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Contrasting responses of terrestrial and aquatic consumers in riparian – stream networks to local and landscape level drivers of environmental change

Richard K. Johnson*, Peter Carlson, Brendan G. McKie

Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, P.O. Box 7050, SE-750 07, Uppsala, Sweden

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Abstract

The biodiversity of streams and riparian zones is highly interlinked by multiple cross-habitat flows of organisms, nutrients and materials, and are thus increasingly recognized as forming an extended “meta-ecosystem” network spanning both within and across entire catchments. However, current understanding of how these extended networks respond to environmental change is limited by the lack of studies quantifying the local and larger-scale drivers of biodiversity in both terrestrial and aquatic systems simultaneously. Using high-resolution species and environmental data from eight boreal riparian – stream meta-ecosystems, half of which were situated in forest and half in agricultural catchments, we quantified land-use impacts and the importance of catchment and local (riparian, instream) scale variables on the diversity and community composition of three epigeal arthropod groups (spiders and staphylinid and carabid beetles) and aquatic macroinvertebrates. All four organism groups responded to quantifiable environmental variables. Staphylinid beetle and spider assemblages differed significantly between forested and agricultural sites and were strongly correlated with riparian variables such as vegetation type and soil properties, but also instream variables such as conductivity and floating macrophytes. By contrast, carabid beetle and aquatic macroinvertebrate assemblages did not differ between forested and agricultural sites and showed similar responses to catchment and local scale variables. Our results indicate that measures that only address local scale drivers of terrestrial biodiversity might be ineffective if the catchment-scale variables regulating aquatic biodiversity and aquatic – terrestrial linkages are not adequately addressed in ecosystem management.

Keywords: Riparian; Epigeal arthropods; Streams; Macroinvertebrates; Biodiversity; Agricultural land use; Ecological linkages

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Introduction

Streams are intricately linked with the surrounding landscape through the riparian areas bordering their channels by multiple flows of organisms, nutrients and materials (Baxter, Fausch & Carl Saunders, 2005; McKie & Malmqvist, 2009; Nakano & Murakami, 2001). Earlier work has shown that boreal riparian – stream networks are highly connected by resource flows (e.g. Bergfur, Johnson, Sandin and Goedkoop 2009, Ramberg et al. 2020, Richardson, Zhang and Marczak 2010). These ecologically linked riparian – stream habitats form key “meta-

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*Corresponding author.
E-mail address: richard.johnson@slu.se (R.K. Johnson).

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ecosystem" networks at landscape scales (Erős & Lowe, 2019; Turunen et al., 2017) that are acknowledged for their aesthetic values as well as their ecosystem services and unique biodiversity (Baxter et al., 2005; Clerici, Paracchini & Maes, 2014). Despite their importance for biodiversity and ecosystem functioning, streams and their riparian zones are often highly degraded systems (Dudgeon et al., 2006). Although the importance of large- and local scale variables for instream biodiversity has been relatively well studied (e.g. Johnson and Hering 2010, Johnson, Goedkoop and Sandin 2004, Truchy et al. 2019), much less is known of land-use effects on the biodiversity of riparian − stream meta-ecosystems (Forio et al., 2020; Turunen et al., 2017); a finding that is disconcerting as knowledge of the key environmental variables, their interactions and relevant spatial scales is critical for making informed management decisions for these biologically diverse and functionally important ecosystems.

Agricultural land use results in marked changes in the structural and functional integrity of riparian and streams habitats, with sensitive species often replaced by more tolerant species (Birkhofer, Smith, Weisser, Wolters & Gossner, 2015;Johnson, Wiederholm & Rosenberg, 1993; Pearce & Venier, 2006; Pearson, Ormerod, Symondson & Vaughan, 2016). For streams, elevated nutrients and inputs of fine sediments are two common drivers of biodiversity loss in general (Townsend, Uhlmann & Matthaei, 2008), and of freshwater insects in particular due to their relative sensitivity to altered habitat (Johnson & Hering, 2009; Johnson et al., 1993). For riparian habitats, land use results in habitat loss and fragmentation, deleteriously affecting the diversity and abundance of many epigeal arthropod species (Forio et al., 2020; Popescu et al., 2021). Spiders comprise an ecologically diverse group of predators with assemblages reflecting changes in not only habitat but also food resources, whilst coleopterans are a functionally more diverse group (spanning multiple ecological guilds) with a broad range of environmental requirements (Pearce & Venier, 2006; Popescu et al., 2021; Ramberg et al., 2020). While many studies have quantified the individual responses of riparian and instream assemblages to land use (e.g. Johnson et al. 1993, Pearce and Venier 2006; Prieto-Benítez et al. 2011; Ramberg et al., 2020), few have considered spatial scales (e.g. Schmidt, Thies, Nentwig & Tscharntke 2008, Schneider, Ekschmitt, Wolters and Birkhofer 2011, Djoudi, Plantegenest, Aviron and Pétillon 2019, Truchy et al. 2019) and to our knowledge only one other study has done both simultaneously (Forio et al., 2020).

In highly connected systems, such as riparian − stream meta-ecosystems, disturbances can directly or indirectly affect the linkages, such as flows of energy and matter, that underpin biodiversity and function by altering food web pathways and reciprocal subsidies (Richardson et al., 2010). Understanding how anthropogenic drivers impact biodiversity and essential ecological linkages is therefore critical for predicting how management of one system can affect the biodiversity and functioning of another system. Agricultural land use results not only in higher relative abundances of tolerant non-insect species (Johnson et al., 1993) and weak-flying, poorly dispersing, adult aquatic insects (Carlson, McKie, Sandin & Johnson, 2016; McKie, Sandin, Carlson & Johnson, 2018) but can indirectly affect terrestrial biodiversity and function if key aquatic subsidies are lost, impaired or unevenly dispersed. Land-use impacts on riparian food webs may be spatially asymmetrical if consumers close to stream edges, such as web-building spiders, benefit from the higher production and limited dispersal of weak flying insects, while at greater distances from the stream channel terrestrial consumer reliance on stream subsidies may decrease.

Using riparian − stream meta-ecosystems as model systems, we simultaneously quantified the joint responses of epigeal arthropod and aquatic macroinvertebrate assemblages to agricultural land use, with particular focus on different spatial scales. Although, many studies have quantified the importance of resource flows within riparian − stream meta-ecosystems for food web structure (e.g. Burdon et al. 2020, Lafage et al. 2019, Webster et al. 1999), few have quantified the effects of land use on biodiversity in these highly connected ecosystems. We expected epigeal arthropod assemblages to correlate more strongly with local habitat characteristics than with catchment land use, whilst aquatic macroinvertebrate assemblages were predicted to be responding to the cumulative effects of catchment land use on instream hydromorphology and nutrients. For species-specific responses, we hypothesized (i) the loss of sensitive epigeal arthropod and aquatic macroinvertebrate species with agricultural land use, and specifically (ii) that diversity and relative abundance of Staphylinidae (Coleoptera) are lower in agricultural sites due to their preference for moist habitats (Bohac, 1999), (iii) that diversity and relative abundance of Carabidae (Coleoptera) are higher in agricultural sites due to their broad habitat preferences (Gailis & Turka 2013; Pearce & Venier 2006), (iv) that diversity and relative abundance of Araneae (Arachnida) are lower in agricultural sites due to loss or altered riparian habitat (Birkhofer et al., 2015), e.g. web-building and ground hunting spiders are expected to be negatively affected if the habitat architecture for webs is changed, and (v) that diversity and relative abundance of aquatic macroinvertebrates, in particular taxa within the three pollution-sensitive groups (Ephemeroptera, Plecoptera, Trichoptera) (Johnson et al., 1993), are lower in agricultural sites due to the cumulative effects of land use on altered instream habitat and food resources.

