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RESEARCH ARTICLE

Context-specific positive effects of woody riparian vegetation on aquatic invertebrates in rural and urban landscapes

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Abstract

1. Woody riparian vegetation (WRV) benefits benthic macroinvertebrates in running waters. However, while some functions are provided by WRV irrespective of surrounding and catchment land use, others are context-specific. In recent large-scale studies, effects of WRV on macroinvertebrates were therefore small compared to catchment land use, raising the question about the relevance of WRV for restoration.
2. Model-based recursive partitioning was used to identify context-dependent effects of WRV on the macroinvertebrates' ecological status in small (catchment area 10–100 km^2) lowland ($n = 361$) and mountain ($n = 748$) streams. WRV cover was quantified from orthophotos along the near (500 m) and far (5000 m) upstream river network and used to predict the site's ecological status. Agricultural, urban and woodland cover at the local and catchment scales along with hydromorphology were considered as partitioning variables.
3. In rural agricultural landscapes, the effect of WRV on the ecological status was large, indicating that establishing near-upstream WRV can improve the ecological status by as much as two of the five classes according to the EU Water Framework Directive.
4. Even in urban landscapes, effects of far-upstream WRV were large if catchments had a moderate share of agricultural land use in addition. The beneficial effects of WRV were only limited in purely urban catchments or in a multiple stressor context.
5. *Synthesis and applications*. While woody riparian vegetation (WRV) can even improve the ecological status in urban settings, it is especially relevant for river management in rural agricultural catchments, where developing WRV potentially are effective measures to achieve good ecological status.

KEYWORDS

agricultural land use, macroinvertebrates, river restoration, urbanization, woody riparian vegetation

1 | INTRODUCTION

In temperate regions most streams and rivers are naturally bordered by trees (Ellenberg, 1988), which influence several aquatic ecosystem processes benefitting riverine biota. These functional links between woody riparian vegetation (WRV), ecosystem processes and biota have been intensively studied and reviewed (e.g. Broadmeadow & Nisbet, 2004; Sweeney & Newbold, 2014). For example, in reaches bordered by WRV, shares of shredding macroinvertebrates were higher than in open reaches (Turunen et al., 2019), indicating the role of leaves as a food source (Lecerf & Richardson, 2010). Biomass and abundance of macroinvertebrates were lower in shaded stream reaches due to lower water temperature and light availability (Kaylor & Warren, 2018; Smith, 1980) limiting instream primary production (Parkyn et al., 2003). With decreasing canopy cover, the abundance of tolerant taxa strongly increased at the expense of sensitive taxa (Kiffney et al., 2003). The decline of sensitive taxa also reflects associated increases in fine sediment input and siltation (Davies & Nelson, 1994). Additionally, sensitive taxa benefit especially from the retention of pesticides by WRV (Bunzel et al., 2014).

The largest effects of WRV on benthic invertebrates are expected in agricultural floodplains, where diffuse nutrient, fine sediment and pesticide input occurs, and from wide and long WRV patches. This is because only some of the functions mentioned above are provided irrespective of adjacent land use and spatial scale, while others are context-specific. Independent of adjacent land use, WRV provides organic material like leaves, twigs and large wood that serve as food and habitat (Oelbermann & Gordon, 2000) or promotes natural channel patterns and dynamics through large wood inputs (Kail et al., 2009) and bank stabilization (Parkyn et al., 2003). Other functions are context specific. Retention of nutrients, fine sediment and pesticides (Arora et al., 2010; Gericke et al., 2020; Ramesh et al., 2021) is only relevant if the adjacent floodplain is actually covered by agricultural fields. Moreover, shading limits primary production and reduces water temperature, which prevents excessive phytobenthos and macrophyte growth especially in streams with high nutrient concentrations (Kiffney et al., 2003; Nebgen & Herrman, 2019). Besides floodplain land use, effects of these functions also depend on the width and length of WRV patches. While already rather narrow, 10 m-wide buffers effectively retain sediments, much wider buffers >20 m are needed to retain nitrogen (Zhang et al., 2010). Shading by WRV causes lower equilibrium water temperatures already after a few hundred meters of continuous canopy cover (Kail et al., 2021), whereas the positive effect of reducing nutrient, fine sediment and pesticide input rather accumulates over long distances (Feld et al., 2018). Although effects of WRV on river biota such as macroinvertebrates are therefore potentially context-specific and likely largest in rivers bordered by agricultural areas, there is little evidence for this and under which conditions, the effects of WRV on macroinvertebrates are largest (but see Effert-Fanta et al., 2019; Tolkkinen et al., 2021). This is relevant for river management because establishing WRV is a widely used restoration measure.

Many studies using standard-resolution land use data have shown that catchment, especially urban, land use has a much larger effect on benthic invertebrates than riparian land use or local habitat conditions (Lorenz & Feld, 2013). This is crucial since main urban stressors like wastewater and stormwater run-off are point sources, which cannot be mitigated by WRV, in contrast to agricultural diffuse source pollution. Furthermore, recent large-scale empirical studies using high resolution data on WRV indicate that catchment land use masks or overrides effects of WRV on macroinvertebrates (Burdon et al., 2020; Le Gall et al., 2022; Palt et al., 2022). This raises the question, in which catchments WRV has positive effects on macroinvertebrates, a biological quality indicator for applied river management.

Against this background, we hypothesized that the effect of WRV on benthic invertebrates is context specific and aimed at identifying conditions, under which WRV has significant positive effects on benthic invertebrates in regression models. Specifically, we first expected that WRV has largest effects in agricultural landscapes, because several of its functions are mainly linked to agricultural land use in the floodplain. Second, we expected WRV far-upstream to be more important compared to near-upstream WRV, since positive effects of some functions potentially accumulate downstream. Third, we expected stressors related to urban catchment land use like point source pollution and stormwater run-off to limit or even override the positive effects of WRV.

