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RESEARCH ARTICLE

More than just a margin: Local and landscape-scale factors regulating the effects of riparian forest buffers on stream-riparian ecosystems in urban and agricultural landscapes

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Abstract

1. Riparian forest buffers are a potentially potent nature-based solution for mitigating environmental degradation and improving biodiversity and ecosystem functioning in stream-riparian networks. However, uncertainties about how buffer size, spatial configuration and land-use intensity shape outcomes and trade-offs hinder management applications.
2. We conducted coordinated field surveys and modelling across four European countries to evaluate how riparian forest properties influence stream-riparian environments, biodiversity, ecosystem processes and macroinvertebrate functional traits along agricultural and urban land-use gradients.
3. Riparian forest buffers had strong effects on habitats, increasing shading and coarse woody debris. Sediment deposition was halved in buffered stream reaches, and longer buffers lowered thermal maxima in stream and riparian habitats by 13%–17%. Buffers further reduced effects of increasing agricultural land use on soluble reactive phosphate concentrations, although this response was highly variable.
4. These environmental changes were associated with multiple effects on biodiversity and ecosystem function. Buffer presence and/or increasing length were associated with 30%–167% increases in microbial detritus decomposition, a 44% increase in

riparian ground beetle diversity, and 18%–77% increases in stream macroinvertebrate diversity and the EPT biotic index, and macroinvertebrate leaf shredding and algal grazing traits. In contrast, algal biomass accrual and web-building spider diversity declined by 33% and 36%, respectively, in buffered reaches.

5. As land-use intensified, riparian forest buffers helped maintain macroinvertebrate functional diversity and shredding, predation, and filtration traits, and saturated fatty acid content in terrestrial predators. In contrast, macroinvertebrate particle-gathering traits declined.
6. The spatial configuration of riparian forest influenced stream ecosystems at local scales: dissolved phosphorus and diatom species richness declined as spatial proximity among upstream riparian forest blocks decreased, while a diatom-based biomonitoring index increased.
7. *Synthesis and applications*. Riparian forest buffers support biodiversity, ecosystem functioning and food webs in human-modified landscapes, and dampen land-use and climate stressors (sediments, nutrients, thermal maxima), motivating their wider use in management. These outcomes were regulated by the presence or size of mostly small, mature buffers and sometimes by proximity among riparian forest blocks upstream, indicating that even modest investments in expanding existing buffer networks are likely to deliver cumulative ecological benefits.

KEYWORDS
biodiversity, blue-green infrastructure, ecosystem functioning, environmental co-benefits, land use, nature-based solution, riparian restoration, stream ecosystem

1 | INTRODUCTION

Lotic (stream and river) ecosystems and their riparian habitats form vital blue-green infrastructure that supports biodiversity, landscape integrity and human well-being (Naiman & Décamps, 1997; Riis et al., 2020). Ecological connections, such as leaf litter inputs into streams and the emergence of the winged adults of aquatic insects, transfer energy and nutrients across ecosystem boundaries and sustain food webs (Gessner et al., 2010; Twining et al., 2025). The ecological integrity of both habitats is important for stream-riparian multifunctionality (Clerici et al., 2014). For example, filtration of water through intact riparian soils and by stream filter-feeders contributes to water purification, and high-quality habitats sustain diverse faunal guilds that support carbon and nutrient cycling processes (Frainer et al., 2018; Singh et al., 2021; Whiles & Dodds, 2002). These cross-ecosystem exchanges are vulnerable to land-use stressors that alter hydrology, degrade habitat quality and disrupt ecological linkages, making stream-riparian networks in modified landscapes particularly susceptible to ecological impairment (Feld et al., 2011; Haase et al., 2023). This challenge underscores an urgent need for expanded management to mitigate degradation and enhance stream-riparian biodiversity, functioning and connectivity.

A primary nature-based solution for improving stream-riparian environments is rehabilitation of riparian vegetation to help buffer land-use and climate-related stressors (Feld et al., 2018; Kumwimba et al., 2024). Riparian buffers can be based on grass, meadow or shrub vegetation, but riparian forest buffers (RFBs, i.e. composed of riparian trees) typically have the strongest effects on local stream environments (Feld et al., 2018; Graziano et al., 2022; Riis et al., 2020). This reflects the capacity of RFBs to intercept nutrients, reduce erosion, moderate microclimate, supply detrital resources, contribute new habitat elements (woody debris, root structures) and provide refugia for sensitive and dispersing species (Carlson et al., 2016; Feld et al., 2011; Johnson & Almlöf, 2016). These effects alter biodiversity, ecosystem functioning and cross-habitat connectivity (Burdon et al., 2025; Mundahl et al., 2023; Mutinova et al., 2020).

Proposals for RFBs in agricultural and urban landscapes often generate stakeholder conflicts (Arnold et al., 2012; Cole et al., 2020), reflecting inter alia concerns over losses of productive land or risks of woody debris damaging infrastructure via flooding and mobilization (Broadmeadow & Nisbet, 2004; Graziano et al., 2022). Consequently, riparian restoration is often largely guided by pragmatic and economic considerations and implemented at the discretion of individual landowners (Graziano et al., 2022; Shr et al., 2025), resulting in patchy, poorly connected riparian networks, with grass buffers favoured (Broadmeadow & Nisbet, 2004; Mitchell et al., 2013; Shr et al., 2025). Nevertheless, support for more extensive riparian restoration increases when landowners expect clear

environmental benefits (Shandas, 2007; Shr et al., 2025), highlighting the need to better understand and communicate the ecological outcomes of RFBs.

Most studies of RFB effectiveness emphasize local-scale effects on single ecosystem attributes, leaving knowledge gaps concerning, for example synergies and trade-offs among multiple potential outcomes, effects of land-use intensity on buffer performance, and the role of buffer spatial arrangement (Cole et al., 2015; Feld et al., 2018; Weigelhofer et al., 2012). We address these knowledge gaps using coordinated field studies and modelling across four European countries to evaluate how riparian forest properties influence stream-riparian habitats, biodiversity and food webs along agricultural and urban land-use gradients. This includes evaluation of the local-scale effects of RFB presence and size. Additionally, we assess the role of spacing among upstream riparian forest blocks as a proxy for connectivity among forested reaches, given that spatial proximity is a primary factor governing connectivity of organisms and materials among forest patches (Pascual-Hortal & Saura, 2006). We hypothesize that:

1. RFBs improve habitat quality by moderating sediments and nutrients, adding new habitat elements and buffering thermal extremes.
2. RFBs increase taxonomic and functional diversity overall and improve ecological status indicators, but reduce taxa that favour unforested habitats.
3. RFBs interact with agricultural and urban land use, either mitigating local land use impacts or being constrained in their efficacy where land-use intensity is high.
4. Greater upstream riparian forest connectivity enhances linkages to regional species pools, reflected in enhanced local biodiversity, and cumulatively reduces land-use stressors such as nutrients and sediments.
5. Ecosystem processes and macroinvertebrate feeding traits that mediate functions associated with the brown (detrital) energy pathway (coarse and fine detritus feeding traits) are enhanced in buffered reaches, reflecting increased terrestrial detritus inputs, whereas algal grazing traits linked to the green (autotrophic) pathway are reduced.
6. Adult aquatic insects with strong dispersal traits—often larger-bodied and environmentally sensitive species—are more abundant in RFBs.

2 | METHODS

2.1 | Study systems and sampling design

As part of the BioDivERsA project CROSSLINK (Burdon et al., 2020), we investigated 36 streams across four European basins (Norway, Sweden, Romania, Belgium, Appendix S1, Figure S1a) affected by riparian forest loss (Clerici et al., 2014). On each stream, we delineated two 50 m long reaches, with, in all but one stream, an upstream unbuffered reach paired with a downstream reach with a RFB present (Figure S1b). The exception was one Belgian stream, where a downstream unbuffered site was used due to site selection constraints (see Appendix S1). The buffered reach was always placed at the downstream end of the buffer (Figure S1b). Our design thus contrasted degraded (control) and buffered (treatment) sites on single streams, allowing us to evaluate shifts in key ecosystem indicators over a relatively small spatial scale.

