DHA and CPOM, but these did not reveal any useful information and are not reported. The mixed-effect SEMs were fitted using the "piecewiseSEM" R package (Lefcheck, 2016). Unless otherwise specified, all multivariate analyses used the "vegan" R package (Oksanen et al., 2022). All analyses were conducted in R (R Core Team, 2022). Data and code can be found in Burdon et al. (2025).

# RESULTS

## Differences in landscape drivers

Across all sites, there were a wide range of values for upstream land cover, water quality, and riparian attributes that contributed to catchment- and local-scale impacts (Tables 2–4). The catchment impact PC1 explained 42.3% of the variation in water quality and land cover (Appendix S1: Section S3: Table S3). There were differences among site types and countries (Figure 3a). Forested reference sites consistently had lower catchment impact PC1 scores when compared to the buffered and unbuffered sites ($F_{2,88} = 4.15$, $p < 0.05$). Sites in Sweden and Norway did not differ but had lower catchment impact PC1 scores than the Belgian and Romanian sites. The Belgian and Romanian sites did not differ. These differences generally reflected poorer water quality in Belgium and Romania (Tables 2 and 3), possibly indicative of increased land use intensity and higher human population densities than in Scandinavia.

The local-scale attributes that contributed to riparian condition varied as expected with the study design, with forested and buffered sites showing higher values than unbuffered sites (Figure 3b). The riparian condition PC1 explained 36.7% of variation in riparian habitat quality (Appendix S1: Section S3: Table S3). There were differences among site types and countries (Figure 3b). Forested reference sites and buffered sites consistently had higher riparian condition PC1 scores when compared

**TABLE 2** Summary statistics of site properties ($n = 103$) across multiple sub-catchments in four European countries.

| Site | Forest (%) | Arable (%) | Natural (%) | Urban (%) | Pasture (%) | Other (%) | Hort. (%) | Water (%) | Wetland (%) |
|---|---|---|---|---|---|---|---|---|---|
| Sweden ($n = 25$) | | | | | | | | | |
| Mean | 59 | 16 | 19 | 1 | 2 | 1 | 0 | 1 | 1.3 |
| Med. | 58 | 14 | 18 | 0 | 2 | 1 | 0 | 1 | 1.2 |
| Min | 47 | 0 | 12 | 0 | 0 | 0 | 0 | 0 | 0.0 |
| Max | 83 | 28 | 34 | 5 | 5 | 5 | 0 | 3 | 3.1 |
| Norway ($n = 29$) | | | | | | | | | |
| Mean | 59 | 2 | 2 | 29 | 0 | 6 | 0 | 2 | 0.0 |
| Med. | 67 | 0 | 0 | 15 | 0 | 2 | 0 | 0 | 0.0 |
| Min | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0 |
| Max | 100 | 11 | 9 | 88 | 0 | 25 | 0 | 11 | 1.0 |
| Romania ($n = 26$) | | | | | | | | | |
| Mean | 65 | 5 | 12 | 2 | 7 | 0 | 8 | 0 | 0.0 |
| Med. | 66 | 3 | 12 | 1 | 6 | 0 | 2 | 0 | 0.0 |
| Min | 28 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0.0 |
| Max | 93 | 20 | 41 | 9 | 26 | 3 | 28 | 0 | 0.0 |
| Belgium ($n = 23$) | | | | | | | | | |
| Mean | 17 | 35 | 25 | 5 | 14 | 4 | 0 | 0 | 0.0 |
| Med. | 12 | 33 | 23 | 4 | 12 | 4 | 0 | 0 | 0.0 |
| Min | 2 | 3 | 4 | 0 | 2 | 0 | 0 | 0 | 0.0 |
| Max | 90 | 76 | 44 | 16 | 27 | 11 | 0 | 0 | 0.0 |

*Note*: Land-cover variables were used for the catchment impact principal components analysis.

**TABLE 3** Summary statistics of site properties ($n = 103$) across multiple sub-catchments in four European countries.

| | Water chemistry | | | | | | | Physical |
|---|---|---|---|---|---|---|---|---|
| **Site** | **SC (μS/cm)** | **pH ([H$^+$])** | **NH$_4$ (mg/L)** | **NO$_3$-N (mg/L)** | **TIN (mg/L)** | **SRP (mg/L)** | **TP (mg/L)** | **Temp. (°C)** |
| Sweden ($n = 25$) | | | | | | | | |
| Mean | 37 | 7.4 | 0.06 | 0.88 | 0.95 | 0.02 | 0.06 | 5 |
| Med. | 28 | 7.4 | 0.03 | 0.61 | 0.64 | 0.01 | 0.04 | 5.3 |
| Min | 11 | 6.8 | 0.01 | 0.02 | 0.05 | 0 | 0.02 | 1.7 |
| Max | 122 | 7.8 | 0.55 | 5.19 | 5.22 | 0.06 | 0.15 | 6.8 |
| Norway ($n = 29$) | | | | | | | | |
| Mean | 193 | 7.7 | 0.05 | 0.8 | 0.84 | 0.03 | 0.05 | 5.8 |
| Med. | 170 | 7.9 | 0.03 | 0.82 | 0.82 | 0.02 | 0.05 | 5.9 |
| Min | 20 | 6.7 | 0 | 0.04 | 0.05 | 0 | 0.01 | 1.1 |
| Max | 552 | 8.1 | 0.21 | 1.55 | 1.57 | 0.09 | 0.13 | 9.2 |
| Romania ($n = 26$) | | | | | | | | |
| Mean | 847 | 7.9 | 3.34 | 2.76 | 6.1 | 0.14 | 0.39 | 12.4 |
| Med. | 403 | 7.8 | 2.45 | 2.41 | 4.94 | 0.11 | 0.41 | 11.4 |
| Min | 49 | 7.4 | 0.19 | 0.81 | 1.45 | 0.04 | 0.13 | 8.1 |
| Max | 4560 | 8.4 | 12.14 | 7.3 | 15.85 | 0.47 | 0.77 | 18.9 |
| Belgium ($n = 23$) | | | | | | | | |
| Mean | 63 | 7.8 | 1.54 | 4.98 | 6.52 | 0.34 | 0.55 | 10.3 |
| Med. | 64 | 7.9 | 0.26 | 3.12 | 3.78 | 0.16 | 0.32 | 10.3 |
| Min | 31 | 7.4 | 0.01 | 0.1 | 0.21 | 0.03 | 0.03 | 9 |
| Max | 93 | 8.3 | 9.8 | 13.66 | 22.47 | 1.82 | 2.26 | 11.1 |

*Note*: Water chemistry variables were used for the catchment impact principal components analysis. Temperature data summarize Autumn (September–October 2017) mean daily stream temperatures.

Abbreviations: SC, specific conductivity; SRP, soluble reactive phosphorus; TIN, total inorganic nitrogen; TP, total phosphorus.

to the unbuffered sites ($F_{2,88} = 36.8$, $p < 0.001$). Sites in Sweden and Norway did not differ apart from higher riparian condition PC1 scores in forested and buffered Swedish sites. Riparian condition scores were higher in Scandinavia when compared to the Belgian and Romanian sites, which did not differ. These differences reflected lower tree densities and canopy cover in Belgium and Romania (Table 4), which were possibly indicative of differences in forest management and fewer conifers than the Scandinavian sites.

## Drivers of FA composition in riparian spiders

FA composition in riparian spiders varied by site type. Riparian spiders in forest reference sites had significantly different FA composition when compared with spiders from buffered ($F_{1,156} = 5.39$, $p < 0.001$, $R^2 = 1.56\%$) and unbuffered sites ($F_{1,161} = 9.00$, $p < 0.001$, $R^2 = 2.41\%$). The FA composition of spiders from buffered sites differed from those in unbuffered sites, but this was not statistically significant at $\alpha = 0.05$ ($F_{1,141} = 3.00$, $p = 0.051$, $R^2 = 0.76\%$). There were differences in the FA composition of different spider taxa ($F_{6,176} = 11.0$, $p < 0.001$, $R^2 = 12.1\%$). Spider taxa also had a significant interaction with site type ($F_{12,176} = 1.29$, $p < 0.05$, $R^2 = 2.82\%$). There were significant differences in FA composition associated with mode of hunting (web vs. ground), spider body size, and country (Appendix S1: Section S3: Tables S4 and S5). Analysis of multivariate homogeneity of group dispersions (variances) indicated that the FA composition of spiders from unbuffered sites was more homogenous than those from forest reference sites ($F_{2,253} = 4.60$, $p < 0.05$). There were no significant differences between the other two site-type contrasts or in mode of hunting, but there were differences in dispersions for spider taxonomic identity and country (Appendix S1: Section S3: Figure S1).