2 | MATERIALS AND METHODS

2.1 | Biological data

Data on macroinvertebrate samples from small lowland (n = 361; 18–189 m MSL) and small mountain streams (n = 748; 58–594 m MSL), taken between 2004 and 2013, were acquired from the three German federal states Hesse, North Rhine-Westphalia, and Saxony-Anhalt (Figure 1). No ethical approval is required for the use of such monitoring data. Sites in lowlands and mountains were analysed separately due to assumed differences in the interaction of aquatic and terrestrial environments.

Macroinvertebrate samples were taken according to the multi-habitat sampling method described in Haase et al. (2004). The species-level taxa lists were processed using the online tool PERLODES (https://www.gewaesser-bewertung-berechnung.de/index.php/perlodes-online.html), which among others computes the river-type specific multimetric index (MMI). The MMI is the core component used to assess the ecological status according to EU Water Framework Directive and to derive restoration needs for river management in Germany. It ranges from 0 and 1 and is divided in five equidistant ecological status classes (bad, poor, moderate, good, high). The MMI reflects the impact of various stressors like hydromorphological degradation, altered hydrology and impacts of land use (Böhmer et al., 2004).

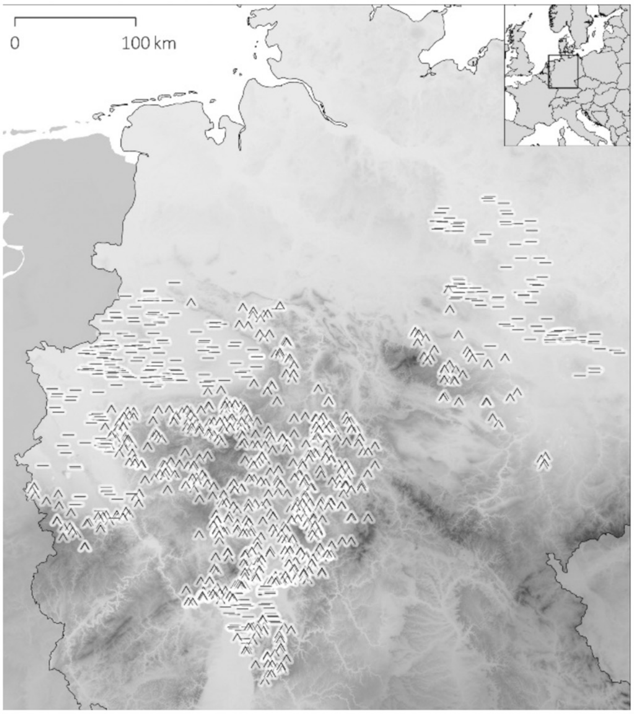

FIGURE 1 Location of macroinvertebrate sampling sites in Germany: Bars show lowland and chevrons mountain streams.

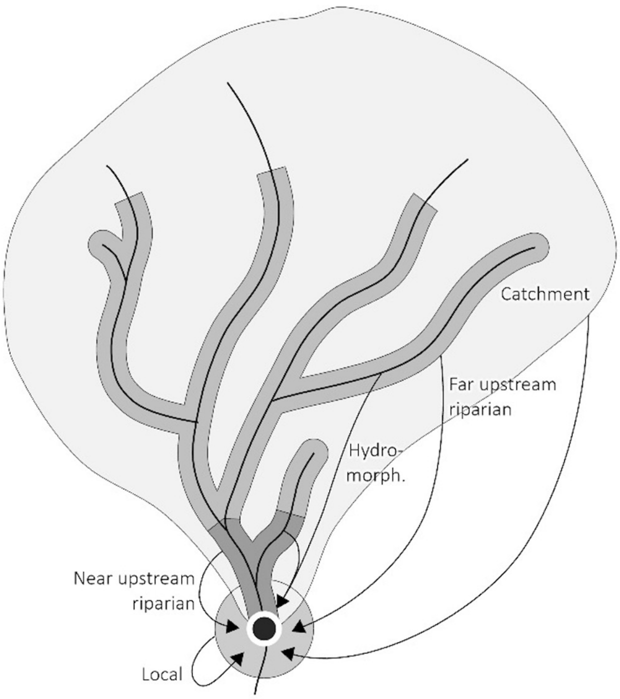

FIGURE 2 Land use was assessed in the catchment, in a circle with a radius of 250 m around the sampling sites and at two upstream lengths of riparian buffers (30 m to either streamside): Near-upstream extents for 500 m, and far-upstream for 5000 m, respectively. Hydromorphological assessments were aggregated for both upstream lengths.

The dataset was pre-processed to exclude data of insufficient quality: Only samples with at least 5 taxa and samples taken between December 1st and April 30th were included to guarantee reliability and comparability. For the same reason, samples with a saprobic index >2.7 were excluded, as these correspond to polluted streams affected by point sources. Sites with barriers within 5000 m upstream of the sampling site were excluded, since these trap sediments, alter the thermal regime to varying degrees, and therefore potentially mask sediment retention and shading by WRV.

2.2 | Riparian land use

Upstream riparian buffers were demarcated for each sampling site at two spatial scales, starting at the sampling site and extending 500 and 5000 m upstream, respectively (Figure 2), referred to as near-upstream and far-upstream in the following. Riparian buffers were delineated using ESRI ArcView (Version 3.3) and included tributaries. Laterally, they covered 30 m to either side starting from the stream banks, hence excluded the water surface, quantifying terrestrial land use only. Water surfaces were taken from official ATKIS landcover data (Amtliches Topographisch-Kartographisches Informationssystem; www.adv-online.de/Products/Geotopography/ATKIS/). For small streams not included as water surfaces in ATKIS, the wetted width was approximated by a mean width measured from orthophotos for all different Strahler orders ($n = 30$ each). The rather small buffer width of 30 m was chosen, as it is relevant in river management and restoration and because many functions like shading mainly depend on woody riparian vegetation (WRV) directly adjacent to the stream.