In Norway, sampling targeted urban streams in the capital city Oslo, draining into Oslo Fjord. In Sweden and Romania, we sampled largely agricultural tributaries of Lake Mälaren's Ekoln Bay and the Argeș River, respectively. In Belgium, we focused on the mixed-use Zwalm catchment, affected by both agricultural and urban pressures. Across these basins, we thus captured both agricultural and urban land-use gradients. The agricultural gradient, spanning sites in Romania, Sweden, and Belgium, encompassed streams typical of south-eastern, central and northern European farmland—from hard-bottomed upland pasture systems to low-gradient, soft-bottomed streams shaped by flat topography and erosive cambisol soils. Urban systems occurred mainly in Norway and Belgium, affected by extensive grey infrastructure, impervious land cover and channel modification (concrete or riprap).

All streams were 1st–3rd order (≈2–6 m wide) with stony substrates (gravel, cobble, bedrock) always present. Hard substrates were less dominant (<30% stream bed cover) in the most agricultural Swedish and Belgian sites, but we ensured comparable substrate composition between paired reaches within single streams. Buffered reaches were characterized by a continuous block of riparian forest (mixed small and large trees) extending ≥70 m along both banks, with a width at least 2–3× the wetted channel. Unbuffered sites lacked a continuous RFB, but sometimes had isolated patches of one or a few trees (<5 m^2). All RFBs were well-established, based either on pre-1970s remnant forest patches that have expanded since 2000, or patchy reforestation along streams that were treeless as recently as the 1980s (see Appendix S1).

2.2 | Field measurements

Our field campaigns were conducted in autumn 2017 and spring–autumn 2018. We thank landowners for site access. None of our measurements required ethical approval. Sampling periods and methods for different field measurements are detailed in Appendix S2; a brief overview is provided here.

2.2.1 | Stream-riparian habitats and water quality

During summer 2018, we conducted detailed stream habitat surveys (Appendix S1, Burdon et al., 2020), including replicate (5–6 transects per reach) measurements of channel dimensions, substrate composition (% cover of inorganic and organic types) and hydromorphological impacts (channel modification, barriers).

Replicate measures of canopy cover (CanopyApp v.1.0.3, University of New Hampshire) were quantified as a proxy for shading in both stream and riparian habitats (Appendix S2). Stream and riparian temperatures were logged continuously during autumn and late spring–summer, respectively, using ibuttons (Maxim Integrated, San Jose, California) placed on substrate or soil surfaces. Coarse woody debris pieces (ø > 10 cm) were counted in both habitats, and riparian tree species richness quantified. Water samples were collected three times per reach (autumn 2017 and spring and summer 2018) and analysed within 24 h for ammonium, total inorganic nitrogen and soluble reactive phosphorus (SRP) concentrations (Appendix S2).

2.2.2 | Algae and sediment deposition

In August 2018, diatoms were sampled from 5 to 10 stones (10–25 cm diameter) collected in fast-flowing habitats, with stone number determined according to mean stone size at each reach (Appendix S2). Stone surfaces were brushed three times, with the sample preserved (96% ethanol) for later species-level microscopic identification.

Eight unglazed tiles (16 × 16 cm) were deployed in four pairs per stream reach for colonization by algal biofilms over ≈30 days in August 2018 (Frainer et al., 2018). After this, algal accrual on the tiles was assessed by quantifying chlorophyll-a biomass using one of two methods suitable for biofilms: in situ using a portable fluorometer, or via laboratory pigment extraction and spectrophotometry (Kahlert & McKie, 2014; McKie et al., 2023).

To quantify sediment deposition, eight artificial turf mats (16 × 16 cm), mimicking macrophyte beds, were deployed in each reach in early autumn 2018 to trap fine particles as they flowed over the stream bottom (Frainer et al., 2018). After 3 days, the mats were retrieved, with entrapped inorganic and organic matter washed through nested sieves. Fine sediment (<2 mm) was then dried, weighed, ashed at 550°C and reweighed to estimate inorganic sediment deposition ($g\,m^{-2}\,day^{-1}$). Sediment deposition was not quantified in the entirely urban Norwegian case study.

2.2.3 | Decomposition of detritus mediated by microbial organisms

We estimated microbially mediated decomposition in stream and riparian habitats using leaf bag- (LBA) and cotton strip assays (CSA), respectively. The LBA used fine (ø = 0.5 mm) mesh bags, excluding most litter-consuming detritivores, each filled with 5.00 ± 0.25 g of locally sourced alder (*Alnus glutinosa*) litter collected at abscission (Frainer et al., 2021). Five litterbags were deployed per reach during autumn 2017 for ≈30 days. Retrieved litter was dried (60°C, 48 h), weighed and combusted at 550°C for determination of ash-free dry mass. Decomposition rate coefficients were calculated as $k = -\ln(mass_{final}/mass_{initial})/time$.

The CSA ran concurrently, using 25 × 80 mm cotton strips (cut from Fredrix Style 548 artists canvas). Two pairs of strips per reach were deployed on riparian soils (Tiegs et al., 2019). Tensile strength (TS) loss was measured with a tensiometer, and breakdown rates ($k_{(TS)}$) calculated as $\ln(TS_{initial}/TS_{final})$ / time.

2.2.4 | Aquatic and riparian invertebrates

Stream benthic macroinvertebrates were sampled from three riffles and three pools per reach using a Surber sampler (500-µm mesh, quadrat 0.0625 m^2) during stable-flow conditions in autumn 2017 or spring 2018. The six subsamples were pooled, and invertebrates identified to the lowest practicable taxonomic level (Appendix S2). Riparian predators (web-building spiders, hunting spiders and beetles) were sampled in summer 2018 using timed visual searches (~10-min, two observers; Burdon et al., 2025) in six 10 × 5 m plots adjacent to each reach (3 per bank, Appendix S2). Predators were collected by hand net and stored frozen for later identification to family and for fatty acid analyses.

2.2.5 | Fatty acid analysis

Riparian spiders and beetles were freeze-dried, homogenized and analysed for saturated (primarily reflecting energy stores) and poly-unsaturated (reflecting high-quality fatty acids) fatty acid content following Ramberg et al. (2020), using gas chromatography–mass spectrometry at the Swedish Metabolomics Centre.

2.3 | Spatial and land-use predictor variables

2.3.1 | Buffer length and upstream riparian forest connectivity

We chose buffer length as our primary measure of buffer size, since extending buffer length longitudinally minimizes encroachment on infrastructure and arable land, and may thus be more acceptable for land owners (Shr et al., 2025). Buffer width and area were strongly correlated with buffer length ($r^2 > 0.85$). Buffer length was measured along stream channels in Google Earth Pro (accessed 2021). Short breaks in forest cover caused by bridges were not considered to interrupt continuous buffers. For unbuffered reaches, we also measured small patches of trees occurring within 50 m of stream banks, summing the length of such patches >25 m^2. These patches typically summed to <100 m in combined length, except at 9 sites where thin roadside tree bands occurred close to the stream along one bank.

We quantified the average distance among riparian forest blocks and occurring upstream of each sampling reach as a proxy for upstream riparian forest connectivity, with all forest patches ≥50 m^2 regarded as discrete riparian forest blocks (Witing et al., 2022).

Forest patches were mapped within a 50 m-wide riparian corridor along both riverbanks using the Copernicus dataset (EEA, 2018), overlaid with a 25 m grid, and inter-patch distances within each upstream corridor calculated using ArcPy as described in Witing et al. (2022).

2.3.2 | Land-use gradients

To capture the agricultural and urban land uses affecting our study reaches, we conducted a principal components analysis of selected catchment land use and local stream habitat variables (Appendix S3), using the rda function in *vegan* (v 2.7.2, Oksanen et al., 2013). The first axis captured a gradient of increasing agricultural catchment land use coupled with increasing fine sediments in benthic substrates, and the second increases in urban catchment cover and the degree of reach bank fixation (Appendix S3, Figure S2). Axes 1 and 2 were used in subsequent statistical analyses as agricultural and urban land-use predictors, respectively.

Comparisons of the distributions of all continuous predictors—two land-use gradients, riparian connectivity and buffer length—among countries are shown in Appendix S4.