Several FAs contributed to the dissimilarity between forest reference and paired site types (i.e., buffered and unbuffered). SIMPER analysis revealed that %

**TABLE 4** Summary statistics of riparian habitat variables at sites ($n = 103$) across multiple sub-catchments in four European countries.

| Site | Tree density (m$^2$) | Canopy cover (%) | Tree and shrubs (%) | Herbs and forbs (%) | Grass (%) | | Mosses and lichens (%) | Plant litter (%) | Rocks (%) | Bare ground (%) | Urban features (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | UM | M | | | | | |
| Sweden ($n = 25$) | | | | | | | | | | | |
| Mean | 0.9 | 60 | 34 | 30 | 17 | 6 | 18 | 32 | 14 | 4 | 0 |
| Med. | 0.8 | 71 | 33 | 23 | 11 | 0 | 11 | 30 | 13 | 3 | 0 |
| Min | 0.0 | 1 | 3 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| Max | 2.3 | 82 | 68 | 70 | 73 | 50 | 67 | 65 | 42 | 12 | 0 |
| Norway ($n = 29$) | | | | | | | | | | | |
| Mean | 0.8 | 58 | 13 | 15 | 3 | 5 | 7 | 26 | 9 | 10 | 20 |
| Med. | 0.7 | 68 | 9 | 12 | 1 | 0 | 1 | 20 | 5 | 6 | 8 |
| Min | 0.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Max | 1.7 | 90 | 36 | 44 | 34 | 55 | 47 | 81 | 24 | 36 | 77 |
| Romania ($n = 26$) | | | | | | | | | | | |
| Mean | 0.5 | 37 | 10 | 0 | 48 | 14 | 1 | 7 | 3 | 16 | 0 |
| Med. | 0.4 | 45 | 4 | 0 | 46 | 0 | 0 | 1 | 0 | 2 | 0 |
| Min | 0.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Max | 1.9 | 77 | 63 | 3 | 97 | 91 | 13 | 36 | 22 | 99 | 0 |
| Belgium ($n = 23$) | | | | | | | | | | | |
| Mean | 0.2 | 33 | 3 | 30 | 15 | 35 | 1 | 5 | 0.1 | 4 | 10 |
| Med. | 0.2 | 40 | 1 | 18 | 10 | 41 | 0 | 0 | 0.0 | 2 | 0 |
| Min | 0.0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0 | 0 | 0 |
| Max | 1.3 | 69 | 20 | 90 | 56 | 83 | 8 | 43 | 1.0 | 23 | 74 |

*Note*: Variables were used for the riparian condition principal components analysis.
Abbreviations: M, managed; UM, unmanaged.

concentrations of the omega-3 short-chain PUFA ALA were significantly higher in riparian spiders from forest reference sites when compared to buffered sites ($p < 0.01$). Concentrations of ALA were also significantly higher in spiders from buffered sites when compared to unbuffered sites ($p < 0.01$). In contrast, concentrations of the omega-3 LC-PUFA DHA were significantly higher in spiders from unbuffered sites when compared to forest reference sites ($p < 0.05$), but the difference was not significant between the paired site types ($p = 0.08$). There were no significant differences in spider %EPA between site types. Ground-hunting spiders generally had higher concentrations of PUFAs than web-building spiders (Appendix S1: Section S3: Table S7). For more results from the SIMPER analyses, see Appendix S1: Section S3: Tables S6 and S7.

Univariate analyses showed that the ratio of EPA to ALA in spiders differed among site types ($F_{2,249} = 4.79$, $p < 0.05$). It was higher in spiders from unbuffered sites than forested sites ($p < 0.05$), possibly reflecting the increased presence of ground-hunting spiders at unbuffered sites ($\chi^2{}_2 = 6.99$, $p < 0.05$). The difference in spider EPA:ALA between buffered and unbuffered sites was not significant. Ground-hunting spiders had lower EPA:ALA in forested sites when compared to buffered sites ($p < 0.05$) and unbuffered sites ($p < 0.01$), but there were no differences in web-building spider EPA:ALA among site types. EPA:ALA in lycosid spiders differed among site types ($F_{2,62} = 3.7$, $p < 0.05$), being lower in forested sites when compared to buffered sites ($p < 0.05$), but there was no significant difference between buffered and unbuffered sites, or unbuffered and forested sites. EPA:ALA in tetragnathid spiders showed similar trends to the Lycosidae, but there were no significant differences between site types.

The RDA model (Figure 4a) explained 24.92% of the total variation in spider FA composition ($F_{9,228} = 9.74$, $p < 0.001$). Most variation in spider FA composition was associated with Axis 1 ($F_{1,228} = 45.6$, $p < 0.001$; Figure 4a), although Axes 2 ($F_{1,228} = 19.4$, $p < 0.001$), 3 ($F_{1,228} = 11.5$, $p < 0.001$), and 4 ($F_{1,228} = 6.04$, $p < 0.01$) were also significant (Appendix S1: Section S3: Figure S2). Significant predictors of spider FA composition in the RDA (Figure 4b) included environmental

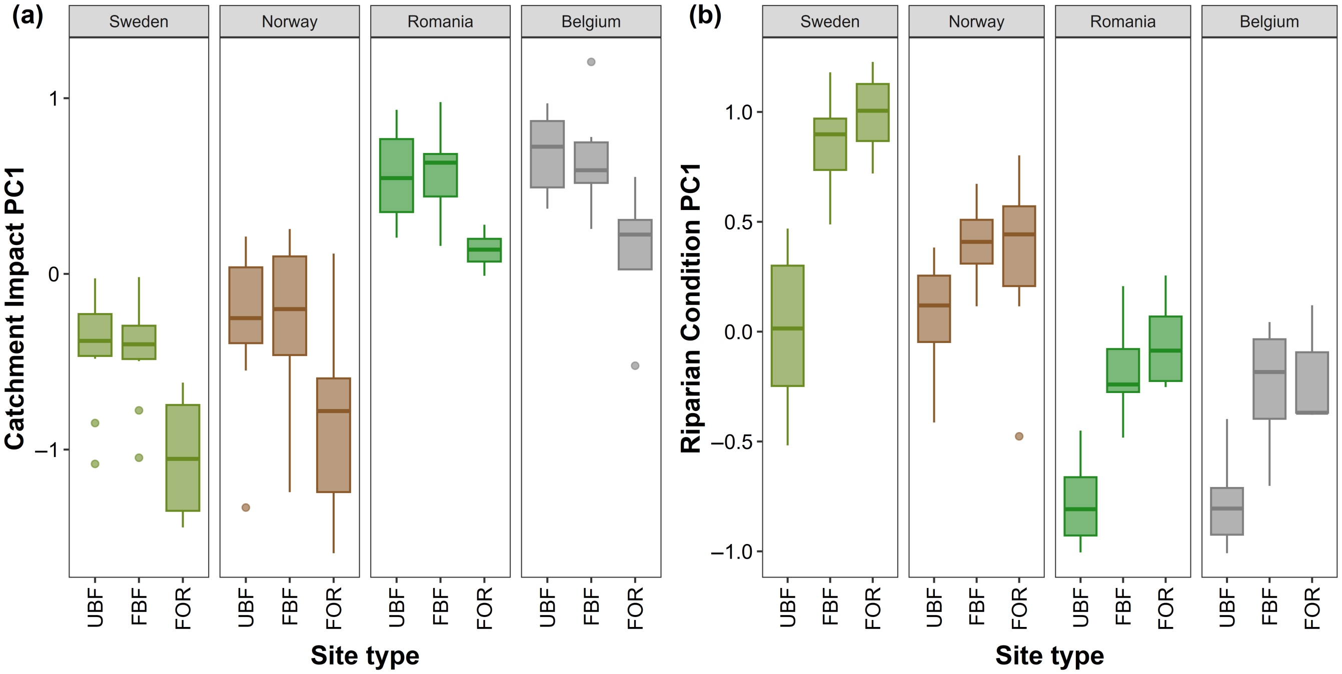

**FIGURE 3** Boxplots showing the distribution of values for the (a) catchment impact PC1 and (b) riparian catchment PC1 by site type and country among multiple sub-catchments in 103 European stream sites. FBF, forest buffer; FOR, forested (or least impacted); UBF, unbuffered (unforested).

