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Author

Gould, L, Franklin, H, Sheldon, F

Published

2025

Journal Title

Aquatic Sciences

Version

Version of Record (VoR)

DOI

[10.1007/s00027-025-01236-5](https://doi.org/10.1007/s00027-025-01236-5)

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Funder(s)

ARC

Grant identifier(s)

LP0668369

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The relative influence of riparian vegetation structure and composition on instream health: a multivariate assessment

L. Gould¹ · H. Franklin¹ · F. Sheldon¹

Received: 12 May 2025 / Accepted: 4 October 2025 / Published online: 30 October 2025
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Abstract

Human activities have pervaded aquatic ecosystems worldwide. As a result, riparian zones (the areas adjacent to rivers and streams) display high proportions of non-native vegetation, which is often considered symbolic of degradation and poor river health. Research suggests that riparian vegetation is essential for maintaining river health. However, whether this is due to the relative effect of vegetation species composition (including non-native vegetation) or vegetation structure (attributes such as canopy cover and linear continuity) is unclear. We used a comprehensive, regional ecosystem-health monitoring dataset to determine the effects of riparian vegetation across several spatial scales on river health and macroinvertebrate community composition. Constrained ordination methods revealed that riparian vegetation structure at the site scale influenced macroinvertebrate assemblages. However, when explicitly assessing the effect of non-native vegetation at the site scale, the proportion of non-native vegetation in the canopy did not influence macroinvertebrate assemblages. Notably, when species composition including both native and non-native species was assessed across all strata (canopy, shrub, and ground), it was found to significantly influence macroinvertebrate assemblages. This is likely driven by the different structural attributes of the various riparian vegetation communities found throughout the region. Therefore, the dominant effect of riparian vegetation structure may reflect the impact of different land uses within the area, rather than a strong influence of vegetation species identity on instream condition. These findings have important implications for riparian restoration. Our results suggest that the common restoration practice of focusing on non-native riparian vegetation removal combined with small-scale native replanting may not improve water quality and macroinvertebrate diversity, particularly where vegetation structure is modified in the process.

Keywords Novel ecosystem · Riparian zone · Restoration · Non-native vegetation · Macroinvertebrates

Introduction

Human activities have altered natural environments on a global scale (Goudie 2019), including aiding the rapid and extensive spread of species outside their native distributions, where they are often referred to as ‘exotic’ or ‘non-native’ components of ecosystems (Pyšek et al. 2004; Buckley and Catford 2016). Consequently, non-native species are indicative of socioecological systems and often symbolic of environmental degradation (Francis et al. 2019). While some non-native species are considered invasive in nature, where their spread is expected to cause environmental or economic

harm (Fernandez et al. 2023; Rilov et al. 2024), many have benign or in some cases beneficial effects within their introduced range (Sax et al. 2022). Therefore, the extent to which these non-natives are drivers, or passengers, of environmental change is unclear (MacDougall and Turkington 2005; Grarock et al. 2014). This is particularly true for rivers and their riparian zones, which have an intense legacy of human intervention (Wohl 2019) and non-native species introductions (Tabacchi et al. 1998; Hood and Naiman 2000; Richardson et al. 2007).

Anthropogenic modification of rivers and associated riparian zones often alters natural disturbance regimes, which facilitates the recruitment and spread of highly adaptive, non-native species (Tabacchi et al. 1998; Richardson et al. 2007). Many current methods of riparian restoration involve restoring native species distributions by clearing non-native and reintroducing native assemblages (Kauffman

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et al. 1995; González et al. 2015; Capon and Pettit 2018; Rood et al. 2020). However, the success of these methods is uncertain as poor evaluation strategies alongside intractable objectives of success often obscure outcomes (Bernhardt et al. 2005; Morandi et al. 2014; González et al. 2015). In many instances, restoration, where the primary objective is native species restoration, may be unattainable in highly modified catchments (Hobbs et al. 2006, 2009; Seastedt et al. 2008).

Hence, if novel riparian ecosystems exist along waterways, is restoring native species compositions at large scales necessary for the ecosystem integrity of these systems? An association between stream macroinvertebrate assemblage composition and the presence of riparian and catchment vegetation has been widely reported in the literature (Peterson et al. 2011; Sheldon et al. 2012; Jonsson et al. 2017), with the general trend of increased diversity associated with more structurally complex riparian zones. However, the response may not be linear and may be locally context specific. Conceptually, the structure and composition of riparian vegetation can influence macroinvertebrate assemblage composition directly through its physical presence or indirectly through its impact on general river health via changes in instream productivity, algal resources, and water quality (Fig. 1).