2.4 | Data analysis

2.4.1 | Preparation

Response variables were grouped into three sets of ecosystem attributes to organize the data by habitat and organism group. Sets 1 and 2 included stream and riparian ecosystem attributes (environmental, biodiversity, food web processes), and set 3 comprised macroinvertebrate functional traits (Appendix S5, Table S1). For sets 1–2, we calculated taxon richness and Shannon diversity for each organism group, and two standard biomonitoring indices widely used in Europe: species richness of the generally sensitive macroinvertebrate orders Ephemeroptera–Plecoptera–Trichoptera (EPT, Wallace et al., 1996), and the diatom index of pollution sensitive species IPS (Indice de Polluo-sensibilité Spécifique Des Clers et al., 1982). We additionally analysed a set of geomorphological variables to assess background (unrelated to RFBs) variation in channel characteristics (Appendix S6).

Macroinvertebrate species trait scores, fuzzy coded as proportions, were obtained from freshwaterecology.info (Schmidt-Kloiber & Hering, 2015). Community-weighted trait means (CWMs) were calculated for six feeding strategies (active and passive filtration, particle gathering, biofilm grazing, leaf shredding, predation) and two adult dispersal modes: aerial active (active flight) and aerial passive (wind or animal vectors). Functional dispersion was computed as an abundance weighted functional diversity index based on a broader trait set reflecting habitat and resource use: feeding, dispersal, locomotion and substrates, resistance forms, respiration and body size. CWMs and functional dispersion were calculated using *functcomp* and dbFD in the R package *FD*, using Gower's distance (Laliberté et al., 2014).

2.5 | Statistical analysis

Statistical analyses were conducted in R v4.5.1 (R Core Team, 2025). Prior to analysis, skewed variables were square-root or log-transformed. All continuous predictor and response variables were further placed on a comparable scale using *Z*-score standardization, facilitating calculation of standardized parameter estimates as measures of effect size.

Permutational multivariate analysis of variance (perMANOVA) was used to conduct global tests of buffer presence and length effects on the variable sets (excluding variables with a high percentage of missing values or high autocorrelation—Appendix S5, Table S1), using the adonis2 function in *vegan*. Permutations were constrained using the 'strata' command to reflect our nested sampling design (stream pairs within country). We present perMANOVA analyses with buffer presence fitted before buffer length; reversing entry order did not alter which terms were significant. No additional predictors were included to simplify interpretation and avoid overfitting. Correlations between response and predictor variables were visualized using nMDS generated with the *vegan* function metaMDS, with envfit used to overlay centroids for buffer presence, and vectors for response variables and the buffer length, land-use gradient and riparian connectivity predictors.

We followed multivariate analyses with univariate linear mixed models (LMMs) for detailed evaluation of the effects of buffer properties and land-use on each variable separately. Buffer presence, buffer length and riparian connectivity were fitted as fixed effects, as were the urban and agricultural land-use gradients and their interactions with buffer presence. Stream pair nested within country was fitted as a random effect. Models were run using the Bayesian implementation of the function lmer in *blme* (v1.0.6, Chung et al., 2013) and reduced with backwards selection based on conditional AIC (cAIC), calculated with *cAIC4* (v.1.1, Säfken et al., 2021). From final models, we report effect sizes (standardized regression coefficients (β) ± 95% confidence intervals) and *p*-values based on Wald *z* statistics for all retained terms, consistent with recommendations on statistical modelling and inference in ecology (Popovic et al., 2024; Sutherland et al., 2023). Effect sizes were broadly classified following Cohen (1992) as small ($\beta < 0.3$), moderate (0.3–0.5) or large (>0.5).

Modelled predictions for effects of buffer length, riparian connectivity and land use by buffer presence interactions were visualized on original variable scales (unstandardized and untransformed) in 'lollipop' plots, using estimated marginal means (EMMs) for three representative values along each predictor (~median, 75th and 85th percentile).

3 | RESULTS

3.1 | Multivariate relationships between buffer properties, land use and ecosystem attributes

3.1.1 | Geomorphology

Buffer presence and length had no effects on stream reach geomorphology overall (perMANOVA, both $p \geq 0.22$, Appendix S6, Figure S4) nor on individual geomorphic attributes (GLMM all $p > 0.1$).

3.1.2 | Effects of buffer properties on stream-riparian ecosystems and macroinvertebrate functions

Buffer presence and length altered stream ecosystem attributes (perMANOVA both $p \leq 0.015$), with buffered and unbuffered reaches separated on Axis 1 of the ordination (Figure 1a). Axis 1 reflected decreasing catchment land use, nutrients and thermal maxima. Increasing buffer length was aligned with shading, coarse woody debris, and macroinvertebrate and diatom richness (Figure 1a). Macroinvertebrate functional diversity, algal accrual and the IPS and EPT indices were also positively associated with Axis 1. Axis 2 mainly represented increasing agricultural land use and decreasing upstream riparian connectivity (Figure 1a). Nutrients and some diversity metrics increased along Axis 2, while microbial detritus decomposition, thermal maxima and the EPT and IPS indices declined (Figure 1a).

Buffered and unbuffered sites were separated on Axis 2 in the riparian ecosystem ordination (Figure 1b), with both buffer presence and length significant (both $p < 0.001$). Buffers were positively associated with shade, coarse woody debris, and beetle and tree richness, and negatively with thermal maxima and ground spider richness. Saturated and polyunsaturated fatty acids, and web-building spider richness, aligned with increasing land use on Axis 1 (Figure 1b).