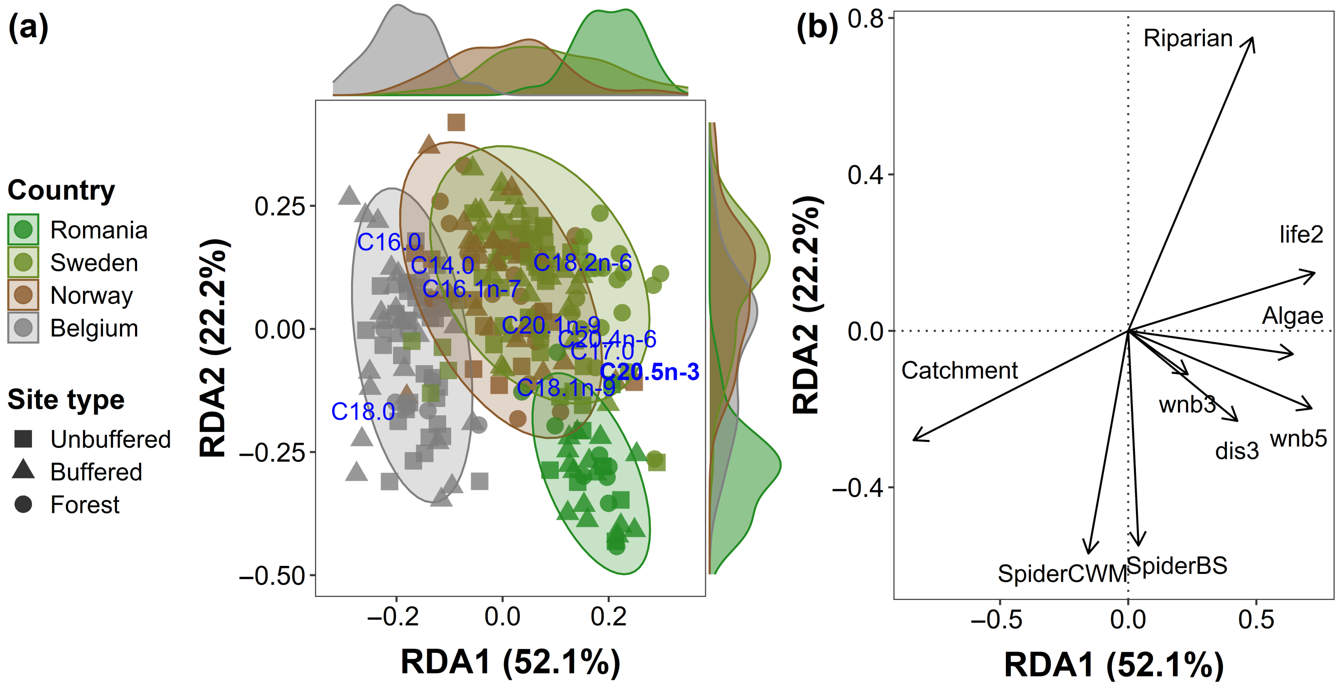

**FIGURE 4** Redundancy analysis (RDA) of fatty acid composition (%FA) in riparian spiders. In (a), standard ellipses indicate differences in the %FA composition of spiders among multiple sub-catchments across four European countries. Density plots along margins show the distribution of values for each country. The 10 most abundant FAs are shown (summing to ≈95% of the mean total). EPA, or eicosapentaenoic acid (20:5n-3), is highlighted in bold. For a full list of the 38 FAs used, see Appendix S1: Section S2: Table S2.
(b) Explanatory variables selected for the RDA: Algae, algae productivity (in milligrams of chlorophyll *a* per square meter per day); Catchment, catchment impact PC1; Riparian, riparian condition PC1; SpiderBS, mean spider body size; SpiderCWM, community-weighted mean (CWM) spider body size. The CWM aquatic invertebrate dispersal traits were wnb5, wing-pair type: 2 similar-sized pairs; wnb3, wing-pair type: 1 pair + 1 pair of small hind wings; life2, adult life cycle: ≥1week–1 month; and dis3, dispersal strategy: aerial passive.

predictors (riparian condition and catchment impact PC1). Biotic predictors included algal productivity, aquatic insect community dispersal traits (CWM Wing-pair types: 2 similar-sized pairs, and 1 pair + 1 pair of small hind wings; Adult life span: 1 week–1 month; and Dispersal strategy: aerial passive), and spider body size and community functional composition (CWM body size). The omega-3 LC-PUFA EPA (20:5n-3) was strongly associated with biotic predictors including algal productivity and aquatic insect dispersal traits (Figure 4a,b). Similar patterns were seen in RDA models for spider hunting modes and selected families (Appendix S1: Section S3: Figure S3).

The first variation-partitioning model ($\mathrm{VP}_{\mathrm{connect}}$) tested our main hypotheses using the FA composition in riparian spiders and predictors selected for the RDA (Figure 4b). The $\mathrm{VP}_{\mathrm{connect}}$ model showed that CWM aquatic insect dispersal traits explained 13.19% of the variation in spider FA composition, with the largest contribution (4.71%) independent of the other predictors (Figure 5a), supporting the notion that aquatic insect dispersal traits are important determinants of aquatic–terrestrial connectivity. The environmental predictors explained 13.51% of the variation in spider FA composition, with an independent contribution of 4.22% (Figure 5a), also highlighting the importance of environmental factors in determining aquatic–terrestrial connectivity. Spider body size and algal productivity explained smaller fractions of variation in spider FA composition. Spider body size accounted for 5.72% of the variation in spider FA composition, with 4.26% independent of the other predictors. Algal productivity explained 6.06% of the variation in spider FA composition, with an independent contribution of 2.02%, suggesting that ecosystem productivity was less important for aquatic–terrestrial connectivity. Aquatic invertebrate dispersal traits and environmental predictors jointly explained 4.30%, and the combined influence of aquatic invertebrates, environment, and algal productivity was 3.27%.

The second variation-partitioning model ($\mathrm{VP}_{\mathrm{riparian}}$) showed that riparian condition explained 6.58% of the variation in spider FA composition, with an independent contribution of 1.69% (Figure 5b). Riparian condition shared fractions with catchment impact (1.49%), and catchment impact jointly with food web attributes including aquatic invertebrate dispersal traits (5.90%). A large fraction of variation in spider FA composition was independently explained by the food web attributes (11.41%). Our third variation-partitioning model ($\mathrm{VP}_{\mathrm{country}}$) explained the most variation in spider FA composition (43.52%), but it highlighted that 19.16% of the variation explained by the predictors selected for the RDA was shared with country and/or spider family, leaving only 3.03% independently explained by the continuous predictors. The results of the $\mathrm{VP}_{\mathrm{country}}$ highlighted that spider identity effects alongside environmental factors associated with the countries used in our study are both important determinants of aquatic-terrestrial connectivity. The fourth variation-partitioning model ($\mathrm{VP}_{\mathrm{bodysize}}$) indicated that the mean body size of spider taxa independently explained

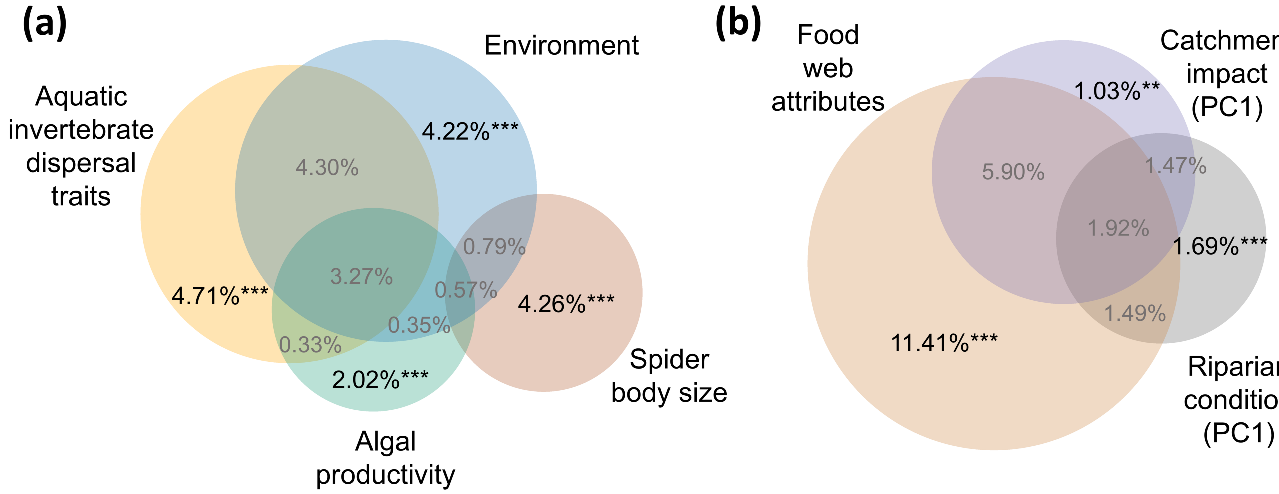

**FIGURE 5** Variation-partitioning analysis of factors contributing to the fatty acid composition (%FA) of riparian spiders. (a) Aquatic invertebrate dispersal: community-weighted mean (CWM) traits for wnb5, wing-pair type: 2 similar-sized pairs; wnb3, wing-pair type: 1 pair + 1 pair of small hind wings; life2, adult life cycle: ≥1 week–1 month; and dis3, dispersal strategy: aerial passive. Environment: catchment impact PC1, riparian condition PC1. Algae, algae productivity (in milligrams of chlorophyll *a* per square meter per day); spider body size: mean spider body size and community functional composition (CWM spider body size). (b) Food web attributes (algae, aquatic invertebrate dispersal traits, and spider body size), riparian condition (PC1), and catchment impact (PC1). Variation <0.25% is not shown. The unexplained (residual) variation in both models was 75.08%. ***$p < 0.001$; **$p < 0.01$.

only 3.63% of the variation in spider FA composition, with little or no shared variation with country or the other continuous variables. For more results from the variation-partitioning analyses, see Appendix S1: Section S3: Figure S4.