The physical structure of riparian vegetation has been shown to influence stream ecology by reducing sediment entering watercourses (Smith et al. 2021), controlling light and temperature regimes (Fellows et al. 2006), and influencing benthic algal composition and thus food quality (Guo

et al. 2016). Extensive root structures associated with riparian vegetation reinforce riparian soils (Smith et al. 2021) and the physical presence of the vegetation along the stream bank can intercept sediment from overland flow (Wilkes et al. 2019). The shading provided by a dense riparian canopy controls the light entering the stream and consequently water temperature regimes (Fellows et al. 2006; Gjerløv and Richardson 2010). Reduced light levels can influence the proportion of diatoms in the periphyton, a high-quality food source for grazing macroinvertebrates, and thus have a direct impact on food quality (Guo et al. 2016; Zhang et al. 2021).

The species composition of riparian vegetation, however, also has the potential to influence instream processes and diversity, particularly through variations in plant species life history traits, such as the timing of leaf fall, and the biochemical properties of the vegetation itself (McNeish et al. 2012). Leaf litter derived from riparian vegetation is a primary source of allochthonous carbon in freshwater ecosystems, forming the basis of instream detrital food webs (Tank et al. 2010). The quantity, quality, and timing of leaf fall can affect the availability of coarse particulate organic matter, which macroinvertebrates use for both habitat and food (Kuglerová et al. 2017). A change in the biochemical properties of instream leaf packs, due to a change in the composition of riparian vegetation, can affect instream litter decomposition dynamics with subsequent effects on secondary products and trophic flows of energy (McNeish et al. 2012). The chemical composition of leaf litter from different riparian species has the potential to indirectly affect macroinvertebrate assemblages via its effect on water quality.

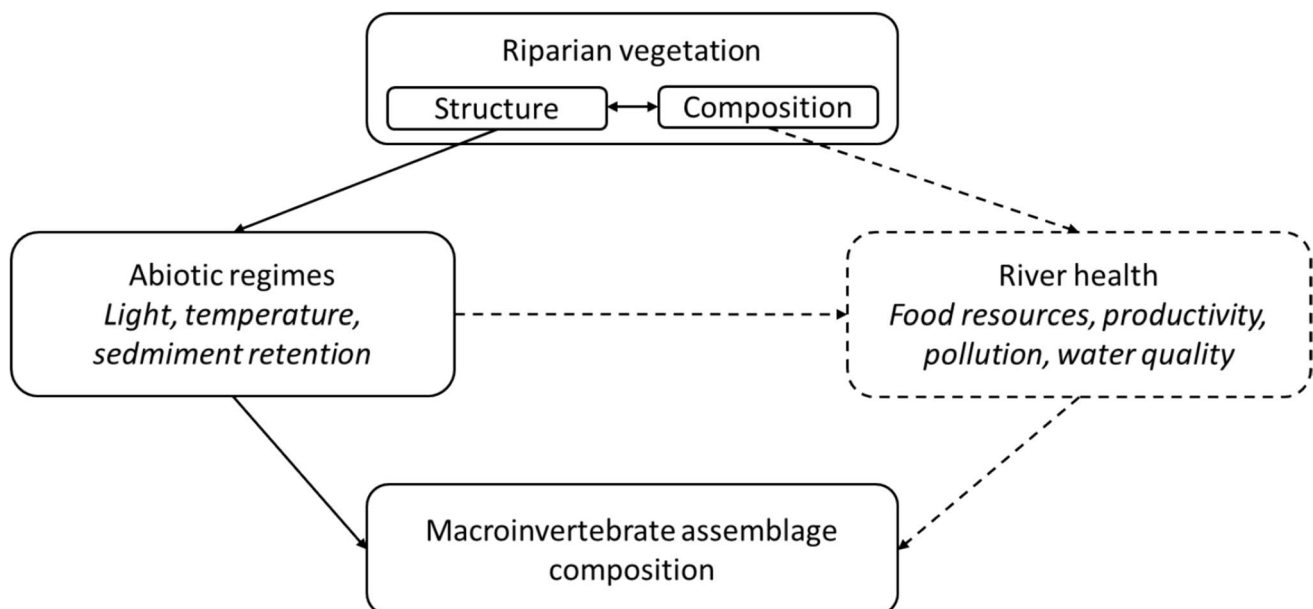


Fig. 1 Conceptual diagram of the direct (*solid line*) and indirect (*dashed line*) links between riparian vegetation structure and composition and macroinvertebrate assemblage composition

Leaf litter from Australian native species has been shown to have contrasting effects on the composition of dissolved organic matter (Franklin et al. 2020a) and nutrients (Franklin et al. 2020b) leached to watercourses from riparian soil during rainfall events, with some dissolved organic matter leachate from native leaf litter inhibiting the photosynthesis of harmful cyanobacteria (Neilen et al. 2019). These studies suggest that the species identity of riparian leaf litter can have implications for water quality and by extension macroinvertebrate diversity.