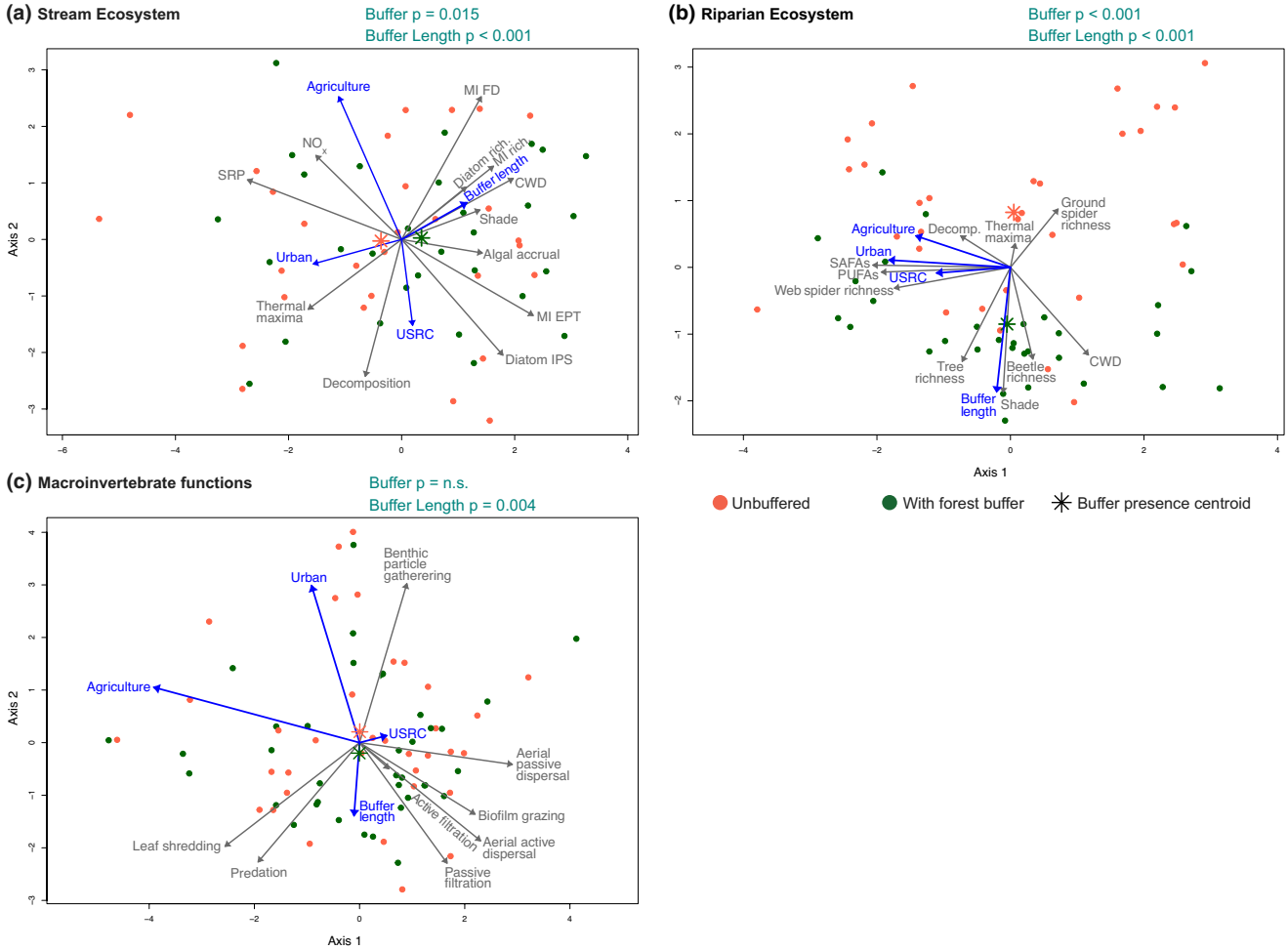

FIGURE 1 nMDS ordination biplots of (a) stream and (b) riparian ecosystems and (c) macroinvertebrate functions, with centroids for buffer presence overlaid. Ecosystem attribute vectors plotted in grey, riparian and land-use predictors in blue. Vector length and direction indicate strength and orientation, respectively, of the association between ordination configuration and each variable. Significance values for buffer presence and length from perMANOVA. All ordinations resolved in three dimensions, first two axes plotted here. Stress: (a) 0.13, (b) 0.12, (c) 0.06. USRC = upstream riparian connectivity, CWD = coarse woody debris, MI = macroinvertebrate, FD = Functional dispersion, SRP=Soluble reactive phosphorus. EPT and IPS are ecological quality indices (see text). Shannon diversity metrics and NH_4 concentrations were excluded from ordinations (a, b) due to high correlation ($r > 0.85$) with richness metrics and SRP, respectively.

Buffer length ($p = 0.004$) but not presence affected macroinvertebrate traits (Figure 1c). Aerial active dispersal and most feeding traits were positively associated with buffer length but negatively with land use on Axis 2. Benthic particle gatherers showed the opposite pattern. Aerial passive dispersal declined with agricultural land use on Axis 1 (Figure 1c).

3.2 | Effects of buffer properties and land use on individual ecosystem properties

3.2.1 | Riparian forest buffer presence

The strongest RFB effects were from buffer presence on the habitat variables stream coarse woody debris, and stream and riparian shading (all $p < 0.001$, Appendices S7 and S8). Predictions for stream woody debris were 190% higher in buffered reaches, and 20%–32% higher for shading (Table 1). Sediment deposition was reduced by a moderate effect of buffer presence ($p < 0.001$), with predicted deposition 46% lower in buffered reaches (Table 1).

Buffer presence had a moderate negative effect on algal biomass accrual and a smaller positive effect on stream microbial carbon processing (both $p \leq 0.013$). Predicted algal accrual was 33% lower and stream litter decomposition 30% higher in buffered reaches (Table 1).

In riparian habitats, buffer presence had large and moderate positive effects on tree richness ($p = 0.002$) and ground beetle richness ($p = 0.043$), with predicted increases of 58% and 44%, respectively (Table 1).

The macroinvertebrate functions biofilm grazing and leaf shredding were altered by small and moderate effects of buffer presence (both $p \leq 0.024$), with predicted increases of 18% and 77%, respectively, in buffered reaches (Table 1).

Several additional buffer presence effects were retained in our models, but were not significant at $p < 0.05$, including small-moderate negative effects on macroinvertebrate richness, ground spider richness and macroinvertebrate gatherers (Appendices S7 and S8).

3.2.2 | Buffer length

Buffer length had small-moderate positive effects on stream ($p < 0.001$) and riparian ($p < 0.024$) shading and on riparian woody debris ($p = 0.036$; Appendices S7–S9, Figures S6b and S8b,c). Increasing buffer length from 0 to 500 m raised predicted stream shading by 31.9% (Figure 2a), with similar outcomes for riparian shading (predicted mean ± SE increase 17.2 ± 7.7%), and riparian woody debris (273%, corresponding to 4.6 ± 4.1 pieces).

Increasing buffer length had moderate and small negative effects on thermal maxima in both habitats (both $p < 0.001$, Appendices S7–S9, Figures S6a and S8a), with increasing buffer length from 0 to 500 m reducing predicted stream and soil thermal maxima by 1.04 ± 0.45°C (12.6%) and 3.72 ± 0.74°C (16.7%), respectively (Figure 2b,c). Further small negative effects retained in our models but not significant at $p < 0.05$ were observed for SRP and ammonium (Appendices S7 and S8).

Macroinvertebrate functional diversity ($p = 0.007$) and Shannon diversity ($p = 0.008$), along with the EPT monitoring index ($p = 0.044$) were altered by small-moderate effects of buffer length (Appendices S7–S9, Figure S6c–e). Increasing buffer length from 0 to 500 m raised predicted Shannon diversity by

TABLE 1 Significant effects of buffer presence on stream-riparian attributes and macroinvertebrate functions, showing effect sizes as standardized model coefficients (β), predicted mean differences ± SE between buffered and unbuffered reaches, and estimated marginal means (EMM) for each reach type.

	Attribute	Effect size (β)	Predicted mean difference (±SE)	EMM unbuffered, buffered
Stream ecosystem	Shading (%)	0.72***	20.4 ± 5.72	30.7, 51.1
	Coarse woody debris (No.)	0.61***	0.95 ± 0.41	0.5, 1.45
	Mineral sediment deposition ($g\,m^{-2}$)[a]	−0.39***	−41.6 ± 45.2	90.4, 48.8
	Algal biomass accrual (μg chl-a $cm^{-2}\,day^{-1}$)	−0.35**	−0.005 ± 0.002	0.015, 0.01
	C processing: microbial ($k\,day^{-1}$)	0.26*	0.012 ± 0.003	0.039, 0.051
Riparian ecosystem	Shading (%)	1.09***	31.8 ± 5.21	29.1, 60.9
	Tree species richness	0.56**	1.49 ± 0.671	2.55, 4.04
	Ground beetle richness	0.38**	0.711 ± 0.38	1.6, 2.31
Macroinvert. functions	Biofilm grazing CWM	0.24*	3.27 ± 1.41	18.3, 21.6
	Leaf shredding CWM	0.36*	2.51 ± 2.57	3.27, 5.78

Note: See Tables S3–S5 for information on all retained terms in the models. In the text, effect sizes are classified following Cohen (1992) as small ($\beta < 0.3$), moderate (0.3–0.5) or large (>0.5). CWM = community weighted mean.

[a]No data for Norwegian case study.

*$p < 0.05$. **$p < 0.01$. ***$p < 0.001$.