Materials and methods

Study area and sites - Eight lowland streams ($<$ 191 m a.s.l.) were sampled in central Sweden, representing two major land use types: forest and agriculture (Fig. 1A). Forested (FOR) sites had agricultural land use < 1%, whilst agricultural (AGR) sites had 8 - 43% of the catchment classified as agriculture. The streams were small- to medium-sized (stream orders 2−4, catchment areas from 9 to 156 km^2), circumneutral (mean pH 6.3 to 8.3) and ranged from nutrient-poor (mean 9 μg TP/L and 18 μg $NO_2+NO_3\_N$/L) to nutrient-rich (mean 198 μg TP/L and 1824 μg $NO_2+NO_3\_N$/L) (Carlson, Johnson & McKie, 2013). For more detailed information see Carlson (2014).

Catchment land use - Catchment land use data for all sites were obtained from the Corine land cover database (http://sia.eionet.europa.eu/CLC2000). Land use within catchments was delineated according to topographic maps with a scale of 1:100 000 (Swedish Geodata; roadmap from Lantmäteriet) and the delineations were digitized using ArcGIS 9 (ESRI, Redland, CA.; http://www.esri.com/). The total area of catchments as well as the areas of the land use types within the catchments was calculated as % agriculture, % coniferous forest, % deciduous forest, % mixed forest, % thickets, % clear cut, % bare rock, % mires and % surface water.

Riparian habitat - The riparian habitat was characterised within a 100 m parallel by 50 m perpendicular square corridor on both sides of the stream. Habitats were characterised at two spatial scales: a 1 m^2 area of the pitfall arrays and a 10 m^2 area around the arrays (see below for description of pitfall arrays). Soil samples were taken within each of the 1 m^2 pitfall arrays once (August) and were analysed for soil pH and organic content (Carlson, 2014). Soil surface temperature was recorded within each pitfall array along one transect per stream every four hours using smart button temperature data loggers (ACR Systems Inc.). Within the 10 m^2 area surrounding the pitfall traps the inorganic substrate and ground vegetation and number of trees were quantified (Appendix A: Table 1). Inorganic substrate was classified

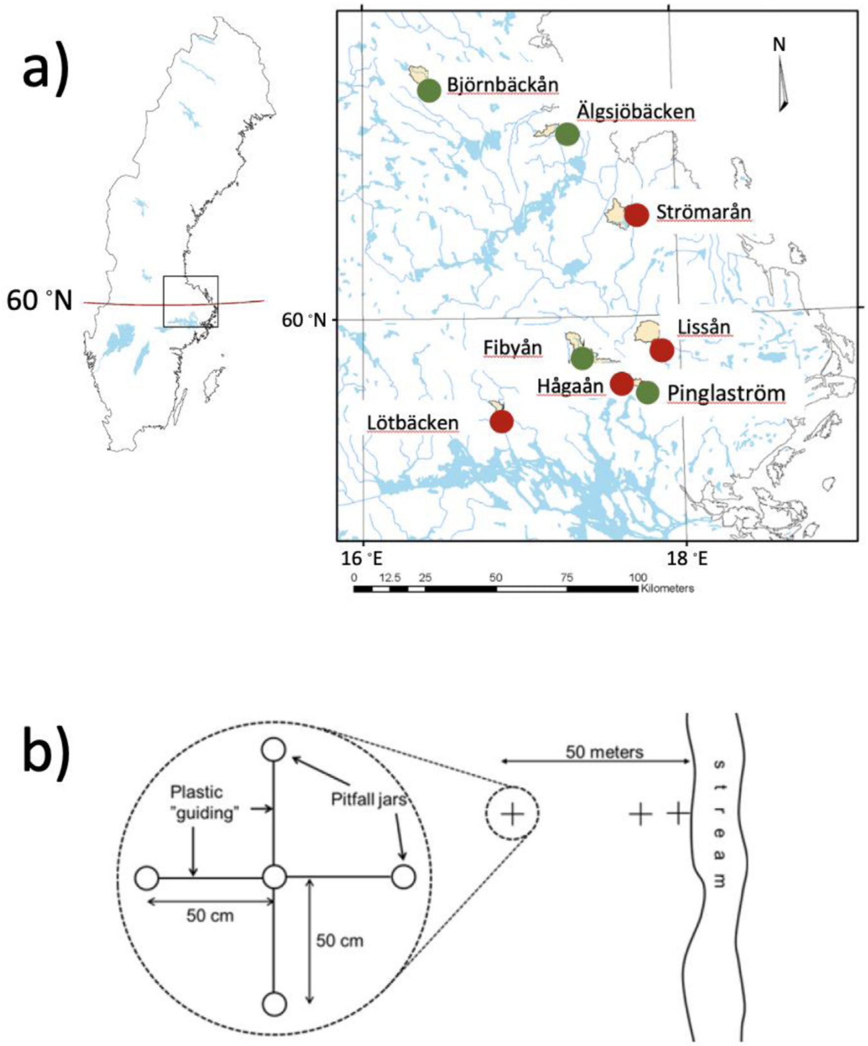

Fig. 1. (a) Distribution of eight study sites located in the boreal region of Sweden (green circles show forested and red circles agricultural streams) and (b) schematic view of the design and placement of the pitfall arrays from the stream edge. Each study site had three transects with three pitfall arrays along each transect.

by size and type (percent coverage), ground vegetation by percent type and tree density (expressed in m^2 of total tree stem area per hectare). Briefly, vertical stem structure of trees under the canopy was estimated by point sampling at 25 m distances from the stream along each transect using a relascope with a gap/chain ratio of 1:50, resulting in the sum of the cross-sectional area of tree stems at breast height (1.3 m above ground) within a radius of 56.4 m from the point taken. Shading was measured using a LI-COR Leaf Area Index (LAI) metre (LAI-2000 model, Lincoln, Nebraska USA). Four measurements were made on a single clear day in early autumn at 1.3 m on each side of each "pitfall trap" location and averaged. LAI values range from 0 (bare ground) to over 10 (dense forest), expressed as m^2 foliage area / m^2 ground area.

Riparian epigeal arthropod sampling - Ground beetles (Carabidae), rove beetles (Staphylinidae), ground-hunting spiders (e.g. Lycosidae) and sheet-web building spiders (e.g. Linyphiidae) were sampled on three occasions in summer (July), autumn (September) and the following spring (April) using pitfall traps. Pitfall traps consisted of glass jars (60 × 70 mm) deployed in three arrays along three transects per stream at 1 and 10 m distances perpendicular to the wetted stream edge (Fig. 1B). A mixture of *c.* 67% ethanol and 33% glycol was used to fill the bottom half of the jars. The traps were emptied after the four-day sampling periods and each group of five jars was combined into one composite sample per array and preserved in 70% ethanol (final concentration). In the laboratory the number of individuals was counted (numbers per unit effort, NPUE) and most individuals were identified to species level. Mean values of abundance and taxon richness from the three sampling events were used here.