WRV was quantified from ATKIS data. Its detailed land use classes were grouped into seven categories: (1) 'arable land', (2) 'grassland', (3) 'natural vegetation', (4) 'urban green space', (5) 'urban', (6) 'water surface' and (7) 'woody vegetation', with some rare land use classes excluded (e.g. quarries, harbours). Given the minimum size of woody vegetation patches in ATKIS of 0.1 ha, smaller landscape features, like single lines of trees along rivers, were missing. Therefore, ATKIS data in the riparian corridor were complemented by WRV identified on orthoimages obtained from the German Federal Agency for Cartography and Geodesy, covering small patches of WRF down to single trees (see Supporting Information S.2 for details).

2.3 | Catchment and local land use

Besides the two upstream riparian buffers, land use was quantified at two additional spatial scales (Figure 2): (1) The catchment scale, that is, area draining to the sampling site, was delineated based on a digital elevation model (DEM, 10 m resolution) and visually checked; (2) The local scale, that is, a circular buffer around a sampling site with a radius of 250 m.

Percentage cover of the three land use categories 'urban', 'agriculture' and 'woodland' was quantified for each scale with ESRI's ArcGIS Desktop 10.8. Urban land use comprises all built-up areas and infrastructure potentially having detrimental effects on stream biota from catchment (e.g. impervious surfaces) to local scale (e.g. light pollution). Agricultural areas are subject to tillage, fertilization and pesticide application, which respectively may result in inputs of fine sediments, nutrients and toxic substances. Woodlands are the predominant potential natural vegetation in temperate regions and should cause the least detrimental effects approximating natural instream conditions. Quantifying woodland cover at catchment and local scale allows distinguishing the effect of WRV in the riparian buffer from adjacent woodland cover, i.e. forest cover in general.

2.4 | Hydromorphology

Stream morphology influences sediment and detritus transport, as well as water temperature. Therefore, the effect of WRV might further depend on instream hydromorphology.

Hydromorphological mapping and assessment results following the work of Gellert et al. (2014) were provided by regional authorities (see Supporting Information S.1 for details). For each sampling site, mean assessment scores for main parameters (1) 'channel pattern', (2) 'longitudinal profile', (3) 'channel bed features', (4) 'cross section' and (5) 'channel bank features' were aggregated based on all available assessment segments 500 and 5000 m upstream of the sampling sites (Figure 2).

2.5 | Statistical analysis

Model-based recursive partitioning (Zeileis et al., 2008) allows to investigate context-specific effects and was therefore used to test the hypotheses. Its core was a linear regression model (*lm*; R Core Team;, 2016), fitted per maximum likelihood estimation, with the macroinvertebrate multimetric index (MMI) as its response and the percentage cover of WRV in the near-upstream and far-upstream riparian buffer as its two predictors. The other variables in the dataset were incorporated as candidate partitioning variables, namely urban, agricultural and woodland cover at the local and catchment scale, as well as hydromorphological assessment results at the near and far-upstream scale.

The recursive approach first tests for the entire dataset if the estimates of the *lm* show any significant parameter instability towards the gradients of any candidate partitioning variable. If statistically significant instability is found (Andrews' sup*LM* test; Zeileis, 2005), the optimal split in the gradient of the partitioning variable causing the highest parameter instability is calculated. This split point optimizes the maximum likelihood for the core model fitted to the resulting child datasets. The process is reiterated until no more parameter instability with respect to the candidate partitioning variables in the *lm* is found for the thus final sub-datasets.

The recursive splitting of the entire dataset can be intuitively displayed in a partitioning tree-diagram similar to other CART approaches. However, this method differs as it does not partition the data into groups of observations with similar response values. Rather it splits the data into groups of observations with similar model trends between the response (MMI) and core predictors (WRV) not used for partition (Garge et al., 2013).

Spearman's ρ correlation coefficient between WRV and woodland cover in the catchment were calculated in order to assess if potential effects of WRV on the MMI were independent or rather a proxy for effects of larger-scale forest cover.

3 | RESULTS

3.1 | Effect of woody riparian vegetation on macroinvertebrates is context specific

The general hypothesis that the effect of woody riparian vegetation (WRV) on the multimetric index (MMI) is context-specific was supported by both datasets being split into sub-datasets. The 361 lowland sampling sites were split into three sub-datasets (LL.1–LL.3) based on two partitioning variables (catchment urban and woodland cover; Figure 3a), whereas the 748 mountain sampling sites were split into eleven sub-datasets (M.1–M.11) based on four different partitioning variables (catchment urban and agricultural cover, local agricultural cover and near-upstream hydromorphology; Figure 4a). Significant effects of WRV were found in all lowland and seven mountain sub-datasets.

Catchment urbanization was the first partitioning variable in both stream types, as it caused the largest differences between sub-datasets regarding the relationship between WRV and the MMI. This allowed distinguishing between rural and urban catchments. In lowlands, macroinvertebrate communities in rural, forested catchments of sub-dataset LL.2 were on average in a moderate to high ecological state (mean MMI = 0.584) and significantly better compared to the prevailing bad state in rural, agricultural LL.1 (0.383) and urban catchments LL.3 (0.366) (Figure 3b; Table S1). The ecological state in mountain sub-datasets differed significantly with MMI scores ranging from good (mean MMI = 0.713) in rural, forested catchments of sub-datasets M.1 to poor (0.121) in hydromorphologically impaired streams in urban, agricultural landscapes of sub-dataset M.11 (Figure 4b; Table S1; Analysis of variance-test: $F = 67.07$, $p < 2e^{-16}$).