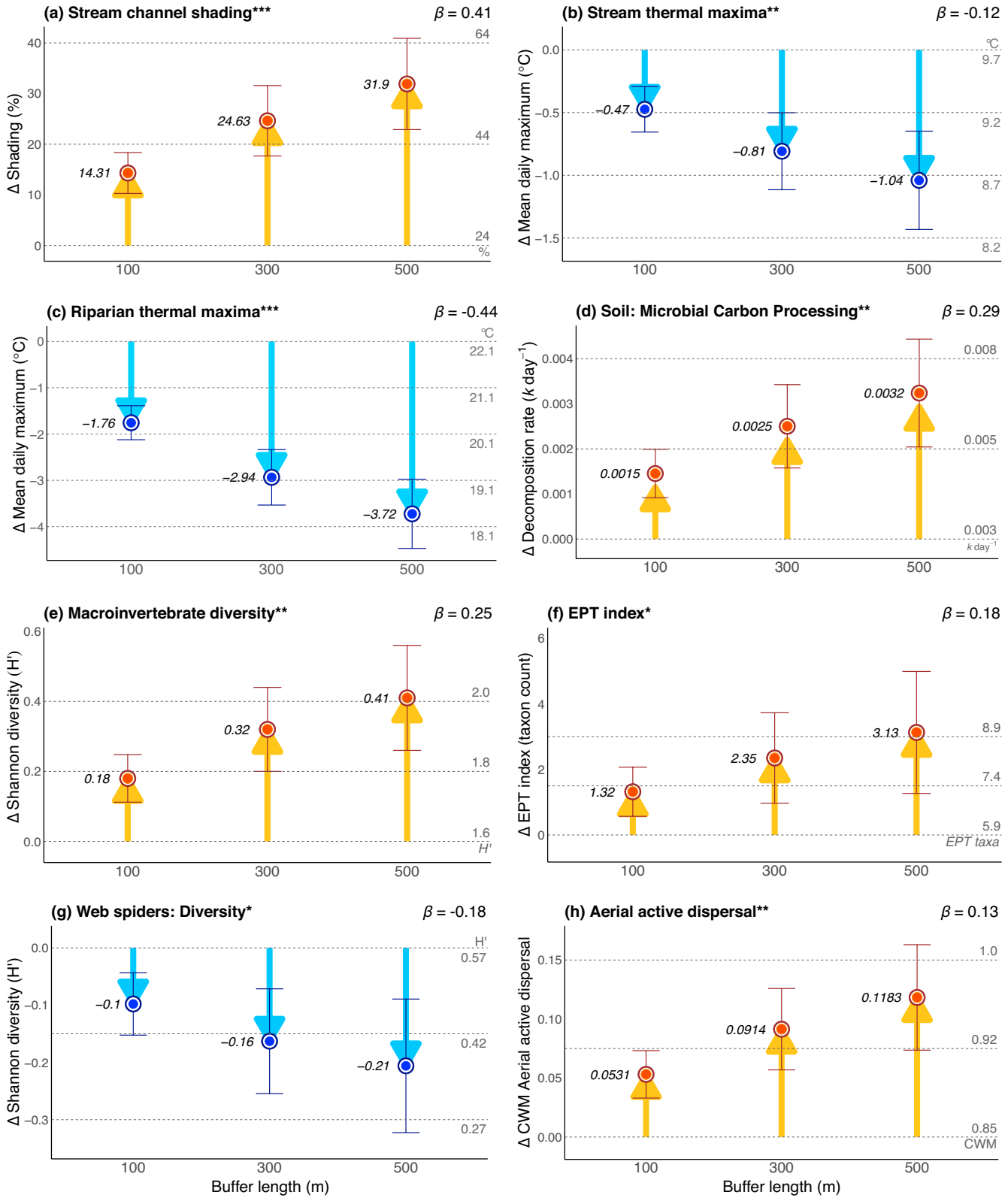

FIGURE 2 Lollipop plots showing predicted effects of increasing buffer length on: (a) stream shading, (b) autumn stream mean daily maximum temperature, (c) late spring–summer riparian mean daily maximum temperature, (d) soil microbial carbon processing, (e) macroinvertebrate diversity and (f) EPT index, (g) web spider diversity and (h) aerial active dispersal capacity of adult aquatic insects. Points indicate differences (Δ, reported in italics) ± SE in predicted EMMs ($\hat{\mu}$) between buffer length = zero and each of 100, 300 and 500 m (the median, 75th and 80th percentiles of buffer lengths). Reference lines show EMMs corresponding to selected levels of Δ. Significance levels: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$. β = standardized regression coefficient for buffer length. See Appendix S7, Tables S3–S5 for information on all retained terms in the models. CWM = community weighted mean.

25% (Figure 2e) and EPT by 53% (~3 taxa, Figure 2f), with a similar outcome for functional dissimilarity (20%, corresponding to an increase of 0.96 ± 0.41).

In riparian habitats, buffer length had moderate positive and weak negative effects, respectively, on microbial carbon processing and Shannon diversity of web-building spiders (both $p < 0.002$, Appendices S7–S9, Figure S8d,e). An increase in buffer length from 0 to 500 m is predicted to increase soil cellulose decomposition by 167% (Figure 2d) and reduce web spider diversity by 36% (Figure 2g).

Among macroinvertebrate functions, only aerial active dispersal was affected by buffer length ($p = 0.010$, Appendices S7–S9, Figure S9a), with a small effect driving a predicted increase of 14% from 0 to 500 m (Figure 2h).

Additional effects of buffer length retained in our models but not significant at $p < 0.05$ included small positive effects on macroinvertebrate richness and predation traits (Appendices S7 and S9).

3.2.3 | Upstream riparian connectivity

Moderate upstream riparian connectivity effects were detected on stream ecosystem attributes (Appendix S7–S9, Figure S6f–h), including negative effects on SRP ($p = 0.009$) and diatom richness ($p = 0.026$), and a positive effect on the diatom IPS index ($p = 0.014$). As mean spacing among upstream riparian forest blocks decreases from 500 to 25 m, SRP is predicted to decline by 50.7 μg L^{-1} (61%), diatom richness by 20% (7 species) and IPS to increase by 14% (Figure 3a–c). A small negative effect on stream thermal maxima was also retained, but was not significant at $p < 0.05$ (Appendix S7).

3.2.4 | Land use and interactions with buffer presence

Agriculture and urban land use had small-moderate positive effects on ammonium ($p < 0.04$), and agriculture on sediment deposition ($p = 0.023$), while a small buffer × agriculture interaction altered SRP ($p = 0.044$, Appendices S7–S9, Table S3, Figure S7a). Predicted SRP was 46% lower in buffered reaches at the 85th percentile of the agriculture gradient (Figure 4a). Ammonium showed a similar response, not significant at $p < 0.05$ (Appendix S7). Riparian woody debris was affected by a moderate buffer × agriculture interaction ($p = 0.046$), with more debris in buffered reaches at low, but not high, land use (Appendices S7–S9, Figure S8f).

Agriculture had large and moderate negative effects on stream microbial carbon processing ($p = 0.008$) and algal accrual ($p = 0.03$), and urban land use had a large positive effect ($p = 0.005$) on algal accrual (Appendix S7, Table S3). Small buffer × land-use interactions influenced algal accrual (urban; $p = 0.006$) and terrestrial predator saturated fatty acid (SAFA) (agriculture; $p = 0.006$, Appendices S7–S9, Tables S3 and S4, Figures S7b and S8g). Predicted algal accrual declined in buffered reaches with increasing urban land use, reaching 50% lower rates at the 85th percentile (Figure 4b). SAFA content was 20% higher in buffered reaches at the 85th percentile of the agriculture gradient (Figure 4c). A small near-significant buffer × agriculture interaction ($p = 0.052$) for stream carbon processing reflected a trend for increasing decomposition in buffered reaches along the agricultural land-use gradient (Appendix S7, Table S3).

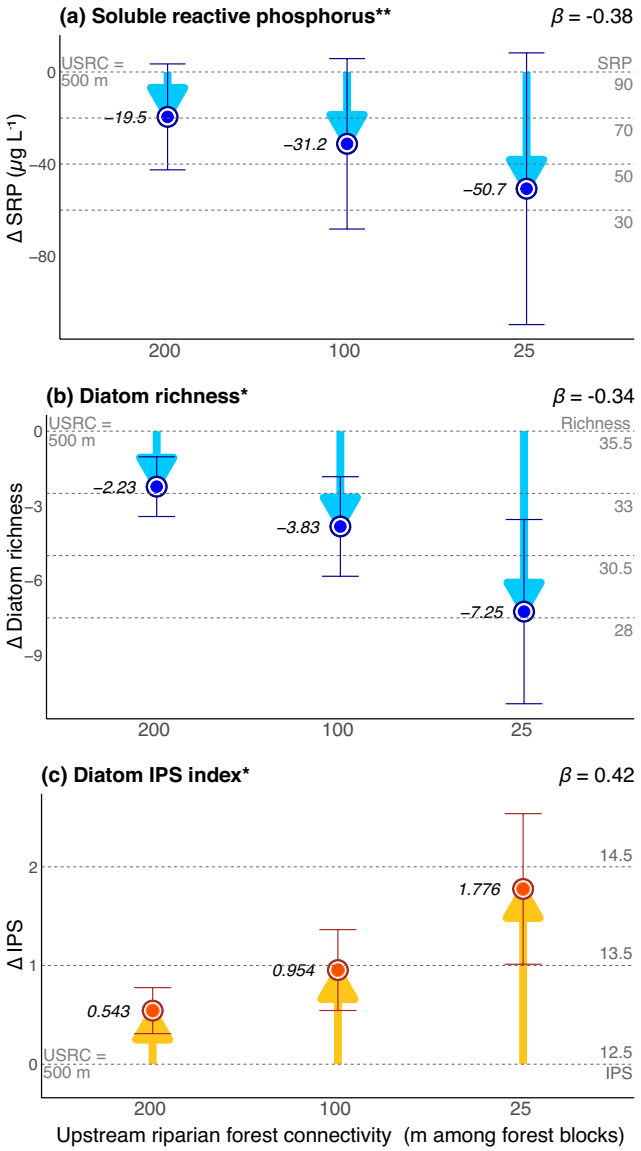

FIGURE 3 Lollipop plots showing predicted effects of increasing upstream riparian forest connectivity (USRC, quantified as decreasing mean distance among forest blocks) on reach-scale (a) soluble reactive phosphorus and diatom (b) richness and (c) IPS index. Points indicate differences (Δ, reported in *italics* adjacent to each plot) ± SE in EMMs ($\hat{\mu}$) between USRC = 500 m and each of 200, 100 and 25 m (the median, 75th and 85th percentiles of the USRC gradient). Reference lines show EMMs on the original scale corresponding to selected levels of Δ. Significance levels: $^{*}p < 0.05$, $^{**}p < 0.01$. β = standardized regression coefficient for USRC. See Appendix S7, Table S3 for information on all retained terms in the models.