Instream habitat − The instream habitat was characterised in autumn from the same section of stream sampled for macroinvertebrates. In each stream, we quantified riffle and pool areas and recorded stream size, flow, substratum types and vegetation and presence of large woody debris (Appendix A: Table 1). Water samples were taken and analysed in the lab for several water quality variables (Appendix A: Table 1) according to certified laboratory protocols.

Aquatic macroinvertebrate sampling - Macroinvertebrate assemblages were quantitatively sampled in mid-autumn (October − November) and late spring (May − June) from one pool and riffle habitat per stream. Three replicate samples were collected from each habitat using a Hess sampler (500 μm mesh) covering a bottom area of 0.086 m^2. Collected organisms were preserved in the field in 70% ethanol (final concentration), sorted and identified to the lowest taxonomic level feasible (mainly to species and genus) and counted (individuals/m^2). Samples with a relatively high number of organisms (> 300/sample) were subsampled by sorting a minimum of 300 individuals in a fraction of the sample, with the remainder of the sample searched for large, rare species not recorded in the subsample. Mean values of abundance and taxon richness from the two sampling events were used here.

Statistical analyses

Environmental variables − Principal component analysis (PCA) and correlation were used to reduce the dimensionality of environmental variables and select a parsimonious set of variables to be used in subsequent ordinations. Three separated PCAs were run for catchment land use and riparian and instream habitat characterisations. PCAs and correlation analysis were conducted using JMP® 14.0.0 (SAS Institute Inc. JMP, 2012).

Permutational multivariate analysis of variance (PERMANOVA) − was used to test for differences in habitat variables and epigeal arthropod and macroinvertebrate assemblage composition between FOR and AGR sites. PERMANOVA was run on Euclidean distances of standardised log-transformed environmental variables and on Bray-Curtis dissimilarities of square-root transformed abundances. PERMANOVA was followed by a multiple comparison test using the function "pairwise.adonis" (Martinez Arbizu, 2019). Permutational analysis of multivariate dispersions (PERMDISP) was tested using the function "betadispser" (Oksanen et al., 2019). When both PERMANOVA and PERMDISP are significant the differences may be due to habitat types (FOR, AGR), dispersion effects or both. PERMANOVA, multiple comparison and PERMDISP were done using the "Vegan" package (Oksanen et al., 2019) and the R software version 3.6.2 (R Development Core Team, 2018). Similarity percentage analysis (SIMPER) was used to identify the organisms that discriminated differences in assemblage composition between FOR and AGR sites, calculated as the contribution of each species to the dissimilarity (%) based on the Bray-Curtis dissimilarity index (Clarke, 1993; Clarke, Gorley, Somerfield, & Warwick, 2014). SIMPER analyses were done using PAST version 4.0 (Hammer, Harper and Ryan, 2001).

Multivariate regression − Multivariate methods were used to quantify the fractions of variation in the taxonomic composition of epigeal arthropod and aquatic macroinvertebrate assemblages that could be explained by catchment, riparian and instream variables, and to rank the importance of the variables that best described these patterns. Separate analyses were done on epigeal arthropod and aquatic macroinvertebrate assemblages. Two complementary approaches were used in analysing responses to catchment and local scale variables. (1) Independent (marginal) effects of single environmental variables (Appendix A: Table 1) and complex (PC) environmental gradients (Appendix A: Table 2) on epigeal arthropod and aquatic assemblages were tested using forward selection without selecting covariables. Marginal effects (lambda) show the amount of variability that can be explained using a single variable in a constrained ordination and were used to rank the individual importance of catchment and local scale variables on epigeal arthropod and aquatic macroinvertebrate assemblages. (2) Forward selection of redundancy analysis was used to quantify and rank the importance of single variables while accounting for variability related to co-variables. The most parsimonious model for explaining variability in taxonomic composition was constructed by selecting the environmental variable that explained the greatest amount of variability. In subsequent steps the influence of other variables was quantified by running any variables already selected as covariables to determine the conditional effects. Significance of the environmental variables on assemblage composition was tested using 999 Monte Carlo permutations. (3) Unconstrained PCA ordination was used to quantify the variation in assemblage composition and diversity explained by complex (PC) environmental gradients. Multivariate regressions were done using Canoco software (version 5.04, ter Braak & Smilauer, 2018; Šmilauer & Leps, 2014).

Wilcoxon tests were used to test for differences in epigeal arthropod and aquatic macroinvertebrate number of taxa, Simpson diversity (1-D) and abundances between FOR and AGR sites. For aquatic macroinvertebrates we also tested if taxon richness of the orders Ephemeroptera, Plecoptera, Trichoptera (%EPT), three sensitive macroinvertebrate groups (Johnson et al., 1993), differed between FOR and AGR sites.

Results

Environmental gradients

Widths of the forested riparian vegetation differed between FOR and AGR streams (Wilcoxon, $p < 0.05$, Appendix A: Table 3): FOR streams had continuous riparian vegetation extending > 100 m from the stream edge, comprised almost entirely (93 − 98%) of mixed-boreal forests (mostly *Pinus sylvestris* and *Picea abies*), whilst for AGR streams riparian vegetation ranged from 5 - 34 m.

Principal components analysis revealed the main environmental gradient characterising our study sites was related to catchment (C-PC1) land use and associated changes in riparian habitat (R-PC1) related to forest cover and extent, soil organic and water content and high forbs (> 30 cm) and in instream habitat (S-PC1) related to geomorphology and woody debris (Appendix A: Table 2). Secondary gradients were related to microhabitat characteristics such as the prevalence of boulders and soil temperature in riparian habitats (R-PC2) and shading, living terrestrial plant parts and nutrients in instream habitats (S-PC2).

PERMANOVA on catchment, riparian and instream characteristics showed that catchment land use and riparian characteristics differed between FOR and AGR sites ($p < 0.05$) (Table 1A), whilst instream variables did not differ ($p > 0.05$). However, several individual variables differed significantly between FOR and AGR sites (Appendix A: Table 3). Catchment land use classified as agriculture accounted for 58.5% of the dissimilarity between FOR and AGR sites, for riparian habitats, forest type (coniferous and deciduous) explained 42% and for streams, nutrients and cobble substrata explained 37.6% of the dissimilarity between FOR and AGR sites.

Taxonomic composition between forested and agricultural sites

A total of 7212 beetles were collected during the three four-day sampling events. Some 259 species were distributed across 44 families (Appendix A: Table 4). Staphylinids were the most common species collected (2355 individuals, 85 species), followed by carabids (828 individuals, 64 species). For spiders, 1231 individuals were collected

Table 1. PERMANOVA results of catchment ($n = 9$), riparian ($n = 15$) and stream ($n = 16$) environmental variables (A) and riparian epigeal arthropod (Carabidae, $n = 64$ taxa, Staphylinidae, $n = 85$ taxa, Araneae, $n = 146$ taxa) and stream macroinvertebrate ($n = 91$ taxa) assemblages (B) between forested and agricultural streams. PERMANOVA was based on Euclidean distances of standardised environmental variables and on Bray-Curtis dissimilarities of square-root transformed abundances. Number of permutations = 999.