3.2 | Effects on macroinvertebrates in rural landscapes

The first specific hypothesis that WRV has large effects on the ecological state (MMI) in agricultural landscapes was supported but even larger effects were found in some urban contexts.

In lowland streams, near-upstream WRV had the largest effect on the MMI in rural, agricultural catchments of sub-dataset LL.1

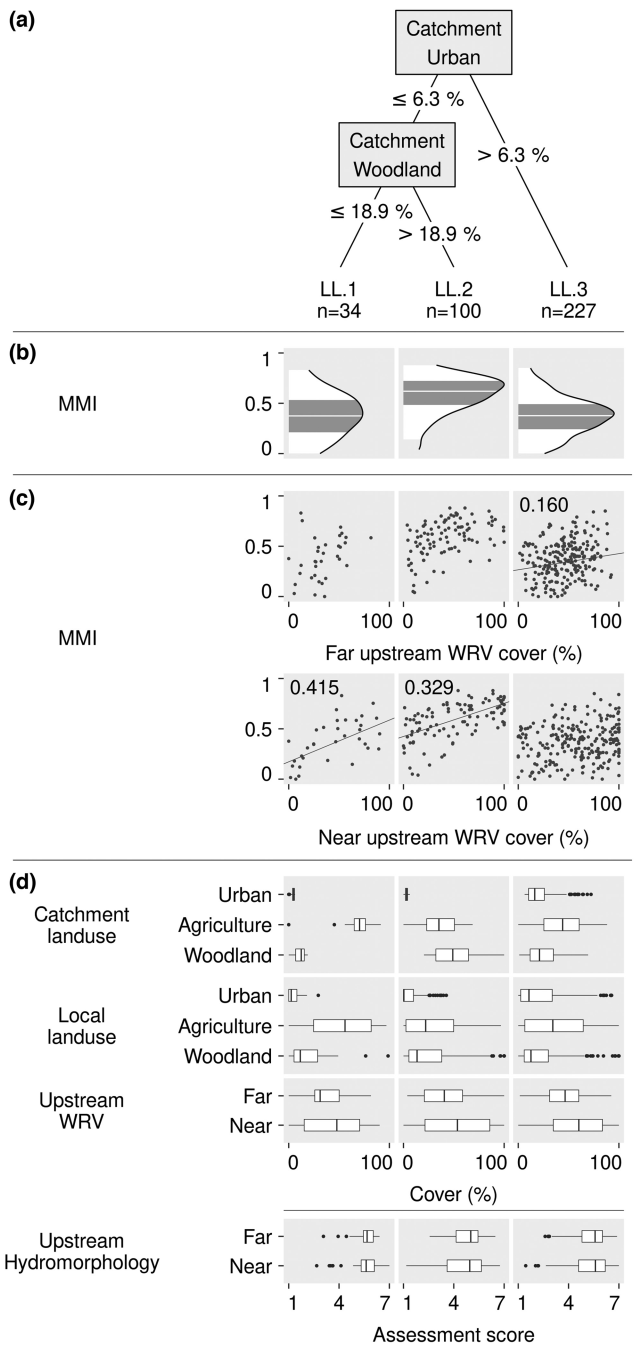

FIGURE 3 Partitioning tree for lowland sites (a). Density distributions of the macroinvertebrate multimetric index (MM) for each final sub-dataset (columns) with boxplot-like coloration of quantiles (b). Relationship between the MMI and the near and far-upstream woody riparian vegetation (WRV) as scatterplots with significant effects indicated by regression coefficient and line (c). Distribution of candidate partitioning variables given as boxplots (d).

(Figure 3c). This sub-dataset was characterized by low urban (4.9%) and woodland (12.4%) median cover in the catchment (Figure 3d). Consequently, median agriculture cover was high at the catchment (70.3%) and local (55.9%) scale (Table S2). The observed positive effect on the MMI likely did not result from sampling sites in forested areas because (i) catchment woodland cover (median = 12.4%) was significantly lower compared to the other two sub-datasets (Table S3) and (ii) did not significantly correlate with near-upstream WRV (Table 1). Therefore, sites in sub-dataset LL.1 were truly located in agricultural landscapes. For the other rural sub-dataset LL.2, median catchment woodland cover was significantly higher (49.0%; Table S3) and correlated with near-upstream WRV (Table 1), implying that the effect of near-upstream WRV on the MMI (Figure 3c) was partly due to effects of larger-scale forest cover.

In mountain streams, WRV had a similarly large effect on the MMI compared to lowland streams in the two rural, agricultural sub-datasets M.5 and M.6 (Figure 4c). Sub-datasets M.5 and M.6 were characterized by low urban (6.1% pooled) and high agricultural (49.2% pooled) median cover in the catchment but differed regarding hydromorphological degradation (Figure 4a). Again, observed effects were likely not resulting from sampling sites in forested areas because (i) median local woodland cover was intermediate in sub-dataset M.5 (17.4%) and even notably lower in sub-dataset M.6 (8.7%) (Figure 4d; Table S2), and (ii) near-upstream WRV was un-correlated with catchment woodland in M.5, while far-upstream WRV weakly correlated positively with catchment woodland cover in M.6 (Table 1). Therefore, sites of sub-datasets M.5 and M.6 were considered to be indeed located in agricultural landscapes. In contrast, the other two rural sub-datasets M.1 and M.2 had higher woodland cover in the catchment (media = 71.1%; Figure 4d), which strongly correlated with far-upstream WRV (Table 1). Median catchment and local cover of agriculture were just 10.6% and 0% (pooled) respectively (Figure 4d; Table S2). Therefore, M.1 and M.2 do not reflect agricultural settings but instead represent larger-scale forest cover.