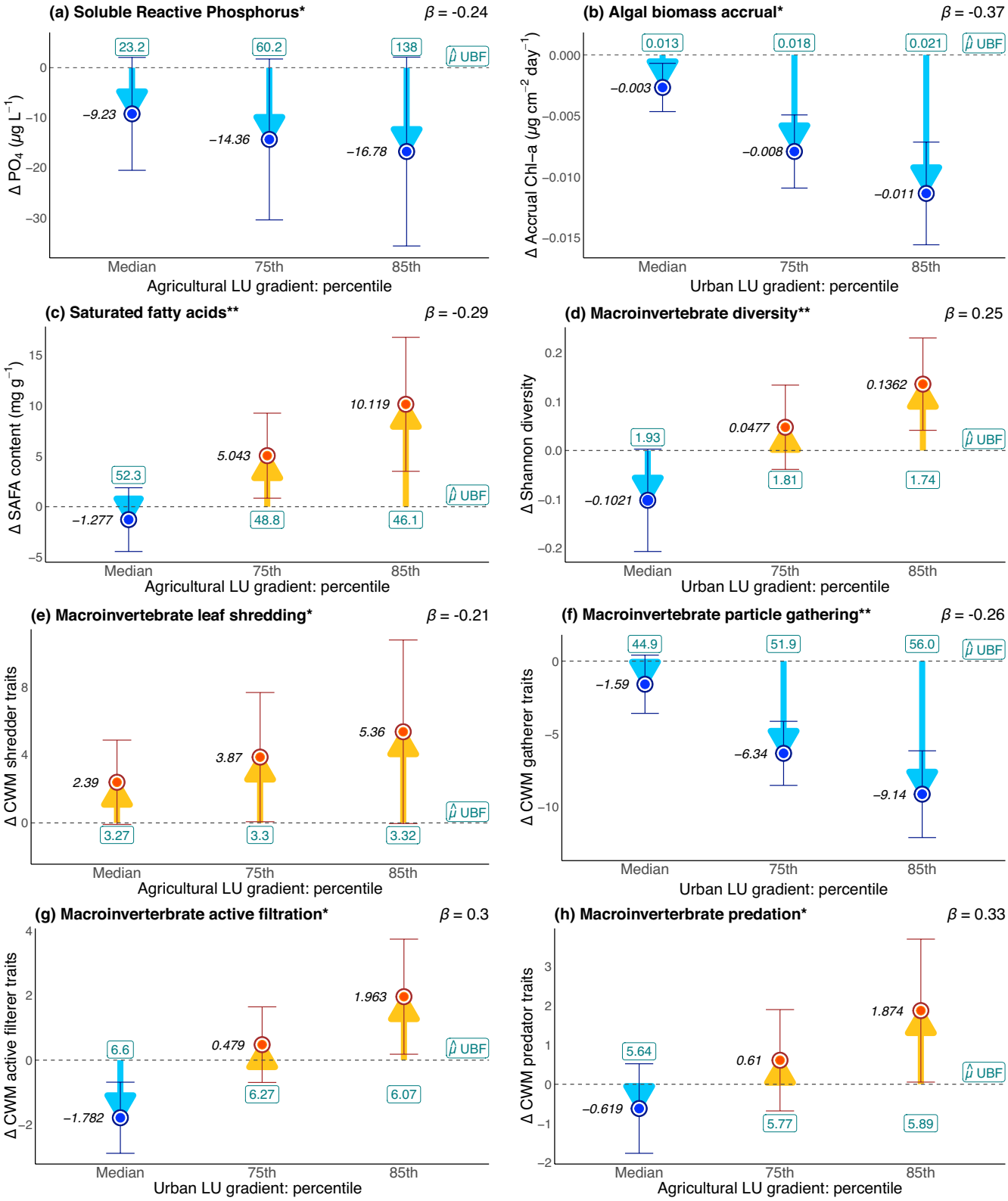

FIGURE 4 Lollipop plots showing predicted differences between unbuffered and buffered sites at the median, 75th and 85th percentiles of either the agricultural (a, c, e, h) or urban (b, d, f, g) land-use (LU) gradients: (a) soluble reactive phosphorus, (b) algal biomass accrual, (c) saturated fatty acid (SAFA) content in terrestrial consumers, (d) macroinvertebrate Shannon diversity, and the macroinvertebrate functions (e) leaf shredding, (f) benthic particle gathering, (g) active filtration, (h) predation. Error bar plots show the difference (Δ, reported in *italics* adjacent to each plot) ± SE in predicted EMMs between buffered and unbuffered reaches at each percentile, based on estimated marginal means ($\hat{\mu}$). The reference line represents zero difference between reach types, with $\hat{\mu}$ for the unbuffered sites (UBF) indicated in the boxes. Significance levels for buffer by land-use interaction: $^{*}p < 0.05$, $^{**}p < 0.01$. β = standardized regression coefficient for the interaction term. See Tables S3–S5 for information on all retained terms in the models. CWM = community weighted mean.

Urban land use had moderate to strong negative effects on all macroinvertebrate community metrics (All $p < 0.017$, Appendices S7 and S8, Table S3). Shannon ($p = 0.017$) and functional ($p = 0.035$) diversity were affected by small-moderate buffer × urban interactions (Appendices S7–S9, Figure S7c,d). Shannon diversity was predicted to be 8% higher in buffered reaches at the 85th percentile of the urban gradient (Figure 4d), with outcomes for functional diversity similar (5% increase, or 0.23 ± 0.25 higher).

Agriculture had a small negative effect on the macroinvertebrate grazing traits, while urban land use had moderate-large negative effects on passive filtration and predation, and a large positive effect on particle gathering (all $p \leq 0.043$, Appendices S7 and S8, Table S5). Small-moderate positive buffer × land-use interactions (Appendices S7–S9, Figures S9b,d,e) altered leaf shredding (agriculture; $p = 0.049$), predation (agriculture; $p = 0.016$) and active filtration (urban; $p = 0.033$) traits. Predicted trait CWMs were 32%–131% higher in buffered reaches at the 85th percentile of the gradient (Figure 4e,g,h). Particle gathering was affected by a negative buffer × urban interaction ($p = 0.016$, Appendices S7–S9, Figure S9c), with 16% lower predicted trait values in buffered reaches at high urban land use (Figure 4f).

Additional buffer × land-use interaction effects on macroinvertebrate traits were retained in our models, but were not significant at the 5% level, including positive interactions between buffers and urban land use for predation and aerial passive dispersal, and negative buffer × agriculture interactions for gathering and aerial passive dispersal (Appendix S7, Table S5).

4 | DISCUSSION

Our spatially extensive field study reveals multiple benefits of riparian forest buffers (RFBs) for stream-riparian ecosystems in human-modified landscapes and identifies key factors regulating these outcomes, including buffer size, upstream riparian forest connectivity, and land use. As hypothesized, RFB presence and/or increasing buffer length dampened land use (nutrients, sediments) and climate-related (thermal maxima) stressors and altered habitats by providing shade and coarse woody debris. RFBs further helped support diversity of several organism groups and microbial carbon processing in both terrestrial and aquatic habitats, fatty acid content in terrestrial predators, and multiple stream invertebrate functions. Several buffer effects were contingent on land use, and landscape configuration was a further modulating factor, with closer proximity among upstream forest blocks linked to lower phosphate concentrations and higher scores for the diatom IPS ecological status index. Some negative outcomes were also detected, highlighting the need to balance the benefits of RFBs with those of unforested habitats in riparian restoration planning.