Source	df groups (residuals)	SS	MS	F model	p
A. Environmental variables					
Catchment	1 (6)	25.121	25.1214	4.8813	0.024
Riparian	1 (6)	55.991	55.991	6.8547	0.031
Stream	1 (6)	25.679	5.679	1.7849	0.111
B. Biological assemblages					
Carabidae	1 (6)	0.32178	0.32178	1.9972	0.087
Staphylinidae	1 (6)	0.29374	0.29374	2.3026	0.023
Araneae*	1 (6)	0.59183	0.59183	3.2590	0.030
Macroinvertebrates	1 (6)	0.12988	0.12988	1.0469	0.456

* PERMDISP was significant $p = 0.03$.

representing 16 families and 146 species: Linyphiidae (803 individuals, 70 species), Lycosidae (211 individuals, 13 species) and Gnaphosidae (24 individuals, 9 species) constituted the three most common families. In further analyses we focus on species within the beetle families Carabidae and Staphylinidae and Araneae.

Assemblage composition − Neither total abundances nor total species richness of epigeal arthropods ($p > 0.194$ and $p > 0.112$, respectively) or aquatic macroinvertebrates ($p = 0.112$ and $p = 0.885$, respectively) differed between FOR and AGR sites (Wilcoxon tests) (Fig. 2). However, among-site variability in the number of epigeal arthropod taxa (Fig. 2A) and their abundances (Fig. 2C) was relatively high in AGR compared to FOR sites. Diversity of carabid beetles was higher in AGR (0.936 ± 0.0152, mean ± 1 SD) than in FOR (0.888 ± 0.017) sites (Wilcoxon, $p = 0.030$), whilst diversity of staphylinids, spiders and aquatic macroinvertebrates did not differ (Fig. 2B). %EPT taxa richness did not differ between FOR (40.6 ± 15.8%) and AGR (42.7 ± 5.1%) sites (Wilcoxon, $p = 0.885$).

PERMANOVA showed significant differences in assemblage composition of staphylinid and spider assemblages between FOR and AGR sites, but not ground beetles nor aquatic macroinvertebrate assemblages (Table 1B). PERMDISP showed a significant dispersal effect for spider ($p = 0.03$) but not staphylinid assemblages. Percent contribution in dissimilarity between FOR and AGR sites by the 10 top ranked species ranged from 26.5% for Araneae to 48.8% for Carabidae (Table 2). Several carabid species were more abundant in AGR than FOR sites, and two species, *Nebria brevicollis* and *Agonum emarginatum*, were not recorded in FOR or AGR sites, respectively. By contrast, 9 of the top 10 ranked staphylinid taxa were more abundant in FOR than AGR sites: *Othius subuliformis* was not recorded in AGR sites and *Anotylus rugosus* was not recorded in FOR sites. Four spider species were recorded in FOR but not AGR sites: two web-builders *Macrargus rufus* and *Tapinocyba pallens* and two free-living ground hunters *Cryphoeca silvicola* and *Drassyllus praeficus*, whilst the web-building *Diplocephalus latifrons* was more abundant in AGR than FOR sites and the web-building *Savignya frontata* was only found in AGR sites. The main aquatic taxa contributing to differences between FOR and AGR sites were two Diptera taxa (Simuliidae, Orthocladinae), the beetle *Elmis aenea* and the amphipod *Gammarus pulex*, while only the stonefly *Nemoura cinerea* was more abundant in FOR than in AGR sites.

Responses to environmental gradients and spatial scale

In unconstrained PCA ordination, the six complex (PC) environmental gradients cumulatively explained from 86% (macroinvertebrates) to 89% (spider) of the variability in epigeal arthropod and aquatic macroinvertebrate assemblages (Fig. 3) and diversity (Fig. 4). Staphylinid and aquatic macroinvertebrate assemblages showed much higher among-site variability (i.e. larger polygons) in FOR compared to AGR sites (Fig. 3B and D). By contrast, spider assemblages were relatively similar among the forest sites (Fig. 3C). Likewise, ordination of species richness revealed differences between FOR and AGR sites along PCA axes 1 and 2 (Fig. 4). Redundancy analysis (lambda values) of epigeal arthropod and aquatic assemblages and complex environmental gradients showed that the strongest correlations were associated with the main PC gradients, in particular R-PC1 but also C-PC1 (Table 3). Ranking the importance of complex gradients showed that aquatic macroinvertebrates were best predicted by catchment land use (C-PC1), whilst epigeal arthropods, especially staphylinids and spiders, were

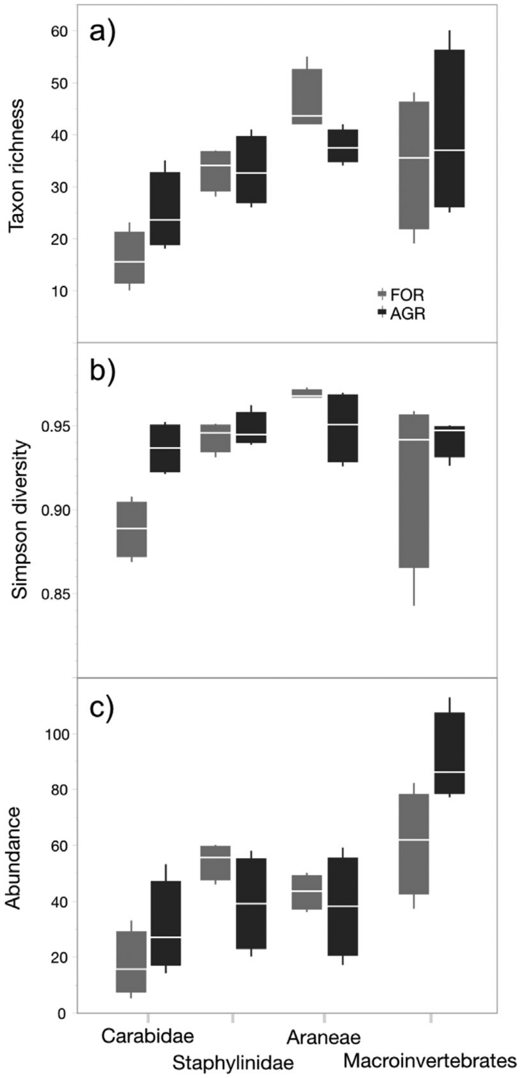

Fig. 2. Taxon richness, Simpson diversity and abundance of epigeal arthropod (numbers per unit effort) and aquatic macroinvertebrates (individuals/m^2) in forested (FOR) and agricultural (AGR) sites. Macroinvertebrate densities are 10x higher than shown on the y-axis. Box and whisker plots show the 25th, 50th and 75th percentiles.