However, the by far largest effects of WRV on the MMI were however not observed in rural sub-datasets but given a combination of urban and agricultural land use (M.8, M.9, M.10), with regression coefficients up to 0.995 (Figure 4c; Section 3.4). In these three sub-datasets, mean catchment and, except for sub-dataset M.10, also mean local urban cover was significantly higher than in agricultural landscapes of sub-datasets M.5 and M.6 (Figure 4d; Table S4).

3.3 | Effects of far- versus near-upstream woody riparian vegetation

The second specific hypothesis that far-upstream is more important than near-upstream WRV was supported in urban but not in rural contexts.

In rural, agricultural catchments (LL.1, M.5, M.6), near-upstream WRV unexpectedly had a more apparent effect on the ecological status (MMI) compared to far-upstream WRV (Figures 3c and 4c). In two sub-datasets (LL.1, M.2), near-upstream had a significant effect on the MMI, whereas far-upstream WRV did not. Only in sites of sub-dataset M.6, which were in a bad hydromorphological and poor ecological state, far-upstream WRV had a significant effect. This suggests that larger-scale WRV was necessary to compensate for

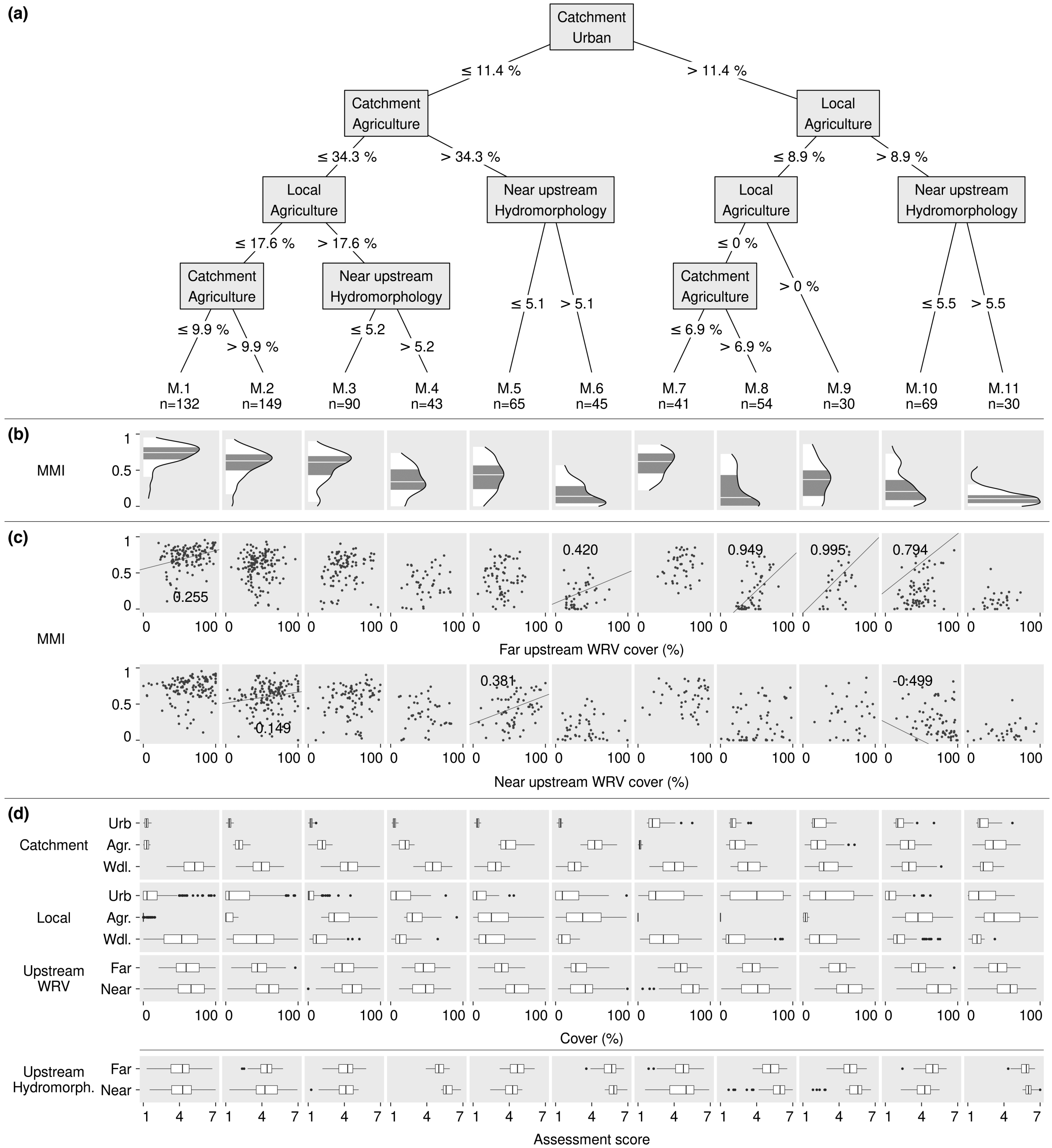

FIGURE 4 Partitioning tree for mountain sites (a). Density distributions of the macroinvertebrate multimetric index (MM) for each final sub-dataset (columns) with boxplot-like coloration of quantiles (b). Relationship between the MMI and the near and far-upstream woody riparian vegetation (WRV) as scatterplots with significant effects indicated by regression coefficient and line (c). Distribution of candidate partitioning variables given as boxplots (d).

instream habitat deficits. In other rural, forested catchments, near-upstream, also had an exclusive significant effect on the MMI in lowlands (LL.2) and mountains (M.2). However, in another forested sub-dataset M.1, the expected significant effect of far-upstream WRV was also found. As catchment agricultural cover was virtually absent (75th-percentile = 7.4%) this effect however was due to larger-scale high forest cover.