RFBs are expected to provide shade, but their capacity to improve other aspects of environmental quality over small spatial scales has been less certain (Brumberg et al., 2021; Cole et al., 2020; Kail et al., 2021). Despite 88% of our buffers being <500 m long, we detected moderate-strong effects on several habitat properties relative to adjacent unbuffered reaches. RFBs increased coarse woody debris, a key habitat feature that shapes channel morphology and flow heterogeneity, and supports diverse biota, including wood-adapted specialists (McKie & Cranston, 1998; Wohl et al., 2016). Furthermore, RFBs reduced deposition of inorganic sediment, a pervasive agricultural stressor that buries substrates and interferes with activities of diverse organisms, including algae and invertebrate and vertebrate consumers (Burdon et al., 2013; Jones et al., 2012; Truchy et al., 2022). Reduced sediment deposition is likely driven by the greater bank stability, increased hydraulic roughness and enhanced sediment retention associated with tree roots and woody debris (Mundahl et al., 2023; Wohl et al., 2016).

Mean daily maximum temperatures declined in both stream and riparian habitats as buffer length increased, highlighting the role of sustained shading over extended stream lengths in supporting development of RFBs as 'climate envelopes' (Johnson & Almlöf, 2016; Kail et al., 2021). The effect size was smaller in stream than riparian habitats, reflecting the greater thermal inertia of continuously flowing water (Caissie, 2006). Nevertheless, model predictions indicate longer RFBs could reduce thermal maxima in both habitats by several degrees, a difference that may be biologically meaningful during summer heat waves (Broadmeadow et al., 2011). Buffers also moderated land-use effects on nutrients, with SRP increasing more slowly along the agricultural gradient in buffered reaches. Potential mechanisms include nutrient sequestration in vegetation and soils, coupled with reduced transport of fine sediment that acts as a nutrient vector, particularly for phosphorus (Kumwimba et al., 2024; Sandström et al., 2020). Additionally, greater upstream riparian connectivity was associated with lower SRP at local scales, with a similar, near-significant effect also retained in our model for stream thermal maxima. This provides evidence that more densely spaced RFB networks can cumulatively dampen stressors and benefit downstream habitats (Witing et al., 2022).

By increasing shading, adding habitat elements (including woody debris), and moderating temperature, nutrients and sediments, RFBs can reduce environmental stress and support biodiversity. Consistent with this, increasing buffer length had small-moderate positive effects on macroinvertebrate Shannon and functional diversity, and the EPT biomonitoring index. Additionally, buffers dampened declines in macroinvertebrate diversity as urban land use increased. Together, these results provide evidence that RFBs can support sensitive species and more even, functionally diverse macroinvertebrate communities in degraded landscapes. Longer buffers also supported more aquatic insects with strong adult dispersal traits, which are often associated with larger-bodied and environmentally sensitive species, highlighting the potential of buffers to enhance stream-riparian connectivity (Burdon et al., 2025; McKie et al., 2018). Terrestrial biodiversity outcomes were more mixed. Taxon richness of riparian trees and hunting invertebrate predators increased with buffer presence, whereas Shannon diversity of web-building spiders declined with increasing buffer length. This may reflect reduced availability and/or diversity of suitable web-building

substrates (e.g. bushes, semi-aquatic sedges) in RFB reaches (Chan et al., 2009), at least in the near-ground zone we sampled.

Diatom responses were driven by upstream riparian configuration rather than local buffer properties. Species richness increased where riparian forest blocks were more widely spaced, suggesting greater open habitat upstream supports higher diatom richness per se at local scales. This might be consistent with a dispersal driven 'mass effect', postulated to be an important process structuring diatom communities (Göthe et al., 2013), where immigration from surrounding open habitats maintains high diversity per se at local scales. In contrast, the IPS biomonitoring metric improved where upstream riparian forest blocks were more closely spaced. This indicates a denser RFB network helps support some environmentally sensitive diatom species, such as those known to be favoured at lower light, temperature and nutrient levels (Hill et al., 2011; Lange et al., 2011).

RFBs modified both green and brown trophic pathways in stream-riparian food webs. Algal biomass accrual declined in shaded reaches, as hypothesized, but macroinvertebrate grazing traits unexpectedly increased. Reduced sedimentation rates in RFB reaches may have aided grazers by reducing sediments in benthic biofilms, improving biofilm food quality (Burdon et al., 2013; Rabení et al., 2005). Shading may also favour diatoms over less palatable cyanobacteria (Guo et al., 2015; Stevenson, 2014). We hypothesize that these conditions help promote more specialized, environmentally sensitive invertebrate grazer species in buffered reaches (Truchy et al., 2022). Macroinvertebrate leaf shredding traits were also more abundant in buffered reaches, and RFB presence and increasing length enhanced microbial detritus decomposition in streams and soils, respectively. These results indicate a likely stimulation of detrital energetic pathways linked to the increase in availability of allochthonous detritus and possibly greater moisture retention in riparian soils (Frainer et al., 2018; Riis et al., 2020).

Land-use effects on food web processes were often modified in buffered reaches. Negative effects of urban land use on algal biomass accrual were amplified in buffered reaches, which we hypothesize reflect combined effects of shading from riparian forest and urban infrastructure, and possibly effects of additional urban stressors on biofilms (e.g. chemicals in runoff, Carles et al., 2021). Buffers also altered land-use effects on macroinvertebrate particle gathering traits, often linked with tolerant species characteristic of degraded conditions (Burdon et al., 2013), which increased along the urban gradient overall, but not in buffered reaches (a similar non-significant interaction between buffer presence and agriculture was also retained in our models). In contrast, buffers reduced negative urban land-use effects on active filtration and enhanced positive agriculture land-use effects on leaf shredding and predation traits. These findings likely reflect improved habitat conditions and—in agricultural streams—possibly also nutrient-driven enhancement of detritus food quality and prey productivity for predators (Davis et al., 2010; Gulis et al., 2006). Saturated fatty acids were higher in terrestrial predators from RFBs at higher levels of agricultural land use, suggesting greater energy storage. More research is required on the potentially cascading consequences of these changes, including for ecosystem metabolism and higher predators. Nevertheless, these results highlight the potential for buffered reaches to act as hotspots supporting diverse food web functions in degraded landscapes.

The buffer effects identified here are most relevant for smaller (2nd–3rd order), mid- to low-altitude, temperate and boreal streams under similar land-use pressures to those we investigated. Our urban-gradient results are thus likely most applicable to cities comparable to Oslo in size (700,000 residents and 500 km^2), which have extensive existing green infrastructure (Łaszkiewicz et al., 2022). However, findings for upstream riparian connectivity may be less transferable to urban settings, as most variation in this predictor variable occurred across the agricultural catchments (Appendix S4). Most of our agricultural reaches are morphologically typical of European lowland agricultural streams (straightened and narrowed, high suspended sediments), although the Belgian catchment is subject to notably extreme inputs of untreated wastewater (Forio et al., 2020). The positive RFB effects on nutrients, sediments and biodiversity under these conditions are promising, but high variability in some responses (e.g. SRP, sediment reduction, leaf shredding) underscores the need for further evaluation across a broader range of human-modified landscapes to improve predictions.

We emphasize that the RFBs evaluated here were well-established, comprising either remnant forest patches that have expanded over recent decades, or reforestation commenced during the 1990s or earlier. Thus, our findings primarily reflect effects of mature buffers with developed canopies and root systems, and highlight the value of planning riparian rehabilitation around existing forest fragments. However, temporal dynamics in buffer effects, including seasonal variation and longer-term trajectories, require more research. In particular, the pace at which biodiversity and ecosystem functioning respond to new riparian reforestation remains poorly understood (Englund et al., 2021; Giraldo et al., 2022), with assessments typically focused on short- to medium-term sediment, nutrient, bioenergy or flood-management outcomes rather than ecological responses (Dunn et al., 2022; Weigelhofer et al., 2012; Wilts et al., 2024).