Table 2. Similarity percentage analysis (SIMPER) of community differences between forested (FOR, $n = 4$) and agricultural (AGR, $n = 4$) sites. Results show the average percent dissimilarity in the riparian epigeal arthropod and stream macroinvertebrate structure between FOR and AGR sites, the top 10 taxa contributing (%) to the community dissimilarity and their cumulative contribution (%). Mean abundance (±1SE) of AGR and FOR sites are shown for epigeal arthropods (numbers per unit effort) and aquatic macroinvertebrates (individuals/m^2). Groups with an asterisk denote significant differences in community composition between FOR and AGR sites (Wilcoxon, $p < 0.05$). Spiders classified as web-building (WS) or free-living (FLS).

Taxon	Average dissimilarity	Contribution%	Cumulative%	Mean AGR	Mean FOR
Carabidae					
Patrobus atrorufus	5.0	8.0	8.0	13.5 ± 7.5	21.2 ± 11.8
Nebria brevicollis	4.5	7.2	15.2	11.0 ± 6.5	0 ± 0
Pterostichus nigrita	4.0	6.3	21.5	14.2 ± 5.3	1.4 ± 0.5
Pterostichus melanarius	3.3	5.3	26.8	11.2 ± 6.7	8.1 ± 3.3
Trechus secalis	3.2	5.1	31.9	6.8 ± 1.9	21.3 ± 13.1
Pterostichus oblongopunctatus	2.3	3.7	35.6	0.5 ± 0.2	5.2 ± 3.0
Clivina fossor	2.2	3.5	39.1	3.1 ± 1.9	0.3 ± 0.3
Pterostichus strenuus	2.2	3.4	42.5	4.2 ± 1.4	0.7 ± 0.5
Agonum emarginatum	2.0	3.2	45.8	0 ± 0	2.5 ± 1.6
Loricera pilicornis	1.9	3.0	48.8	2.7 ± 1.6	0.4 ± 0.3
Staphylinidae*					
Anotylus rugosus	3.5	6.0	6.0	23.5 ± 10.2	0 ± 0
Aleocharinae indet.	3.3	5.7	11.7	37.8 ± 7.8	97.1 ± 14.6
Tachinus sp.	2.4	4.2	15.9	9.1 ± 4.9	31.7 ± 21.1
Arpedium quadrum	2.0	3.4	19.3	1.0 ± 0.4	10.5 ± 6.1
Acidota crenata	1.8	3.2	22.5	0.02±0.02	7.8 ± 4.9
Othius subuliformis	1.8	3.1	25.6	0 ± 0	4.5 ± 0.6
Omalium caesum	1.7	3.0	28.6	0.9 ± 0.4	12.5 ± 9.9
Philonthus decorus	1.6	2.8	31.4	2.8 ± 1.9	7.5 ± 7.5
Xantholinus tricolor	1.6	2.8	34.1	0.4 ± 0.3	6.0 ± 2.7
Proteinus brachypterus	1.5	2.6	36.7	2.8 ± 1.7	7.3 ± 3.9
Araneae*					
Macrargus rufus (WS)	3.0	3.9	3.9	0 ± 0	9.8 ± 3.0
Diplostyla concolor (WS)	2.4	3.1	7.1	15.6 ± 11.9	5.9 ± 1.2
Tapinocyba pallens (WS)	2.2	3.0	10.0	0 ± 0	6.1 ± 1.8
Diplocephalus latifrons (WS)	2.1	2.8	12.8	14.0 ± 6.2	4.1 ± 2.0
Centromerus arcanus (WS)	1.9	2.6	15.4	0.3 ± 0.3	5.9 ± 1.8
Agroeca brunnea (FLS)	1.9	2.5	17.9	0.8 ± 0.8	7.1 ± 1.8
Savignya frontata (WS)	1.7	2.2	20.1	3.6 ± 0.9	0 ± 0
Trochosa terricola (FLS)	1.7	2.2	22.3	4.1 ± 2.7	8.3 ± 4.2
Cryphoeca silvicola (FLS)	1.6	2.1	24.4	0 ± 0	2.8 ± 0.8
Drassyllus praeficus (FLS)	1.6	2.1	26.5	0 ± 0	1.6 ± 0.2
Aquatic macroinvertebrates					
Simuliidae	2.9	5.8	5.8	10,634 ± 3355	4746 ± 2114
Orthocladiinae	2.8	5.6	11.4	9912 ± 4645	4331 ± 1902
Elmis aenea	2.6	5.3	16.7	3728 ± 1222	748 ± 428
Gammarus pulex	2.6	5.3	22.0	3675 ± 2710	558 ± 447
Pisidium sp.	2.4	4.9	26.9	2081 ± 7357	118 ± 109
Limnius volckmari	2.2	4.3	31.2	1462 ± 674	1411 ± 1350
Oligochaeta	2.0	4.1	35.3	5780 ± 2001	3248 ± 1547
Chironomini	2.0	4.0	39.3	1051 ± 303	2250 ± 2106
Nemoura cinerea	1.6	3.2	42.5	69.7 ± 24.0	1041 ± 616
Tanytarsini	1.5	3.0	45.5	2460 ± 629	2035 ± 927

best predicted by riparian variables (R-PC1). However, all three epigeal arthropod groups correlated with catchment (C-PC1) and riparian (R-PC1) characteristics, but staphylinid assemblages were also significantly correlated with instream characteristics (S-PC1).

Redundancy analysis also revealed significant relationships between assemblage composition and single environmental variables (Table 3). Carabid assemblages correlated with one catchment, five riparian and one instream variables. Forward selection resulted in a three-variable model:

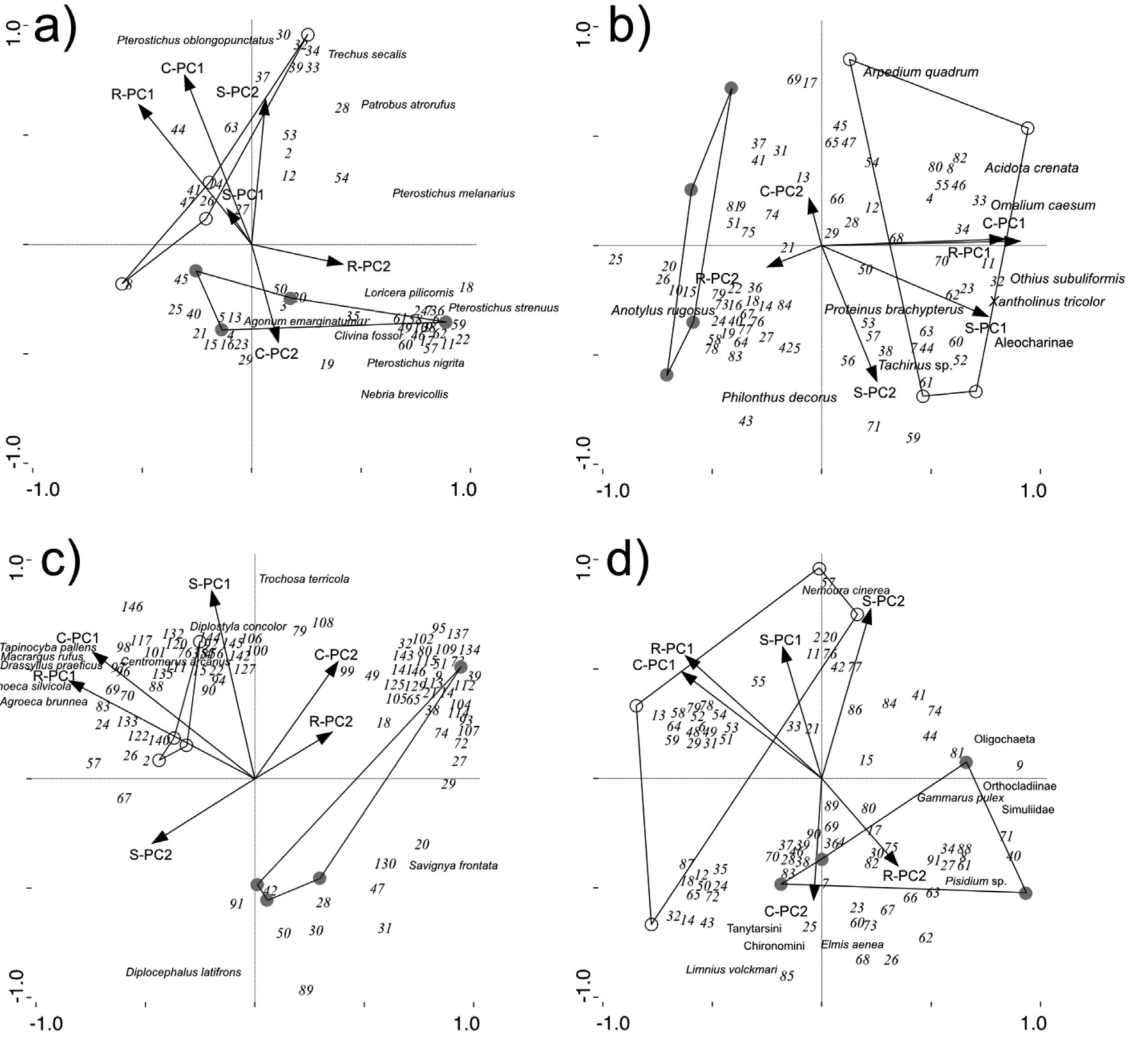

Fig. 3. PCA ordination of carabid (a), staphylinid (b), spider (c) and aquatic macroinvertebrate (d) assemblage composition and six environmental gradients (PC axes) in eight boreal streams and riparian habitats. Taxa names show the 10 top ranked taxa discriminating between forested and agricultural sites (Table 2). Numbers refer to taxa and their names are listed in Appendix A: Table 4. Arrows show PC axes 1 and 2 for catchment (C-PC1 and C-PC2), riparian (R-PC1 and R-PC2) and instream (S-PC1 and S-PC2) sites (Appendix A: Table 2). Forested sites (open circles) and agricultural sites (shaded circles) are enclosed by polygons.

riparian tree density (34%, $p = 0.007$), riparian deciduous forest (24.3%, $p = 0.037$) and catchment clear-cut (17.1%, $p = 0.036$). Nine riparian variables, notably high forbs (30.3%, $p = 0.002$) and coniferous forest (29.1%, $p = 0.001$), three catchment and three instream variables were strong predictors of staphylinid assemblages. Forward selection resulted in a two-variable model: high forbs (30.3%, $p = 0.002$) and shading (LAI, 17.4%, $p = 0.048$). Like rove beetles, spider assemblages were correlated with nine riparian, three catchment and two instream variables. Forward selection resulted in a two-variable model: high forbs (32.8%, $p = 0.002$) and instream nutrients (NO_2+NO_3, 23.9%, $p = 0.006$). Aquatic macroinvertebrate assemblages correlated with catchment forest type, four riparian and only one instream variable (inorganic substrates >6−20 cm, 25.9%, $p = 0.013$). Forward selection resulted in a two-variable model: width of the riparian habitat (28%, $p = 0.002$) and water colour (23.1%, $p = 0.014$).

Discussion

Agricultural land use is a pervasive threat to the biodiversity, function and ecosystem services of streams and their adjacent riparian habitats (Strayer & Dudgeon, 2010). As ecosystems are increasingly considered open, connected by resource flows acting at different spatiotemporal scales (Soininen, Bartels, Heino, Luoto & Hillebrand, 2015), biodiversity loss and changes in community composition in one system can affect another system if these linkages are lost or impaired. We hypothesized that responses to environmental variables and different spatial scales (catchment land use and