In urban catchments, in line with expectations, far-upstream was more important than near-upstream WRV (LL.3, M.8, M.9, M.10). Sub-dataset M.10 was distinct as there was a negative

TABLE 1 Spearman's ρ rank correlation coefficient between near or far-upstream woody riparian vegetation (WRV) and catchment woodland cover for sub-datasets of lowland (LL) and mountain (M) sites. Asterisks indicate significant correlations at $p<0.5$ (*) and $p<0.01$ (***). Bold coefficients indicate if significant effects on the macroinvertebrate multimetric index exist.

	Spearman's ρ	
Sub-dataset	Near-upstream WRV	Far-upstream WRV
LL.1	**−0.086**	0.115
LL.2	**0.404*** **	0.547***
LL.3	0.128	**0.291*** **
M.1	0.153	**0.614*** **
M.2	**−0.103**	0.354***
M.5	**−0.144**	0.330*
M.6	0.019	**0.300* **
M.8	0.211	**−0.066**
M.9	−0.449*	**−0.182**
M.10	**0.044**	**0.240* **

additional effect of near-upstream WRV. However, further inspection revealed a spatial cluster of sites within M.10 located in the vicinity of Frankfurt am Main, a major metropolitan area (Figure 5). For these sites near-upstream WRV cover was upwards of 50% but the poor ecological state indicated that other stressors not covered by the predictors were present. Excluding these sites from the sub-dataset, far- and near-upstream WRV would both have a positive effect on the MMI.

Therefore, the expected stronger effect from far-upstream WRV was actually only found in forest or urban context but not in other rural landscapes contradicting the second specific hypothesis.

3.4 | Limiting effects of urban catchment land use

The third specific hypothesis that urban catchment land use limits effects of WRV was supported in lowland but not in mountain sites.

In lowland streams, WRV had the expected small effect on the ecological state (MMI) (Figure 3c) in urban catchments of sub-dataset LL.3 characterized by high median urban cover in the catchment (16.4%; Figure 3a). However, the regression coefficient and variance explained (R^2 = 5%) were very low compared to the significant effects of near-upstream WRV in the other lowland sub-datasets LL.1 and LL.2 (R^2 = 32% and 31% respectively) (Figure 3c).

Against expectations, effects of WRV on macroinvertebrates' MMI in mountain sites were largest in urban sub-datasets M.8, M.9 and M.10 (Figure 4c). These urban sub-datasets were characterized by high catchment (16.2% pooled) and partly by very high local (42.9% pooled for M.8 and M.9) median urban cover. Similar to rural agricultural sub-datasets M.5 and M.6. (Section 3.1), effects in urban sub-datasets were most probably not due to large-scale forest cover because catchment woodland cover (i) was significantly lower than in forested, rural sub-datasets (M.1 and M.2; Table S4) and (ii) did not correlate with far-upstream WRV in sub-datasets M.8 and M.9 (Table 1) nor with near-upstream WRV in sub-dataset M.10. Therefore, sub-datasets M.8, M.9, M.10 were located in landscapes with a mix of urban and agricultural cover and this is where the largest effects of WRV in mountain streams were unexpectedly observed.

4 | DISCUSSION

This study confirmed that the effect of woody riparian vegetation (WRV) on the ecological status of macroinvertebrates is context-specific and successfully identified conditions under which positive effects exist. This has important implications for river management as practitioners can lean upon the context in which WRV may be an effective measure benefiting aquatic biota when more sophisticated, for example spatially explicit (Witing et al., 2022), tools are not feasible.

4.1 | Effect of woody riparian vegetation on macroinvertebrates is context specific

The results confirmed the effect of WRV on the multimetric index (MMI) was context-specific. This helps to explain conflicting results reported in reach-scale and large-scale empirical studies. On the one hand, there is overwhelming evidence for positive effects of WRV on ecosystem processes and river biota from reach-scale empirical studies, summarized in several reviews (Broadmeadow & Nisbet, 2004; Sweeney & Newbold, 2014). These reach-scale studies usually compared close-by sites with differing configurations of WRV (e.g. Anderson & Poage, 2014; Parkyn et al., 2003). Due to their spatial proximity, large-scale stressors were probably similar as they originate at the catchment scale, hence the sites had a similar context (Melo et al., 2020). Consequently, these reach-scale studies do not allow comparing general effect of WRV across variable landscape contexts. On the other hand, studies investigating larger numbers of sampling sites at larger spatial scales reported only minor effects of WRV on macroinvertebrates (Burdon et al., 2020; Le Gall et al., 2022; Palt et al., 2022). In the present study, model-based recursive partitioning allows bridging the gap between reach-scale and large-scale studies by identifying the context in which WRV indeed had expected large effects on the ecological status of macroinvertebrates. Hence, without the need to a priori define context thresholds (Tolkkinen et al., 2021), model-based recursive partitioning may offer insights into larger datasets (e.g. monitoring data) missed otherwise and therefore might be underused in ecological studies (but see e.g. Müller et al., 2015). Being model-based, this approach can be adapted to other research questions, too. For instance, thresholds or abrupt changes in the relationship between biotic integrity and WRV (Dala-Corte et al., 2020), could be investigated by formulating an underlying model with corresponding properties.