Continuous reforestation of all available riparian habitat is unlikely to be optimal in all catchments. Rather, the challenge is to design spatially heterogeneous riparian habitats that maximize biodiversity, ecosystem functioning and connectivity at the catchment scale (Witing et al., 2022). This requires RFB planning that balances trade-offs, not only those observed in this study but also trade-offs with, for example open habitats supporting flowering plants and pollinators, and existing land uses (Broadmeadow & Nisbet, 2004; Cole et al., 2015; Graziano et al., 2022). Encouragingly, we detected multiple ecological benefits of our RFBs despite their generally small size, suggesting that even modest increases in buffer number and size could improve environmental quality, biodiversity and ecosystem function (Forio et al., 2020; Kowarik et al., 2023; Witing et al., 2022). Further research is needed to identify buffer configurations that maximize cumulative benefits across spatial scales, and the potential

for ongoing adjustment in buffer configurations as a component of adaptive management to environmental change. Nevertheless, the multiple benefits of RFBs documented here support their expanded use as nature-based solutions in agricultural and urban landscapes.

AUTHOR CONTRIBUTIONS

Brendan G. McKie, Nikolai Friberg, Martin Volk, Geta Rîşnoveanu, Peter Goethals, Richard K. Johnson, Maria Kahlert and Francis J. Burdon conceived the ideas and designed the field studies and methodology; Francis J. Burdon, Marie Forio, Benjamin Kupilas, Petra T. Mutinova, Cristina Popescu, Darmina Niță, Geta Rîşnoveanu, Valentin Dinu, Mihaela Sava, Jasmina Sargac and Ellinor Ramberg collected the data; Felix Witing generated GIS-based metrics. Brendan G. McKie and Maria Kahlert harmonized taxonomic data. Brendan G. McKie, Francis J. Burdon and Amélie Truchy designed the statistical analyses. Brendan G. McKie analysed the data, created plots and led writing. All authors edited drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

We have no conflicts of interest to disclose.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.2280gb67r (McKie et al., 2026).

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SUPPORTING INFORMATION

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

Appendix S1. Spatial distribution of sampling sites and detailed site-selection criteria.

Figure S1. (a) Map showing location of paired reaches in the Norwegian, Swedish, Belgian and Romanian case study basins in relation to land use and river networks; (b) Spatial arrangement of paired sample reaches on a single study stream, with the unbuffered (UBF) placed upstream of the start of the forest buffer, and the riparian forest buffer (RFB) placed at the downstream end of the buffer.

Appendix S2. Field measurements: Overview of methods and timing.

Figure S2. Biplot of principal component analysis of local and catchment scale characteristics of our stream reaches. The biplot depicts vectors for catchment land use/land cover (black labels) and local channel (brown text) characteristics, with country identity overlaid.

Appendix S4. Comparison of four continuous predictor variables among the levels of the random block factor Country.

Figure S3. Box plots for comparison of the data distribution of the continuous predictors used in the linear mixed models among the levels of the random blocking factor: Country: (a) Spacing among upstream riparian blocks (blue) and buffer length (green); (b) The agricultural (pink) and urban (grey) LUI gradients.

Appendix S5. Ecosystem attribute sets.

Table S1. Composition of ecosystem attribute sets from (1) stream and (2) riparian habitats, and (3) macroinvertebrate functions.

Appendix S6. Additional results Geomorphology.

Table S2. Mean ± 1 standard deviations for the geomorphological variables included in Figure S4, presented as global values and broken down by country.

Figure S4. nMDS ordination of stream reach geomorphology. Sites plotted as points and buffer presence centroids as asterisks (light red = buffer absent, dark—green = buffer present). Vectors for geomorphological variables are plotted in light grey, with vectors for catchment level predictors (Agricultural and Urban land use, and upstream riparian forest connectivity, USRC) and buffer length overlaid in blue. Ordination in 3 dimensions, first two axes plotted. Stress = 0.12. Neither buffer presence nor length affected these geomorphological attributes (perMANOVA both $p > 0.22$).

Appendix S7. Retained effects in LMMs for stream-riparian attribute sets 1–3: Effect sizes and significance.

Table S3. Linear mixed models of variables in the stream ecosystem attribute set: Effect sizes (standardized regression coefficients β) for main effects and interactions retained following model reduction based on the conditional Akaike's information criteria. The goal of model selection is to identify the most parsimonious description of the data; non-retention of terms does not imply ecological irrelevance, but rather a lack of support in the present dataset. In the text, effect sizes are classified following Cohen (1992) as small ($\beta < 0.3$), moderate (0.3–0.5) or large (>0.5).

Table S4. Linear mixed models of variables in the riparian ecosystem attribute set: Effect sizes (standardized regression coefficients) for main effects and interactions retained following model reduction based on the conditional Akaike's information criteria. The goal of model selection is to identify the most parsimonious description of the data; non-retention of terms does not imply ecological irrelevance, but rather a lack of support in the present dataset. In the text, effect sizes are classified following Cohen (1992) as small ($\beta < 0.3$), moderate (0.3–0.5) or large (>0.5).

Table S5. Linear mixed models of variables in the macroinvertebrate functions attribute set: Effect sizes (standardized regression coefficients) for main effects and interactions retained following model reduction based on the conditional Akaike's information criteria. The goal of model selection is to identify the most parsimonious description of the data; non-retention of terms does not imply ecological irrelevance, but rather a lack of support in the present dataset. In the text, effect sizes are classified following Cohen (1992) as small ($\beta < 0.3$), moderate (0.3–0.5) or large (>0.5).

Appendix S8. Graphical summary of all retained effect sizes.

Figure S5. Effect sizes (standardized β-coefficients ±95% CI) for terms retained in GLMMs of (a) riparian forest properties and (b,c) the land-use gradients and their interactions with buffer presence, on ecosystem attributes (Table S1). Attribute colours: dark grey = habitat element, red = environmental buffering, purple = food web attribute, green = community metric, dark blue = invertebrate function. In the text, effect sizes are classified following Cohen (1992) as small ($\beta < 0.3$), moderate (0.3–0.5) or large (>0.5).

Appendix S9. Fitted value regressions overlaid on raw data.

Figure S6. Effects of the total forest buffer length (a–e) and upstream riparian forest connectivity (f–h) on stream ecosystem attributes: (a) mean daily maximum temperatures, (b) channel shading, (c–e) macroinvertebrate Shannon diversity, functional diversity and EPT index, (f) soluble reactive phosphorus, (g–h) diatom richness and IPS index. Graphs depict linear models based on fitted values from GLMMs overlaid onto raw data, with 95% confidence interval. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. See Table S3 for standardized model coefficients. See main text Figures 2 and 3 for specific model-based predictions.

Figure S7. Interactions between buffer presence and the agricultural (a) and urban (b–d) land use gradients on stream (a) soluble reactive phosphorus concentrations, (b) algal biomass accrual and macroinvertebrate (c) Shannon diversity and (d) functional dissimilarity. Graphs depict linear models based on fitted values from GLMMs overlaid onto raw data, with 95% confidence interval. $^{*}p < 0.05$, $^{**}p < 0.01$. See Table S3 for standardized model coefficients. See main text Figure 4 for specific model-based predictions.

Figure S8. Effects of total forest buffer length (a–e) and interactions between buffer presence and the agricultural land use gradient (f–g) on riparian ecosystem attributes: (a) mean daily maximum temperatures, (b) channel shading, (c) coarse woody debris, (d) microbial carbon processing, (e) web spider Shannon diversity (f) coarse woody debris, (g) invertebrate predator saturated fatty acid content. Graphs depict linear models based on fitted values from GLMMs overlaid onto raw data, with 95% confidence interval. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$. See Table S4 for standardized model coefficients. See main text Figures 2 and 4 for specific model-based predictions.

Figure S9. Effects of total forest buffer length (a) and interactions between buffer presence and the agriculture- (b, e) and urban (c, d) land use gradients on macroinvertebrate functions, quantified as community weighted mean (CWM) trait affinities: (a) aerial active dispersal, (b) leaf shredding, (c) benthic particle gathering (d) active filter feeding, (e) predation. Graphs depict linear models based on fitted values from GLMMs overlaid onto raw data, with 95% confidence interval. $^{*}p < 0.05$, $^{**}p < 0.01$. See Table S5 for standardized model coefficients. See main text Figures 2 and 4 for specific model-based predictions.

Appendix S10. References for supplementary material.

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