Riparian ecosystems are disproportionately susceptible to non-native vegetation recruitment with many riparian zones in disturbed landscapes dominated by non-native species (Planty-Tabacchi et al. 1996; Hood and Naiman 2000; Richardson et al. 2007). In restoring riparian zones, the removal of non-native species may sacrifice vegetation structure, and if vegetation structure, rather than composition, is a more significant driver of macroinvertebrate assemblage composition, this practice of vegetation removal may in fact be deleterious to river health, at least in the short to medium term. Thus, to achieve optimal restoration outcomes it is paramount that restoration techniques are pragmatic and objective, particularly in highly modified catchments.

South East Queensland (SEQ) is a highly modified region of Australia. The clearance of catchment vegetation there has been extensive since European settlement began in 1823, with only a quarter of the original native vegetation intact (Bunn et al. 2010; Saxton et al. 2012). These alterations have resulted in highly modified riparian ecosystems that are composed of intermixed non-native and native vegetation assemblages (Leigh et al. 2013). These riparian zones can be considered ‘novel’ ecosystems (*sensu* Hobbs 2009), as they contain a mix of historical (endemic native) and non-native (exotic) species. Moreover, the effects of land conversion combined with novel vegetation assemblages suggest these systems have fundamentally and irreversibly changed, which means that their restoration to an historical state is no longer possible. In this region, the native and non-native riparian vegetation tends to be non-deciduous, or evergreen, reflecting the dominance of evergreen trees in the Australian flora combined with the sub-tropical climate with a limited seasonal signal. Previous studies suggest that around 60–80% vegetation cover, in the mid-dense cover category (Peterson et al. 2011), needs to be returned to the upstream riparian and gully regions to significantly improve river health (Sheldon et al. 2012). Active restoration practices at this scale would be overwhelming and financially impractical (Leigh et al. 2013). It is therefore important to examine the effects of altered riparian vegetation structure and composition on river health to aid in the development of pragmatic riparian restoration strategies for the region.

This study represents a targeted examination of the aquatic-terrestrial links that drive ecosystem health. It builds

on the broader work of Sheldon et al. (2012), which determined the spatial scale of land use that had the strongest influence on indicators of river health; in that study riparian cover was the strongest health predictor as measured by aspects of macroinvertebrate assemblage composition. The present study first assesses how catchment-scale land use influences riparian vegetation assemblages at the site scale. Next, multivariate techniques are used to determine the relative influence of riparian vegetation structure and composition on measures of water quality and instream processes as well as on macroinvertebrate assemblages at the site scale. We hypothesise that the structural attributes of riparian vegetation at the site scale will have a greater influence on instream processes and macroinvertebrate assemblages compared to the composition of riparian vegetation species assemblages. By assessing the impact of land use at multiple spatial scales, findings at the site scale can be interpreted within the context of the broader catchment network.

Methods

Study area

The study was conducted in SEQ, a subtropical region covering an area of approximately 23,000 km² and a total of 48,000 km of stream networks across 15 major river systems (Bunn et al. 2010; Leigh et al. 2013) (Fig. 2). Mean maximum monthly temperatures for SEQ range between 21 and 29 °C, with an average annual rainfall of 900–1800 mm, most of which falls during the austral summer (October–February). The catchments of SEQ have been heavily modified since European settlement in 1823, with two-thirds of the region’s woody vegetation cleared for agriculture and urban development (Abal et al. 2005).