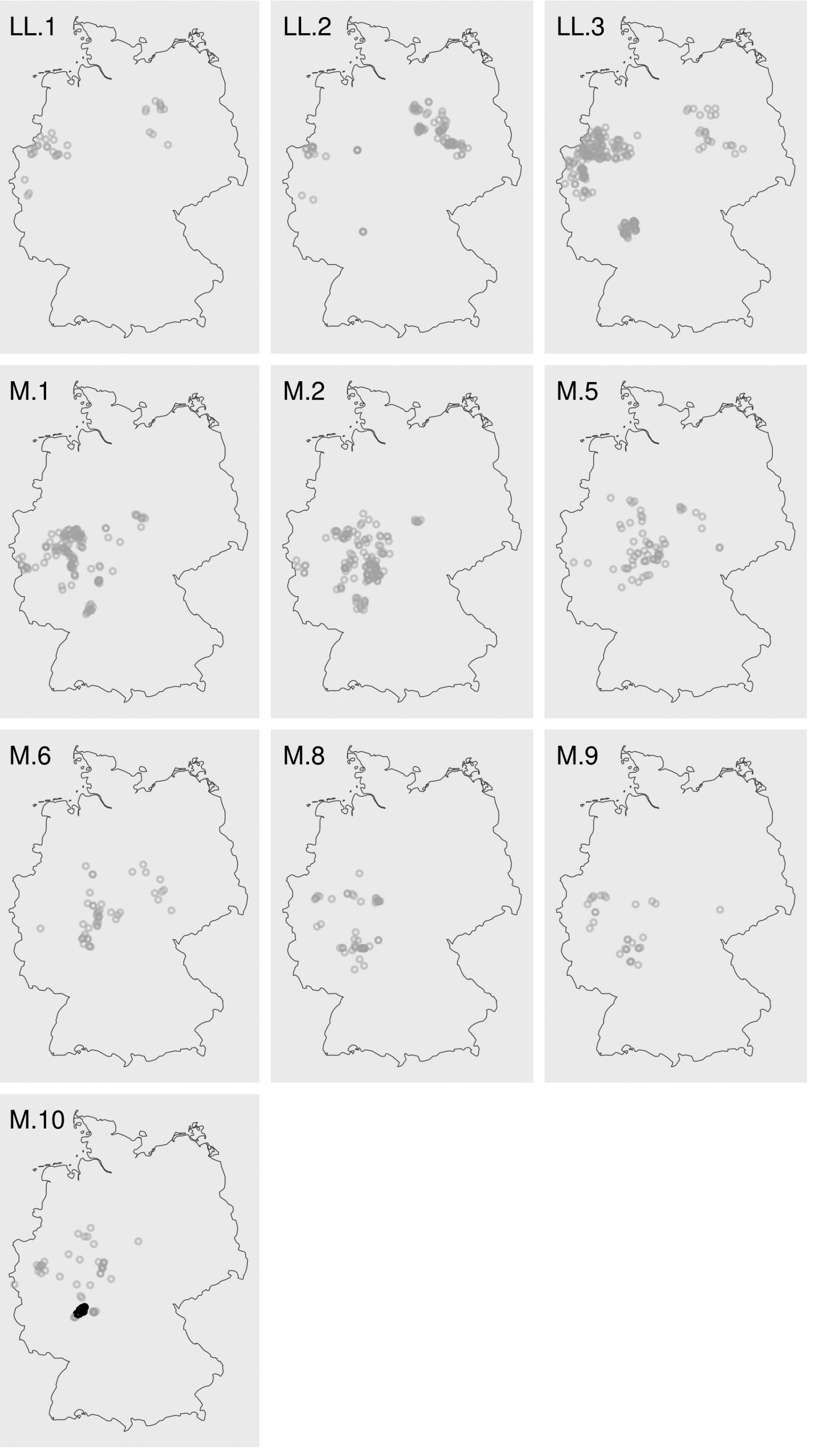

FIGURE 5 Sites in sub-datasets in in lowlands (LL) and mountains (M) with significant effects of woody riparian vegetation. Sites in sub-dataset M.10 contributing to a negative effect in black.

4.2 | Effect on macroinvertebrates in agricultural landscapes

As hypothesized, WRV had large positive effects on the ecological status (MMI) in rural, agricultural catchments, indicating that WRV mitigates stressors resulting from agriculture. This is consistent with the large number of reach-scale studies and several respective reviews, especially on nutrient (Dodd & Sharpley, 2016), fine sediment (Ramesh et al., 2021) and pesticide (Reichenberger et al., 2007) retention. These agricultural stressors are known to affect macroinvertebrates. While a moderate increase in nutrient concentrations alone may increase macroinvertebrates' abundance, they are especially sensitive to fine sediment input (Matthaei et al., 2010; Piggott et al., 2015) and pesticides (Williams & Sweetman, 2019).

Results were consistent in lowlands (LL.1) and mountains (M.5 and M.6) (regression coefficient between 0.381 and 0.420). As the MMI is discretized evenly into five ecological status classes between 0 and 1, these coefficients imply that by restoring lacking woody riparian cover from 0% to 100%, the ecological status could be improved by as much as two status classes confirming that woody riparian buffers are indeed a powerful restoration tool in an agricultural context. Similarly, Tolkkinen et al. (2021) found an increase of one status class along the gradient of WRV cover from 10% to 60% in agricultural landscapes.