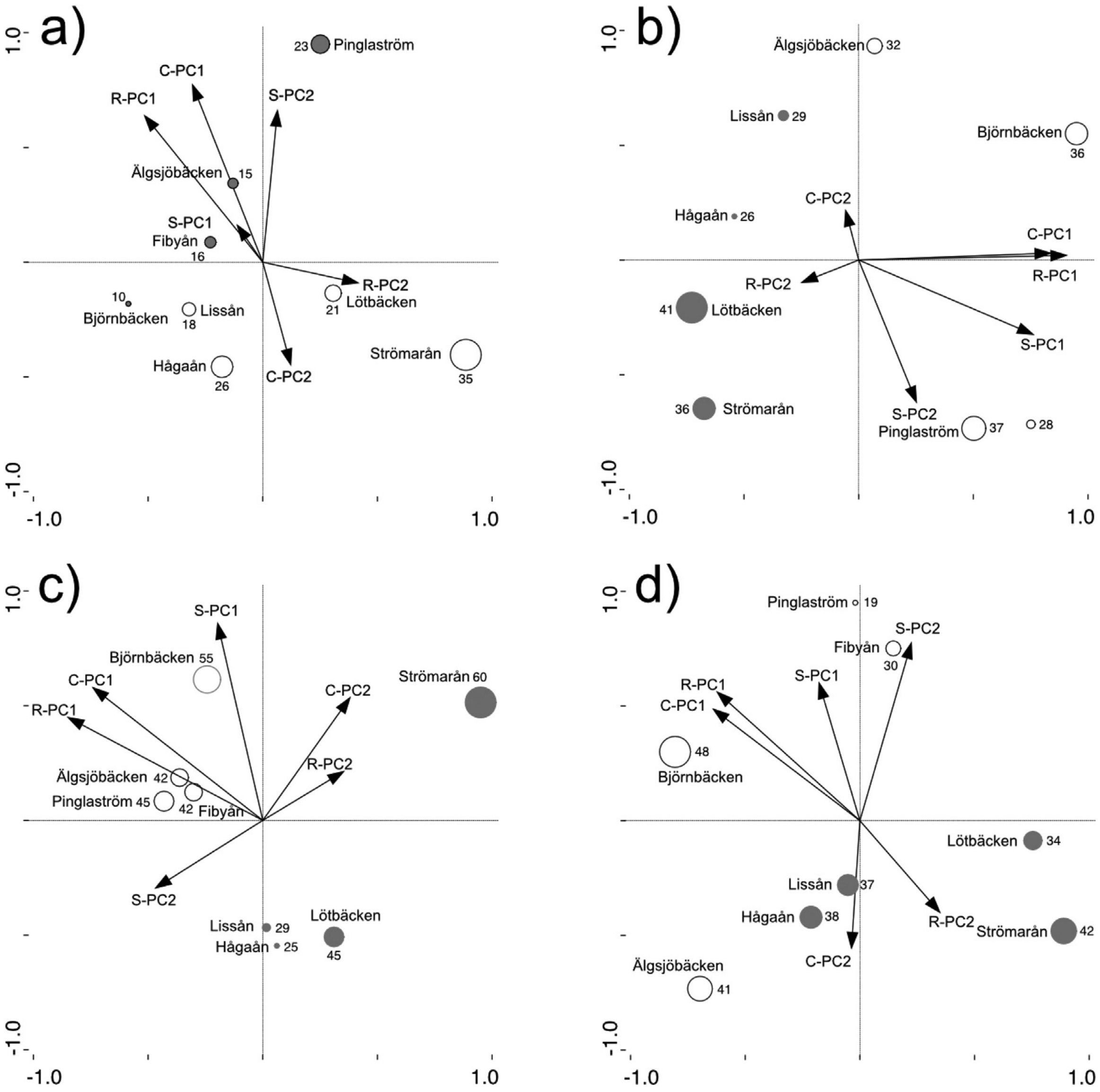

Fig. 4. PCA ordination of species richness (shown as circles and numbers) of carabid (a), staphylinid (b), spider (c) and aquatic macroinvertebrate (d) assemblages and six environmental gradients (PC axes) in eight boreal stream and riparian habitats. Arrows show PC axes 1 and 2 for catchment (C-PC1 and C-PC2), riparian (R-PC1 and R-PC2s) and instream (S-PC1 and S-PC2) sites (Appendix A: Table 2). Open circles=forested sites; Shaded circles=agricultural sites. Numbers show taxon richness.

local habitat) would differ between riparian epigeal arthropod and aquatic macroinvertebrate assemblages. Specifically, we predicted that epigeal arthropods are responding more to local scale variability in riparian habitat, whilst aquatic macroinvertebrate assemblages are responding more to the cumulative effects of catchment land use as well as local (riparian and instream) environmental variables. Multivariate regressions of epigeal arthropod assemblages with single environmental variables and with complex environmental gradients supported these principal hypotheses, whilst partial support was found for aquatic macroinvertebrate assemblages. As anticipated, the main environmental variables underpinning riparian and aquatic biodiversity loss and changes in assemblage composition differed and were species-specific.

Catchment and local scale variables explained significant amounts of variability in aquatic macroinvertebrate assemblages, partially supporting our cumulative-effects hypothesis. Aquatic macroinvertebrate assemblages were correlated with catchment land use and variables indicative of nutrient effects on streams (e.g. floating macrophytes). However, unexpectedly epigeal arthropods (staphylinids, spiders) were also correlated with these variables. Moreover, catchment and local scale variables were correlated (e.g. C-PC1 & R-PC1, $\rho = 0.762$; C-PC1 & S-PC1, $\rho = 0.476$) and therefore difficult to disentangle. Other studies have shown aquatic macroinvertebrate assemblages to be correlated with both large-scale (regional, catchment) and small-scale (habitat) environmental variables (Johnson et al., 2004; Li, Chung,

Table 3. Lambda (% variation explained), pseudo-F values and p values for assemblage composition of epigeal arthropod and aquatic macroinvertebrates against selected environmental variables and complex environmental (PC axes) gradients in eight boreal streams and riparian habitats. $p < 0.05$*, $p < 0.01$**, $p < 0.001$***, $p < 0.1$†. Variables that were significant in model calibrations, but not as individual predictors, are not shown.

	Carabidae			Staphylinidae			Araneae			Aquatic macroinvertebrates		
	%	F	P	%	F	P	%	F	P	%	F	P
Catchment variables												
agriculture (%)				26.5	2.2	*	26.3	2.1	*			
deciduous forest (%)	27.7	2.3	*	23.0	1.8	*	29.1	2.5	**	23.9	1.9	*
coniferous forest (%)				27.4	2.3	**	26.2	2.1	*	22.8	1.8	*
Riparian variables												
agriculture (%)							23.0	1.8	†			
deciduous forest (%)	25.6	2.1	*	26.4	2.2	*	24.4	1.9	*			
coniferous forest (%)				29.1	2.5	**	29.6	2.5	**	21.6	1.7	†
open grass (%)	20.1	1.5	†				23.2	1.8	*	27.3	2.3	**
tree density at 25 m (m^2/ha)	34.0	3.1	*	26.1	2.2	*	32.8	2.9	**	25.1	2.0	*
altitude (m a.s.l.)				24.2	1.9	*						
width (m)	29.9	2.5	*	26.1	2.1	*	31.3	2.7	**	28.0	2.3	**
soil water content (%)				24.1	1.9	*	23.8	1.9	*			
soil organic content (%)				25.7	2.1	*	28.4	2.4	**			
soil temperature (°C)	22.7	1.8	*	28.3	2.4	***	23.5	1.8	*	22.8	1.8	†
high forbs >30 cm (%)	32.9	2.9	**	30.3	2.6	**	32.8	2.9	**	27	2.2	**
Stream variables												
algae (%)							22.8	1.8	†			
floating macrophytes (%)				25.1	2.0	*	24.8	2.0	*	23.2	1.8	†
inorganic substrates >6–20 cm	28.8	2.4	*				22.3	1.7	†	25.9	2.1	*
conductivity (mS/m)				27.7	2.3	*	25.8	2.2	*			
water colour (Absf)				24.2	1.9	*				21.7	1.7	†
Complex (PC) gradients												
C-PC1	26.5	1.9	†	29.9	2.1	*	30.7	2.3	*	25.7	1.7	†
R-PC1	27.5	1.9	†	32.1	2.3	*	33.8	2.6	**			
S-PC1				27.8	1.9	*						

Bae, Kwon & Park, 2012) as well as other taxonomic groups (Johnson & Hering, 2010). Interestingly, our study showed that riparian habitat variables were as good as measures of water quality and instream substratum for predicting aquatic macroinvertebrate assemblages. Aquatic macroinvertebrate assemblages were correlated with several measures of riparian vegetation type and extent, emphasizing the importance of riparian vegetation for instream food webs (Quinn, Cooper, Stroud & Burrell, 1997; Webster et al., 1999) and shading effects on water temperatures (Johnson & Almlöf, 2016). Although the significance of terrestrial leaf litter and woody debris for instream function has been well studied (Webster et al., 1999), much less is known of how other riparian – stream interactions affect aquatic biodiversity (Baxter et al., 2005; Burdon et al., 2020).