## Aquatic insect dispersal trait syndromes

CWM abundances of selected dispersal traits (Table 1) were strongly correlated with negative or positive associations (Figure 6), indicating the presence of two trait syndromes associated with aerial active and passive dispersing aquatic insects, respectively. We subsequently focused on these two modalities for dispersal strategy traits in our statistical models exploring trophic connectivity in riparian spiders, since they were indicative of the broader dispersal trait syndromes present in aquatic insects (Figure 6).

## Trophic connectivity in riparian spiders

The LME models showed that trophic connectivity measured by spider %EPA (Figure 7) and EPA:ALA (Appendix S1: Section S3: Figure S5) was strongly correlated with the CWM abundances of aerial active dispersing aquatic insects (Table 5). Trophic connectivity (spider %EPA) showed considerable shared variation (25%) explained by the influence of aerial active insects and country, and aerial active insects, country, and spider taxa (i.e., β-diversity) combined; this shared variation decreased to 18% when spider EPA:ALA was considered. There were significant differences in CWM trait abundances of aerial active dispersing aquatic insects among countries ($F_{3,81} = 36.5$, $p < 0.001$), with universally lower abundances in Belgium and higher abundances in Romania and Norway compared to Sweden. Trophic connectivity was also correlated with CWM abundances of aerial passive dispersing aquatic invertebrates (Appendix S1: Section S3: Figure S6), although this influence was not significant after accounting for aerial active dispersing aquatic insect CWM abundances (Table 5). There were no significant correlations between other FAs (%ALA) and CWM abundances of aerial dispersing aquatic insects. Although there was some evidence for a nonlinear positive association between algal productivity and trophic connectivity (Appendix S1: Section S3: Figure S7), further analysis accounting for random effects (e.g., site and taxa) indicated each relationship was linear.

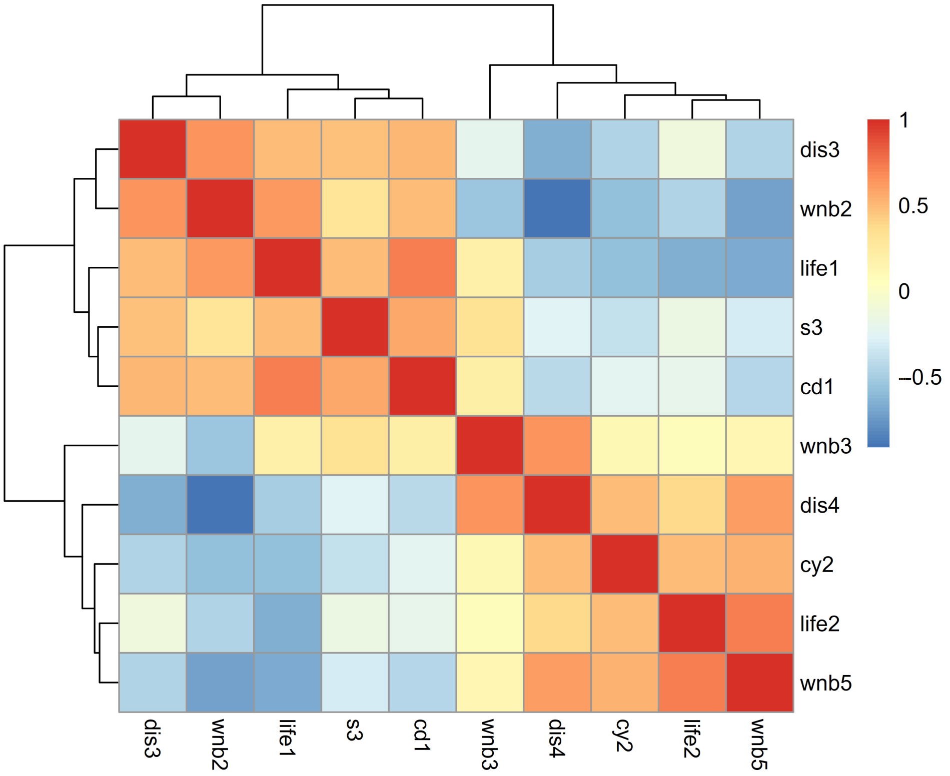

**FIGURE 6** Correlation heatmap of log[$x + 1$] community-weighted mean (CWM) abundances of 10 aquatic invertebrate dispersal traits hypothesized to contribute to trophic connectivity. The results show two broad functional trait syndromes associated with aerial passive (dis3) and active (dis4) dispersing aquatic insects.

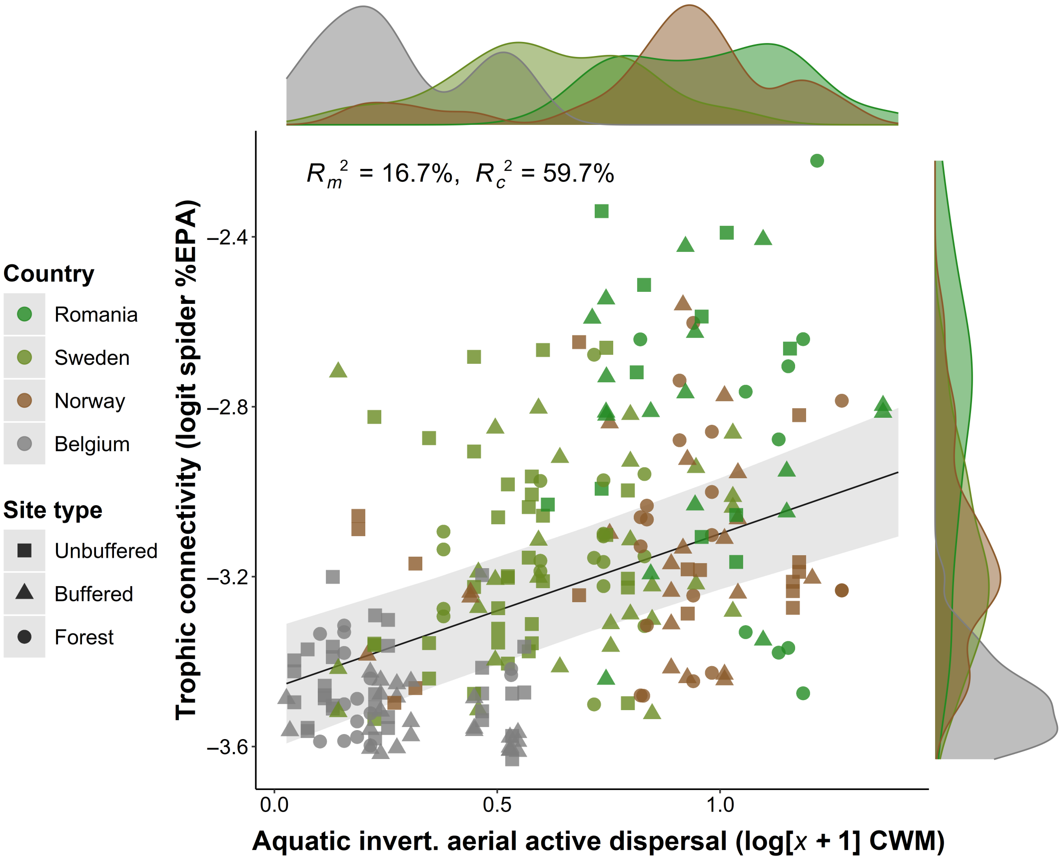

**FIGURE 7** Trophic connectivity [logit % concentrations of eicosapentaenoic acid (EPA, 20:5n-3) in riparian spiders] was correlated with log[$x + 1$] community-weighted mean (CWM) abundances of "aerial active" dispersing aquatic insects (dis4). The regression line represents the parameter estimate (±95% CI) from a linear mixed-effects model. Density plots along margins show the distribution of values for each country.