4.3 | Far-upstream versus near-upstream woody riparian vegetation

Contrary to expectations, far-upstream WRV was less important for the ecological status (MMI) compared to near-upstream WRV in most agricultural streams. This suggests that positive effects of WRV probably did not just result from retention of nutrients, fine sediment and pesticides even in agricultural contexts, as these functions accumulate over longer distances downstream (Feld et al., 2018). Rather WRV cover in the near-upstream riparian scale plays an important role, which is consistent with other studies. For one, retention of pollutants by WRV may be less effective in some lowland streams than previously thought. This is because fine sediment retention by WRV is highest at moderate hillslopes but not in flat terrain (Liu et al., 2008), as a minimum hillslope is required to cause surface runoff that can be retained by WRV. Moreover, while WRV can retain substantial amounts of nutrients from surface and sub-surface flow the effect on total load is often reduced due to groundwater being the main emission pathway in lowlands (Gericke et al., unpubl.) and agricultural drainage also bypassing the retention in WRV.

Positive effects of near-upstream WRV hence likely resulted from other functions like shading. In comparable lowland streams, maximum daily water temperature already substantially decreased 400 m downstream of an increase in WRV cover (Kail et al., 2021), hence after a similar length to the 500 m near-upstream scale used in this study. Moreover, shading substantially reduces gross (by 60%) and net primary production (by 90%), especially in agricultural catchments with high nutrient loads (Nebgen & Herrman, 2019).

4.4 | Limiting effects of urban catchment land use

As hypothesized, WRV along lowland streams had a smaller effect in urban compared to rural catchments, suggesting that urban catchment cover limits the positive effects of WRV. The split point of 6.3% separating the rural and urban datasets in the partitioning tree (Figure 3a) is similar to reported thresholds of 2%–5% urban catchment cover to cause substantial losses of sensitive macroinvertebrate species (Kail et al., 2012). Stressors related to urban areas are manifold (Walsh et al., 2005) but macroinvertebrates seem to be mainly affected by hydrological alterations (Richards & Host, 1994) and water pollution related to stormwater run-off (Walsh & Webb, 2016).

In mountain streams, the ecological status was also lower above the first split point, that is in catchments with an urban cover >11.4% compared to rural sub-datasets. However, in these urbanized catchments, within a limited range of lower MMI scores, far-upstream WRV had the by far largest effect found in this study (sub-datasets M.8–M.10). Solely considering the regression coefficients, increasing woody riparian cover from 0% to 100% would results in an improvement of the ecological status by as much as five status classes, that is from bad to high. However, as only few sites in these sub-datasets had a high WRV cover (Figure 4c), such an extrapolation of the regression model is questionable. Nevertheless, within the limited range of WRV cover, results indicate that increasing WRV cover might be an appropriate restoration measure even in urban catchments increasing poor ecological statuses to at least moderate, which is two status classes.

This was unexpected given the larger negative effect of urban catchment land use on macroinvertebrates compared to small effects of riparian land use since many stressors originating from urban land use are related to inputs from point-sources unaffected by WRV (Lorenz & Feld, 2013). Yet, these studies might have underestimated the importance of WRV since the low resolution land use data used did not include small WRV patches and rather wide buffers were investigated (50–100 m in width). Most functions however mainly depend on WRV within 30 m of the river banks (Broadmeadow & Nisbet, 2004; Sweeney & Newbold, 2014). This study complemented official land use data with small WRV patches delineated on orthophotos and focused on a relatively narrow 30 m buffer. This might have led to finding an increased importance of WRV. Nevertheless, an effect from WRV was missing both in sub-datasets M.7, where agricultural pressures were entirely absent, and M.11, where sites were additionally impaired morphologically and by high local agricultural cover. Therefore, the unexpected effect of WRV only occurred in streams affected by urbanization in concert with a moderate level of catchment agriculture, while predominantly urban catchment cover or a more pronounced multi-stressor context did actually limit the positive effects of WRV.

5 | CONCLUSIONS

In the Central European lowland and mountain streams investigated, effects of woody riparian vegetation (WRV) on the ecological status of macroinvertebrates (MMI) were large, but context specific, depending on catchment land use, local land use and hydromorphology. WRV had large positive effects in rural, agricultural catchments, improving the ecological status by up to two out of five status classes. Results indicate this was not only due to pollutant retention by far-upstream WRV but also caused by other functions at the near-upstream scale like shading and related effects on water temperature and primary production. WRV even had a surprisingly strong significant effect if urban and agricultural land use combine at the catchment scale. While the context-specificity of the relationship between WRV and the macroinvertebrate community is hardly surprising, this analysis succeeds in confirming strong positive WRV effects on macroinvertebrates using a large dataset.

These findings have important implications for river management as results indicate that WRV are indeed a powerful tool for improving the ecological status of macroinvertebrates in streams impacted by agricultural stressors supporting their relevance in river restoration. Furthermore, the fact that already near-upstream WRV unexpectedly had a larger statistical effect than its far-upstream counterpart in most contexts stresses that already smaller-scale restoration measures can provide relevant functions such as shading, that is, control of excess temperature and primary production. This suggests that achieving ambitious restoration goals is not necessarily limited by the availability of riparian zones along several kilometres of river length. Rather, river managers are encouraged to pursue restoration measures already if more limited areas become available. Establishing WRV along several kilometres far-upstream potentially may also be an effective measure in urban contexts to at least reach a moderate ecological state. Only in catchments affected by multiple stressors, urban catchment and local agriculture potentially limit the beneficial effects of WRV.

While further studies are recommended confirming statistical effects actually stem from the candidate functions provided by WRV, our results suggest achieving good status in agricultural as well as some urban landscapes is possible—and achievable by a fairly simple measure.

AUTHOR CONTRIBUTIONS

Martin Palt, Daniel Hering and Jochem Kail conceived the ideas; Martin Palt designed the methodology and analysed the data; Martin Palt and Jochem Kail led the writing of the manuscript. All authors contributed critically to the drafts and gave the final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interests.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.pzgmsbcrf (Palt et al., 2023).

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SUPPORTING INFORMATION

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

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