Agricultural land use influences not only riparian and aquatic biodiversity directly, as shown here and elsewhere (e.g. Burdon et al. 2020; Johnson et al. 1993; Venier, 2006), but if the proportion of non-flying to flying aquatic macroinvertebrates increases, land use can result in knock-on effects on the cross-habitat resource flows that maintain biodiversity (Stenroth, Polvi, Fältström & Jonsson, 2015). Our study showed that three of the 10 species discriminating between FOR and AGR sites were non-insects (*Gammarus pulex, Pisidium* and Oligochaeta) with higher abundances in the AGR streams. On the one hand, a shift in assemblage composition to non-insects constitutes a reduction in the proportion of in-stream production that can be potentially transferred to terrestrial systems by emerging flying insects (Carlson et al., 2016; McKie et al., 2018; Muehlbauer, Collins, Doyle & Tockner, 2014). On the other hand, the higher abundances of stress-tolerant insect species (e.g. many dipterans) often found in nutrient-rich agricultural streams might partly compensate for and maintain the resources that support terrestrial biodiversity, as well as reciprocal flows back to aquatic habitats. In our study, three aquatic insect taxa (simuliid black flies, orthocladiine midges and the beetle, *Elmis aenea*) were more abundant in AGR than in FOR streams. Shifts in aquatic assemblages to non-flying macroinvertebrates and weak-flying aquatic insects associated with agricultural land use can negatively impact riparian biodiversity through the loss of riparian consumers that rely on aquatic flying insects as a food resource. However, paradoxically, terrestrial consumers close to the stream edges might benefit if dispersal of weak-flying insects is truncated to the stream edges (Carlson et al., 2016).

Contrary to our predictions, neither spider diversity nor abundances were lower in AGR sites. Furthermore, although assemblages differed significantly between FOR and AGR sites, the dispersion effect was also significant, complicating interpretation of among-site differences. Consistent with expectations, the strongest relationships were generally noted with local scale (riparian) such as high forbs, soil organic matter and the extent and density of riparian vegetation. That spider assemblages were responding to local variables agrees with several earlier studies (De Mas, Chust, Pretus & Ribera, 2009; Mader et al., 2016; Schmidt et al., 2008). Species-specific responses revealed strong general patterns associated with land use between FOR and AGR sites: seven of the top 10 discriminating species were either not recorded in AGR sites or had lower abundances compared to FOR sites. The four species not recorded in AGR sites have been shown to be associated with forest leaf litter such as pine needles (i.e. two web-builders *Macrargus rufus, Tapinocyba pallens* and the free-living *Cryphoeca silvicola*) or under stones (the free-living *Drassyllus praeficus*) (Harvey, Nellist & Telfer, 2002). By contrast, the two web-building species found in higher abundances at AGR sites can be characterised as habitat generalists (e.g. *Diplocephalus latifrons* and *Diplostyla concolor*) (Harvey et al., 2002; Rushton, Topping, & Eyre, 1986). Given the differences in spider assemblages between AGR and FOR sites, we expected to find a difference in vegetation along the stream edges. Although AGR streams had higher abundances of forbs $>$ 30 cm, which should favour certain web-building spiders, we found no clear pattern that web-building spiders tracked these differences.

Staphylinid assemblages differed between FOR and AGR sites and consistent with expectations responses were species-specific: nine of the top 10 ranked staphylinid species were more abundant in FOR sites. These findings support our conjecture that staphylinid beetles are less tolerant of the environmental conditions prevailing in arable landscapes (Carlson et al., 2013). The one exception was the spiny-legged rove beetle *Anotylus rugosus* which had relatively high abundances in AGR sites and was not found in FOR sites. This species is widely distributed in central and northern Europe and has been recorded in a wide range of habitats, including the margins of aquatic systems (Eyre, Lott & Luff, 2001). Our findings that staphylinid assemblages correlated with vegetation type (e.g. high forbs) and soil properties (e.g. organic content) are consistent with those of Pearce and Venier (2006), but disagree with a study by Silva et al. (2009) who found significantly higher abundances and species richness of staphylinids in AGR than FOR sites. Part of the discrepancy between these two studies might be explained by the effects of different hydrogeomorphic conditions on riparian vegetation and soil conditions (Bendix & Steella, 2013; Gregory, Swanson, McKee & Cummins, 1991).

Many carabid species are habitat generalists and known to predominate in agricultural landscapes (Gailis & Turka, 2013), a finding which was supported by our study. While total abundances did not differ between FOR and AGR sites, seven of the top 10 carabid species were more abundant in AGR than FOR sites. Our findings of higher diversity in AGR sites and differences in species composition between FOR and AGR sites also corroborates a number of earlier studies (e.g. Gailis and Turka 2013, Pearce and Venier 2006). Niemelä, Koivula and Kotze (2006) showed that forestry resulted in shifts in assemblage composition to species commonly occurring in open habitats, whilst Pearce and Venier (2006) found both increased diversity and shifts in species composition associated with forestry. Likewise, Birkhofer et al. (2015) found that species richness did not differ with land use, although the average functional distinctness was higher in grasslands than in forested or in arable lands, and differences in assemblage composition between land-use types was related to differences in body size, dispersal ability, feeding and substratum preferences. Finally, similar to spider populations, as predators the observed differences in species composition and abundances of carabids between AGR and FOR sites could be related to food resources (i.e. stream subsidy effects) (e.g. Terui, Negishi, Watanabe and Nakamura, 2018).

Implications for management - Riparian epigeal arthropod and aquatic macroinvertebrate assemblages due to their relatively small size, short generation times and predictable responses to quantifiable environmental gradients are frequently used to assess disturbance and recovery (Gerlach, Samways & Pryke, 2013; Resh & Rosenberg, 1993). An underlying premise of our study was that riparian beetle and spider assemblages would respond more strongly to local scale variables, whilst aquatic macroinvertebrates were responding more to the cumulative effects of catchment and local variables. Consistent with our predictions, epigeal arthropod responses to land-use impacts on local habitat were species-specific and predictable, supporting their use in monitoring degradation and recovery. Aquatic macroinvertebrates responded to both catchment and local (both riparian and instream) scale variables. These findings support the use of epigeal arthropods for quantifying local (habitat) effects of land-use on biodiversity, whilst instream macroinvertebrate assemblages are more suitable for assessing cumulative land-use effects on instream biodiversity.

Increasingly, managers emphasise the value “green infrastructure”, comprising networks of natural or seminatural areas in landscapes otherwise characterised by extensive anthropogenic disturbance and transformation, in order to preserve biodiversity and support ecosystem service delivery. Riparian − stream networks might exemplify the green infrastructure principle, but are often highly degraded, limiting their potential to support biodiversity and ecosystem functioning. Given the importance of aquatic subsidies for terrestrial food webs and biodiversity (Baxter et al., 2005;

Nakano & Murakami, 2001; Ramberg et al., 2020), our results indicate that measures that only address local scale drivers of terrestrial biodiversity might have limited efficacy if the catchment-scale variables regulating aquatic biodiversity and aquatic − terrestrial linkages are not adequately addressed in management. For example, in a recent study Forio et al. (2020) found cumulative benefits of increasing vegetation in the riparian zones for aquatic macroinvertebrates, whilst local vegetation patches were enough to benefit terrestrial invertebrates.These studies highlight the need for management planning that simultaneously addresses both the importance of catchment- and local-scale drivers of biodiversity loss and the terrestrial and aquatic components of riparian − stream networks, to effectively fulfil the role of green infrastructure in degraded agricultural landscapes.

Declaration of Competing Interest

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

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Supplementary materials

Supplementary material associated with this article can be found in the online version at doi:10.1016/j.baae.2021.10.006.

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