Two families of spiders, representing web-building and ground-hunting guilds, respectively, showed different correlations between bioindicators representing trophic connectivity and CWM abundances of aerial dispersing aquatic insects (Table 5). In the web-building tetragnathid spiders, there was a significant positive influence of aerial active dispersing aquatic insects on % EPA and EPA:ALA. These results were contrasted by a significant positive correlation between aerial passive dispersing aquatic insects and %ALA in the same spider family. In the ground-hunting Lycosidae, %EPA was significantly associated with both aerial active and passive dispersing insects. Although there were no significant associations with %ALA, lycosid EPA:ALA was significantly correlated with aerial active dispersing aquatic insects. The standardized parameter estimates indicated that the correlation of aerial active dispersing aquatic insects and EPA:ALA was stronger in the Tetragnathidae (0.59; 0.30–0.88 95% CI) than in the Lycosidae (0.39; 0.13–0.66 95% CI); similar results were observed with web-building spiders when compared to ground-hunting spiders (Appendix S1: Section S3: Table S8).

For the SEM, we focused on EPA:ALA since this appeared to be the best indicator of trophic connectivity driven by a dietary pathway with aquatic prey. The first SEM showed that trophic connectivity in spiders (EPA:ALA) was positively associated with the CWM abundances of aerial active dispersing aquatic insects and ecosystem size (wetted channel width), with a negative influence of woody riparian vegetation indicated by riparian condition (Figure 8a). These predictors explained almost 25% of the variation in trophic connectivity (Table 6). In turn, aerial active dispersing aquatic insects were positively associated with riparian condition and algal productivity, with a negative influence of catchment impact. The positive influence of riparian condition on aerial active dispersing aquatic insects was despite a negative indirect effect on aquatic invertebrates mediated through reduced algal productivity, presumably due to shading by woody riparian vegetation. The CWM abundances of aerial passive dispersing aquatic insects were not significantly associated with EPA:ALA in spiders. The aerial passive dispersing aquatic insects were negatively influenced by catchment impact and had a negative

**TABLE 5** Results from linear mixed models testing the correlation of two community-weighted mean aquatic insect dispersal trait abundances (passive, aerial passive dispersal; active, aerial active dispersal) with selected fatty acid (FA) responses in riparian spiders.

| Spider group and FA | Predictor | Estimate | 95% CI | *p* | $R_m^2$ | $R_c^2$ |
|---|---|---|---|---|---|---|
| All (*n* = 252) | | | | | | |
| %EPA | (Intercept) | −0.15 | −0.51 to 0.22 | 0.431 | 18.8 | 60.0 |
| | Passive | 0.05 | −0.07 to 0.18 | 0.421 | | |
| | Active | 0.37 | 0.23 to 0.51 | **<0.001** | | |
| %ALA | (Intercept) | −0.11 | −0.40 to 0.18 | 0.468 | 4.3 | 64.7 |
| | Passive | 0.10 | −0.06 to 0.26 | 0.219 | | |
| | Active | 0.12 | −0.07 to 0.32 | 0.211 | | |
| EPA:ALA | (Intercept) | −0.05 | −0.43 to 0.32 | 0.775 | 15.2 | 59.5 |
| | Passive | −0.09 | −0.24 to 0.07 | 0.262 | | |
| | Active | 0.44 | 0.27 to 0.60 | **<0.001** | | |
| Tetragnathidae (*n* = 55) | | | | | | |
| %EPA | (Intercept) | −0.02 | −0.27 to 0.23 | 0.884 | 25.0 | 45.2 |
| | Passive | 0.14 | −0.14 to 0.42 | 0.319 | | |
| | Active | 0.42 | 0.13 to 0.70 | **0.005** | | |
| %ALA | (Intercept) | −0.02 | −0.30 to 0.27 | 0.915 | 10.0 | 77.1 |
| | Passive | 0.35 | 0.08 to 0.61 | **0.011** | | |
| | Active | −0.07 | −0.35 to 0.22 | 0.643 | | |
| EPA:ALA | (Intercept) | −0.00 | −0.26 to 0.25 | 0.971 | 26.4 | 45.3 |
| | Passive | −0.14 | −0.42 to 0.14 | 0.310 | | |
| | Active | 0.59 | 0.30 to 0.88 | **<0.001** | | |
| Lycosidae (*n* = 69) | | | | | | |
| %EPA | (Intercept) | −0.03 | −0.24 to 0.19 | 0.792 | 30.5 | 42.0 |
| | Passive | 0.27 | 0.03 to 0.51 | **0.025** | | |
| | Active | 0.39 | 0.15 to 0.62 | **0.002** | | |
| %ALA | (Intercept) | 0.04 | −0.24 to 0.33 | 0.754 | 5.8 | 66.0 |
| | Passive | 0.26 | −0.01 to 0.53 | 0.059 | | |
| | Active | −0.02 | −0.29 to 0.26 | 0.897 | | |
| EPA:ALA | (Intercept) | −0.05 | −0.30 to 0.20 | 0.686 | 13.5 | 42.2 |
| | Passive | −0.05 | −0.32 to 0.21 | 0.684 | | |
| | Active | 0.39 | 0.13 to 0.66 | **0.004** | | |

*Note*: *p*-values in bold are significant at $\alpha = 0.05$.

Abbreviations: ALA, alpha-linolenic acid (18:3n-3); EPA, eicosapentaenoic acid (20:5n-3); $R_c^2$, conditional $R^2$ (in percentage); $R_m^2$, marginal $R^2$ (in percentage).

influence on algal productivity. Spider community composition represented by CWM body size was positively influenced by ecosystem size and negatively associated with riparian condition. There were significant correlated error terms between spider CWM body size and aerial passive dispersing aquatic insects; aerial dispersing aquatic insects (active and passive); and spider CWM body size and trophic connectivity (EPA:ALA). Correlated error terms helped improve model fits and the interpretability of results when the test of directed separation specified unlikely causal paths that were significant at $\alpha = 0.05$.

The SEM testing EPA:ALA in tetragnathid spiders revealed similar pathways (Figure 8b). There was a significant influence of aerial active dispersing aquatic insects on tetragnathid EPA:ALA, whereas the aerial passive dispersing aquatic insects and ecosystem size paths were nonsignificant. These predictors explained almost 33% of the variation in trophic connectivity for this spider family (Table 6). The aerial active dispersing aquatic insects were in turn positively associated with algal productivity and negatively influenced by catchment impact. The aerial passive dispersing aquatic insects were negatively influenced by catchment impact and riparian condition

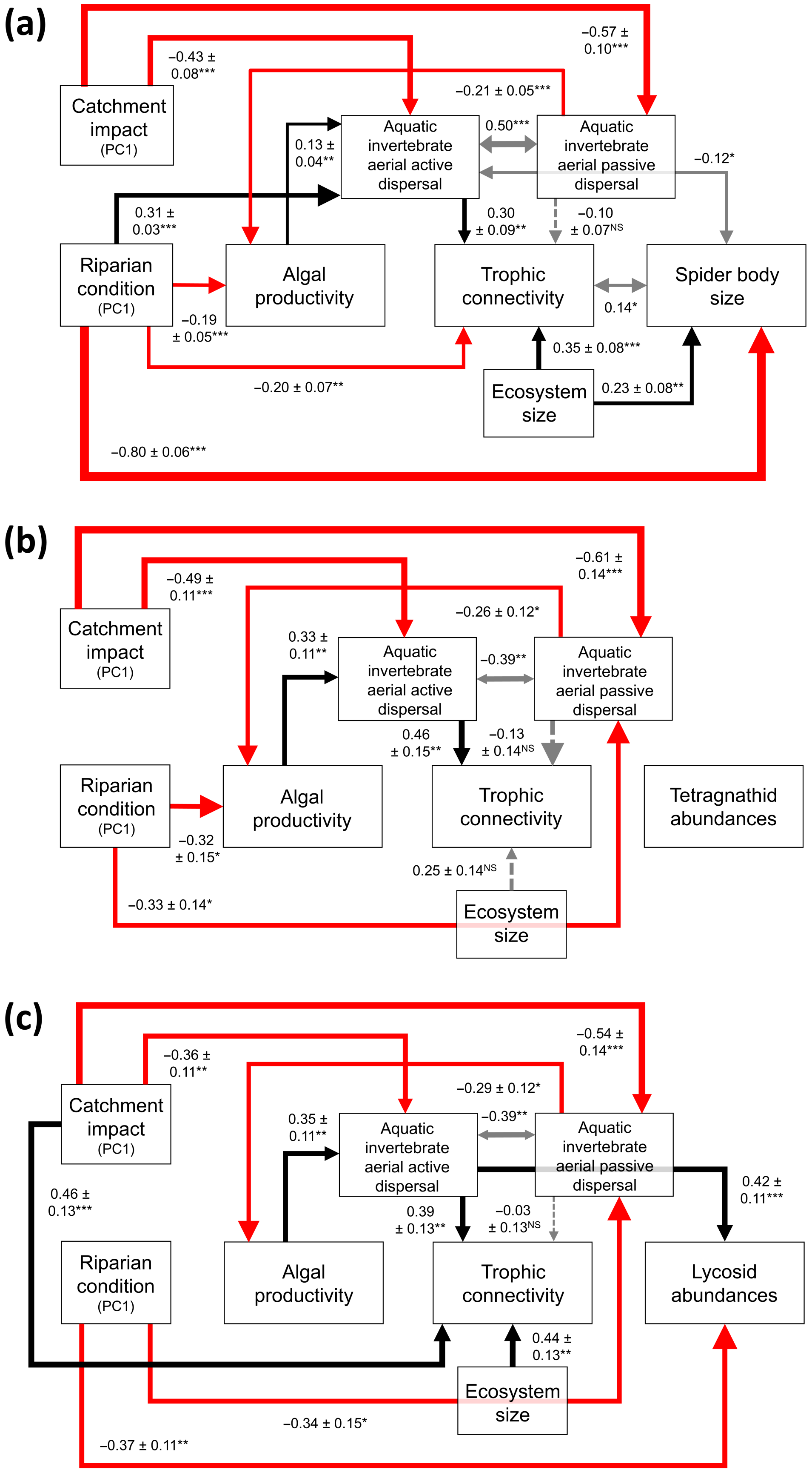

**FIGURE 8** Legend on next page.

**TABLE 6** Coefficient of determination values for response variables used in the structural equation models (SEMs) illustrated in Figure 8.

| SEM | Response | $R_m^2$ (%) | $R_c^2$ (%) | $R^2$ (%) |
|---|---|---|---|---|
| (a) All spiders | Trophic connectivity | 24.8 | 56.7 | |
| | Spider body size | 48.1 | 76.0 | |
| | Aquatic invertebrate aerial active dispersal | 39.6 | 95.0 | |
| | Aquatic invertebrate aerial passive dispersal | 26.1 | 73.4 | |
| | Algae productivity | 6.1 | 88.6 | |
| (b) Tetragnathidae | Trophic connectivity | | | 32.6 |
| | Tetragnathidae abundances | | | n/a |
| | Aquatic invertebrate aerial active dispersal | | | 42.8 |
| | Aquatic invertebrate aerial passive dispersal | | | 25.9 |
| | Algae productivity | 10.6 | 64.7 | |
| (c) Lycosidae | Trophic connectivity | | | 34.9 |
| | Lycosidae abundances | | | 27.3 |
| | Aquatic invertebrate aerial active dispersal | | | 28.9 |
| | Aquatic invertebrate aerial passive dispersal | | | 19.8 |
| | Algae productivity | 4.7 | 65.8 | |

*Note*: Where appropriate, marginal ($R_m^2$) and conditional ($R_c^2$) coefficient of determination values are reported for piecewise mixed-effects models used in the SEMs. In all other instances, $R^2$ reports the total variance in the response explained by the predictors used in the SEM.
Abbreviation: n/a, not applicable.

and exerted a negative top-down influence on algal productivity. Woody riparian vegetation, as indicated by riparian condition, negatively influenced stream algae. Tetragnathid spider abundances were not associated with any drivers. There was a significant negative correlated error term between aerial dispersing aquatic insects (active and passive).

The SEM testing EPA:ALA in lycosid spiders revealed similar pathways with some differences (Figure 8c). Catchment impact, aerial active dispersing aquatic insects, and ecosystem size exerted positive influences on lycosid EPA:ALA, whereas the aerial passive dispersing aquatic insects path was nonsignificant. These predictors explained almost 35% of the variation in trophic connectivity for this spider family (Table 6). The aerial active dispersing aquatic insects were positively associated with algal productivity and negatively influenced by catchment impact. The aerial passive dispersing aquatic insects were negatively influenced by catchment impact and riparian condition and exerted a negative top-down influence on algal productivity. Woody riparian vegetation, as indicated by riparian condition, negatively influenced algae. Lycosid abundances were positively associated with aerial active dispersing aquatic insects and negatively correlated with riparian condition. There was a significant negative correlated error term between aerial dispersing aquatic insects (active and passive). SEMs

**FIGURE 8** Results from piecewise structural equation models (SEMs) testing different causal pathways affecting aquatic-terrestrial trophic connectivity in (a) all riparian spiders, (b) Tetragnathidae, and (c) Lycosidae. Trophic connectivity is indicated by the ratio of eicosapentaenoic acid (EPA, 20:5n-3) to alpha-linolenic acid (ALA, 18:3n-3) in riparian spiders. Community-weighted mean (CWM) trait values are used to describe aquatic macroinvertebrate and spider communities. In panels (b) and (c) estimated abundances (in number of individuals per square meter per hour) following a CPUE (catch per unit effort) approach are used for each spider family. Algae productivity (in milligrams of chlorophyll *a* per square meter per day); ecosystem size, mean wetted channel width (in meters). Bolded lines indicate significant positive (black) and negative (red) relationships. Gray double-arrowed lines indicate correlated error terms. Dashed lines indicate nonsignificant (NS) relationships where $\alpha = 0.05$. The width of the lines is standardized and thus indicates the relative strength of the relationships with standardized path coefficients indicated (±1 SE). Marginal $R^2$ values ($R_m^2$) indicate the goodness of fit for endogenous variables excluding variance explained by the random effects, Conditional $R^2$ values ($R_c^2$) indicate variance explained by the fixed and random effects. Model statistics: (a) Fisher's $C = 22.7$, $p = 0.304$, df = 20, corrected Akaike information criterion ($\text{AIC}_\text{c}$) = 2273. (b) Fisher's $C = 16.9$, $p = 0.854$, df = 24, $\text{AIC}_\text{c} = 713$. (c) Fisher's $C = 33.7$, $p = 0.143$, df = 26, $\text{AIC}_\text{c} = 824$. ***$p < 0.001$; **$p < 0.01$; *$p < 0.05$.

testing web-building and ground-hunting spider responses (Appendix S1: Section S3: Figure S8) showed similar patterns to the Tetragnathidae and Lycosidae, respectively.

# DISCUSSION

Our investigation of how local and landscape-level factors influence trophic connectivity in temperate stream-riparian meta-ecosystems revealed that aquatic invertebrate dispersal traits independently explained the most variability in the FA profile of riparian spiders. The shared variation explained by algal productivity pointed to the role of primary production in contributing to this connection. The omega-3 LC-PUFA EPA (20:5n-3) in riparian spiders was positively associated with CWM abundances of aerial actively dispersing insects, further suggesting this PUFA is a useful biomarker to measure trophic connectivity between aquatic and terrestrial food webs. Trait syndromes associated with aerial actively dispersing aquatic insects included univoltine life cycles, suggesting that synchronized seasonal emergence during spring might be a strong faunal attribute contributing to cross-ecosystem linkages in our study. Our SEM evaluating the importance of environmental factors demonstrated how riparian and catchment land uses mediate indirect effects on trophic connectivity via impacts on aquatic insects. Thus, our study elucidates the mechanisms underpinning patterns observed in previous studies (Ohler et al., 2024), and further shows how human disturbances in aquatic ecosystems might indirectly propagate to connected terrestrial food webs (Burdon, 2021).

## Trait-based ecology and trophic connectivity

Developing a general, predictive understanding of ecological systems requires an improved understanding of how and to what extent structural and functional relationships can cross scales and contexts. We used the FA composition of riparian arachnids to explore the potential proximate and ultimate drivers of trophic connectivity between coupled stream-riparian meta-ecosystems. Our results indicated that aquatic insect dispersal traits were strong predictors of FA composition in riparian arachnids. Two of the dispersal traits selected for our RDA model reflected wing configurations of pollution-sensitive stream insect orders including Ephemeroptera (wing-pair type: 1 pair + 1 pair of small hind wings), Plecoptera, and Trichoptera (wing-pair type: 2 similar-sized pairs). The prominence of dispersal traits associated with these EPT stream insects further suggests that human impacts on stream ecosystems can indirectly propagate across traditional ecosystem boundaries by weakening aquatic-terrestrial food web linkages (Burdon, 2020).

Our results showed a negative influence of catchment land use on aerial dispersing insects, with the potential to indirectly impact aquatic-terrestrial connectivity by reducing prey for riparian spiders. Similarly, water pollution associated with human land uses (e.g., mining) has been shown to indirectly affect riparian spiders through negative direct impacts on stream insects (Kraus et al., 2014; Paetzold et al., 2011). In our study, poor water quality in the Zwalm River catchment could help explain the reduced aquatic-terrestrial connectivity implied by the EPA concentrations in riparian spiders collected from the Belgian sites. Our results indicated that woody riparian vegetation may ameliorate wider catchment impacts by increasing abundances of aerial active dispersing aquatic insects such as species of Ephemeroptera, Plecoptera, and Trichoptera, thus helping to preserve aquatic-terrestrial connectivity through positive indirect effects on riparian spiders. This indirect positive effect of riparian vegetation on aquatic-terrestrial connectivity contrasted with the direct effects of habitat loss on terrestrial consumers shown by Laeser et al. (2005). Those authors investigated numerical responses by spiders, whereas our analyses focused on the functional integrity of aquatic-terrestrial linkages indicated by omega-3 LC-PUFA concentrations in riparian predators.

Another key dispersal trait highlighted by our analyses reflected a life-history attribute (adult life cycle: ≥1 week–1 month) consistent with plecopteran and trichopteran species. The three dispersal traits (wing-pair type: 2 similar-sized pairs, 1 pair + 1 pair of small hind wings; and adult life cycle: ≥1 week–1 month) were associated with a trait syndrome that included univoltine life cycles, suggesting that synchronized seasonal emergence during spring could be another important faunal attribute contributing to cross-ecosystem linkages. Our sampling occurred during the spring–summer period when the emergence of many EPT species typically peaks in temperate stream ecosystems of the northern hemisphere (Raitif et al., 2018). Although beyond the scope of the present study, increasing water temperatures typically lead to earlier emergence and semivoltinism in aquatic insects (Bonacina et al., 2023) and may increase the emergence period for some insects (Cheney et al., 2019). This environmental plasticity could explain some of the differences among countries in our study, with Romania recording warmer stream temperatures and stronger indicators of aquatic-terrestrial connectivity than the other more northern catchments. The last key dispersal trait reflected aerial passive dispersal, which included the numerically abundant yet small-bodied chironomid dipterans. Future research should further investigate if trophic connectivity is conserved over different seasons and/or latitudes since temporal and spatial changes in habitat conditions and emerging insect species could alter the linkage between stream and riparian food webs (Kowarik et al., 2021; Nash et al., 2023; Ohler et al., 2024). For instance, differences among sites might be greatest in spring and summer when aquatic insect emergence peaks and then converge in autumn due to reduced aquatic emergence (Parmar et al., 2022).

Our main hypotheses focused on the role of stream primary productivity, aquatic invertebrate dispersal traits, and recipient terrestrial predators in influencing cross-ecosystem connectivity in temperate streams. We used a variety of statistical approaches to explore the contribution of these nonexclusive proximate drivers of trophic connectivity. The variation-partitioning analysis showed that dispersal traits associated with univoltine EPT insects explained the greatest independent proportion of FA composition in riparian arachnids, highlighting an important role for certain trait combinations (or trait syndromes) in food web attributes described by trophic connectivity. Other studies have used dispersal traits to explore the potential for cross-ecosystem food web linkages between stream and riparian habitats, but our study is the first to use fixed traits in combination with biomarker analyses that reflect the realized trophic connectivity in these meta-ecosystems. Several authors have suggested that riparian land uses and hydrological disturbances can affect the size structure, dispersal ability, and longevity of adult aquatic insects available to emerge from river reaches, thus potentially influencing the spatial extent and type of terrestrial consumers supported by aquatic prey (Greenwood & Booker, 2016; Kopp & Allen, 2020; McKie et al., 2018). Accordingly, the dispersal traits of stream insects should influence recipient ecosystems by determining the distance resource subsidies travel from the donor ecosystem and the period they are available to consumers.

These two aspects may have been underestimated in our study, since riparian sampling occurred within a narrow range (5 m) from the stream and occurred only once during the spring–summer period. However, despite the relatively narrow riparian width used in our study, Muehlbauer et al. (2014) found that lateral aquatic-terrestrial connectivity was best described by a negative power function in which 50% of the stream signature was concentrated near stream banks (1.5 m), suggesting that we captured the vast majority of the potential interaction between stream insects and riparian spiders. We found evidence that aerial active dispersing insects were more associated with trophic connectivity in riparian spiders than the aerial passive dispersing insects. Muehlbauer et al. (2014) found that a nontrivial portion (10%) of the maximum aquatic-terrestrial subsidy level was detected 0.5 km from the water's edge, indicating that aerial active dispersing insects may be important for the distance these subsidies travel into the recipient landscape. Furthermore, Didham et al. (2012) found that Ephemeroptera and Trichoptera species were more frequently captured in the canopy lateral to streams, suggesting that long-distance dispersal of stream insects may be underappreciated in forested landscapes.

Riparian vegetation type may also determine the spatial signature of stream subsidies by influencing insect dispersal (Collier & Smith, 1997); although Petersen et al. (2004) recorded little difference in lateral dispersal between moorland and forested streams. Carlson et al. (2016) found that abundances of adult aquatic insects were greater at agricultural than at forested sites, but most (64%) were caught close to the stream edge because these insects typically possessed traits indicative of more limited adult dispersal (e.g., small adult size and weak flying strength). In contrast, catches of adult aquatic insects declined relatively little with increasing distance from the forest streams because they generally possessed aerial active dispersal traits, leading McKie et al. (2018) to hypothesize that Swedish agricultural reaches had diminished aquatic-terrestrial trophic connectivity. Further, Raitif et al. (2018) quantified an emergent aquatic insect flux of 4-g dry mass $m^{-2}$ $year^{-1}$ in French agricultural streams, which was dominated by Trichoptera (56%) and Ephemeroptera (19%) compared to the Chironomidae (25%). Other study systems may differ. Baxter et al. (2005) reported that 60%–99% of emergent biomass can be Diptera, indicating that these taxa may not only be numerically abundant but also potentially important functionally. Our study suggests that small-bodied, numerically abundant taxa with shorter life spans and more passive aerial dispersal may contribute to trophic connectivity in European streams, but this contribution is relatively minor compared to the role of larger, more actively dispersing aquatic insects.

Correlations among phenotypic traits (syndromes) include the life history and behavioral syndromes used by evolutionary biologists (Roff, 1992; Sih et al., 2004), whereas Raffard et al. (2017) define associations between correlated suites of response and effect traits as functional syndromes (FS). Effect traits can determine how and to what extent an organism influences energy flow and matter transformation in an ecosystem, whereas response traits determine how an organism responds to environmental conditions (Díaz et al., 2013; Violle et al., 2007). The concept of FS is important in the context of our study for two reasons. Firstly, changes in response traits along environmental gradients might also be associated with effect traits as part of a FS, and combined help explain the faunal attributes contributing to changes in cross-habitat trophic connectivity in our study. Secondly, the presence of FS helps explain why three associated traits used in our RDA models (wing-pair: 2 similar-sized pairs, 1 pair + 1 pair of small hind wings; and adult life cycle: ≥1 week–1 month) were analogous with the single trait (aerial active dispersal) found to be highly correlated with trophic connectivity in our mixed models, since these traits broadly belong to the same FS.

## Fatty acid biomarkers in aquatic-terrestrial food webs

Our study shows that the omega-3 LC-PUFA EPA is a useful indicator of trophic connectivity. These results concurred with Chari et al. (2020), who found that EPA concentrations in riparian spiders were negatively correlated with distance from a South African river and generally elevated in summer when stream insect emergence was greatest. Twining, Parmar, et al. (2021) showed that riparian spiders collected in spring alongside a German lake had elevated EPA levels relative to their upland counterparts, and a mixing model indicated that aquatic insects comprised 74% of the riparian spider diet compared to almost zero for upland spiders. Likewise, Parmar et al. (2022) and Shipley et al. (2024) found that EPA levels were consistently elevated in aquatic insects when compared to their terrestrial counterparts. Although we did not measure this LC-PUFA in stream invertebrates or adult aquatic insect prey, there is ample evidence that benthic insect abundances and biomass are correlated with emergence (Statzner & Resh, 1993), and that such "productivity gradients" are positively associated with riparian spiders (Burdon, 2020; Burdon & Harding, 2008). Several field experiments have demonstrated that reductions in emergence aquatic insect biomass can negatively affect spiders (e.g., Kato et al., 2003; Recalde et al., 2016), thus bolstering the contention that reduced aquatic insect prey availability is responsible for diminished concentrations of EPA in riparian predators. Future research should consider omega-3 LC-PUFA concentrations in emergent aquatic insect prey to more reliably quantify the interaction strength between stream and terrestrial food webs, since high fluxes of omega-3 LC-PUFA impoverished prey might drive positive numerical responses in predators despite resulting in reduced EPA concentrations. However, Shipley et al. (2024) also found that in human-dominated landscapes, predator biomass and PUFA biomass were lower for a given level of species richness when compared to natural systems, suggesting a negative shift in function. Our results indicate that diminished export of aquatic insect prey in human-impacted streams could help explain the pattern observed by Shipley et al. (2024).

In contrast to EPA, the results of our SEM and LME analyses using docosahexaenoic acid (DHA, 22:6n-3) were equivocal, indicating recipient consumer effects among other contingencies. Depending on habitat use and dietary availability, spiders can use two distinct pathways (trophic vs. metabolic) to meet their omega-3 LC-PUFA needs (Mathieu-Resuge et al., 2022). Generalist predators like ground-hunting spiders that were relatively more common in unbuffered habitats may have an increased ability to synthesize DHA from precursor short-chain PUFAs like ALA (18:3n-3), thus helping to explain the higher concentrations of DHA in spiders from these more open and degraded reaches. Twining, Parmar, et al. (2021) found that nestlings of Blue Tit (*Cyanistes caeruleus* Linnaeus), a generalist avian invertivore, were able to convert dietary ALA into DHA through internal synthesis. This ability contrasted with other avian insectivores such as Tree Swallow nestlings (*Tachycineta bicolor* Veillot), who rely on aquatic dietary pathways for their omega-3 LC-PUFAs (Twining, Lawrence, et al., 2018). It is also possible that in our study, higher abundances of DHA-rich, but weaker flying taxa like Diptera led to higher DHA concentrations in recipient spiders in unbuffered habitats, but we saw little direct evidence for this pathway in our SEMs. Instead, more tolerant stream insects that actively disperse (e.g., baetid mayflies) could still be important for aquatic-terrestrial linkages in unbuffered habitats. The increased productivity of unbuffered habitats might also mean that both terrestrial and aquatic prey are more available, meaning spiders have greater body condition. Body condition can be a better indicator of the nutritional status of a spider than body size (e.g., mass) alone (Anderson, 1974) and thus increased DHA concentrations could be indicative of this environmentally plastic trait. Future research should account for individual body size and condition, along with establishing PUFA variability in prey and DHA origin in spiders (endogenous vs. dietary).

In our study, ALA in spiders was greatest in forested sites. In tetragnathids, %ALA was positively associated with abundances of aerial passive dispersing aquatic insects. While caution is needed when attributing causality, we tentatively suggest these results could reflect an alternative trophic pathway to that underpinned by algal productivity. Arce Funck et al. (2015) found that certain aquatic fungi produced high levels of ALA, suggesting that the abundance of this FA might be linked to allochthonous inputs of terrestrial organic matter, helping to explain the correlation of concentration of this omega-3 short-chain PUFA in tetragnathids with abundances of aerial passive dispersing aquatic insects.

However, aquatic insects typically show only modest increases in ALA relative to their terrestrial counterparts (Mathieu-Resuge et al., 2022). While some terrestrial plants are known to produce ALA in large quantities (Blomquist et al., 1991; Hixson et al., 2015), terrestrial insects can also be rich in this PUFA (Parmar et al., 2022) indicating that the elevated ALA in tetragnathids might directly come from terrestrial prey sources. A terrestrial influence potentially helped to explain why increasing proportions of riparian woody vegetation at the local scale depressed EPA:ALA in spiders (i.e., an apparent direct negative effect on trophic connectivity), as shown in the first SEM.

Riparian woody vegetation had a positive association with EPT stream insects that in turn positively influenced EPA concentrations in riparian spiders, both as an overall proportion and relative to concentrations of ALA. The surfeit of spider EPA relative to ALA associated with active dispersing stream insects in our statistical models is indicative of aquatic-derived trophic subsidies as opposed to a metabolic pathway relying on ALA as a precursor compound (Mathieu-Resuge et al., 2022). Our study further highlights that riparian spiders may be an important conduit of these essential macronutrients to terrestrial food webs, in addition to the stream insects that form prey subsidies for a wider range of consumers including birds, bats, and lizards (Baxter et al., 2005).

We aimed to assess the relative importance of underlying stream primary productivity gradients in driving cross-ecosystem resource flows. We hypothesized that realized trophic connectivity may be ultimately determined by extrinsic biotic and abiotic factors, including proximate pathways mediated by aquatic insects and terrestrial predator communities. Although we found evidence that aquatic invertebrate dispersal traits explained the most variability in riparian spider FA composition, there was a notable shared component jointly explained by dispersal traits and algal productivity, in addition to the small independent contribution of algae. Algal productivity is important for the production of PUFAs, but there is evidence that the increased light and nutrient availability typical of agricultural and urban streams can alter the nutritional quality of periphyton (Cashman et al., 2013). By decreasing the availability of PUFAs relative to forested streams with biofilms dominated by EPA-rich diatoms, these land use types may have hidden consequences for stream and riparian consumers (Cashman et al., 2013; Twining, Brenna, Hairston, & Flecker, 2016). However, we found little direct evidence for this pathway, and our SEMs showed how increasing woody riparian cover might negatively affect algal productivity. Increased shading may lead to negative indirect effects on trophic connectivity through reduced in-stream autochthonous production. However, this negative effect is potentially offset by increased abundances of EPT stream insects with dispersal traits that increase connectivity to terrestrial food webs. Further considering in-stream habitat variables such as flow conditions and benthic substrate could reveal additional positive indirect effects of woody riparian vegetation on trophic connectivity via aquatic insect communities (Burdon et al., 2013).

## Spider communities in stream-riparian networks

We hypothesized that riparian habitat properties affect terrestrial predator communities, potentially affecting their ability to consume aquatic prey via direct and indirect pathways. We identified body size as a key trait describing the difference between arachnid communities dominated by small, web-building spiders (e.g., Linyphiidae, Tetragnathidae) and those typified by large, ground-living spiders (e.g., Lycosidae, Pisauridae). These different community types were in turn influenced by riparian vegetation structure, with woody vegetation associated with smaller web-building spiders and open, grassy unbuffered riparian reaches associated with larger, ground-hunting spiders (Popescu et al., 2021; Ramberg et al., 2020). Such differences could affect the strength of trophic connectivity since Allen et al. (2024) found in a global meta-analysis that web-building spiders had ~30% more allochthonous diet contributions from aquatic systems than that for ground-hunting arthropods. Consistent with this finding, we saw evidence of a stronger association between aerial active dispersing stream insects and web-building tetragnathid spiders when compared to ground-hunting lycosids.

However, spider community type explained a relatively small amount of the variation in the FA composition of spiders, and most of this was shared with environmental predictors that included riparian vegetation structure. There were differences in the FA composition of different spider families, and in our first SEM we specified a correlated error term between trophic connectivity and spider community type, since it was ecologically plausible that aquatic subsidies affect spider communities and spider niche requirements affect their ability to access aquatic prey (Nash et al., 2023). As a possible example of this inextricable relationship, spiders from the family Agelenidae were most frequently encountered in the Belgium sites. The Agelenidae typically construct a horizontal, sheet-like web low to the ground, whereas the dominant web-builder in riparian zones (Tetragnathidae) constructs an orb-web above or near the water. The Belgian sites were also conspicuous with low

CWM abundances of active aerial dispersing insects, raising the possibility that reductions in aquatic prey subsidies also contributed to differences in spider communities.

## CONCLUSIONS

Our study demonstrates how landscape-level influences on stream habitats can indirectly propagate across traditional ecosystem boundaries by weakening aquatic-terrestrial food web linkages. Human impacts in the upstream catchment had a negative influence on aquatic insects, thus indirectly reducing the trophic connectivity with riparian spiders. We found that the proportion of the omega-3 LC-PUFA EPA and the ratio of EPA to ALA in riparian spiders were positively associated with abundances of "aerial active" dispersing aquatic insects, underscoring the potential of these biomarkers as indicators of trophic connectivity. We also found evidence that enhanced riparian condition (woody vegetation) had a positive indirect effect on trophic connectivity via influences on aquatic insect communities, but that this was negated by direct and indirect influences associated with shading. Our study highlights that functional trait syndromes may be important for linking response and effect traits over gradients of environmental change. Further understanding the reciprocal influence of functional diversity in the key organismal groups driving cross-ecosystem linkages will improve our understanding of how biodiversity losses affect meta-ecosystem functioning (Baruch et al., 2021; Scherer-Lorenzen et al., 2022). Overall, our results further demonstrate how the dynamics of seemingly distinct ecosystems are intimately linked by spatial resource flows (Polis et al., 1997), thus suggesting pervasive changes in cross-habitat connectivity associated with the profound transformation of landscapes in the Anthropocene.

### AUTHOR CONTRIBUTIONS

All authors contributed to the design of the study. Francis J. Burdon, Geta Rîşnoveanu, Marie A. E. Forio, and Benjamin Kupilas selected sites. Francis J. Burdon, Ellinor Ramberg, Jasmina Sargac, Cristina Popescu, Nita Darmina, Corina Bradu, Marie A. E. Forio, and Benjamin Kupilas carried out field sampling. Francis J. Burdon, Ellinor Ramberg, Cristina Popescu, Nita Darmina, and Corina Bradu processed samples. Danny C. P. Lau and Ellinor Ramberg conducted the FA analyses. Francis J. Burdon conceived the conceptual framework and analyzed the data. Francis J. Burdon wrote the initial draft and edited the manuscript. All authors discussed the results and contributed to the final version.

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### CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

### DATA AVAILABILITY STATEMENT

Data and code (Burdon et al., 2025) are available in Dryad at https://doi.org/10.5061/dryad.931zcrjxz.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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