Freshwater Ecosystem Health Monitoring Program data

Data from a long-term regional monitoring program, the Freshwater Ecosystem Health Monitoring Program (EHMP), was used for this analysis. EHMP data collected twice yearly during the austral spring (pre-wet) and austral autumn (post-wet) between 2002 and 2008 at sites representative of third- and second-order streams distributed across major stream class types (upland, lowland, coastal and wallum) was used (see Bunn et al. 2010). To assess overall river health each site monitored is given an annual score which represents the seasonal aggregation of 14 separate river health indices into five broad indicators, which are further aggregated into a single score for a site (Table 1; see also Sheldon et al. 2012). Before aggregation, data for each index are converted to a standardized

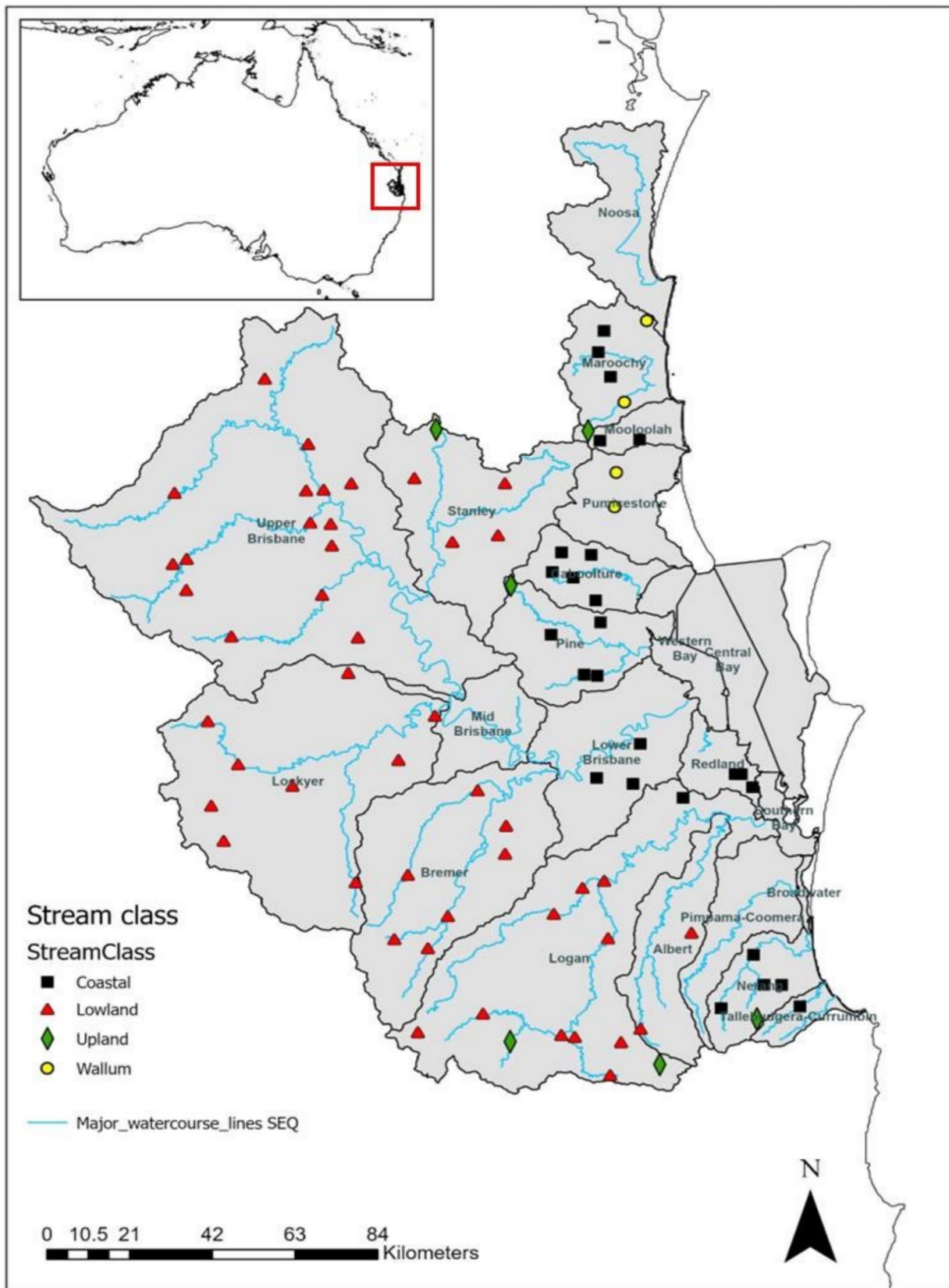


Fig. 2 Map of South East Queensland, Australia, showing the location and stream class of 83 sampling sites used in the multivariate analyses

score by comparing the observed value at a site with a reference condition such that standardized scores ranges from 0 (maximum deviation from reference condition) to 1 (equal to reference condition) (Bunn et al. 2010). To represent river health in this analysis, standardized scores for 11 of the 14 indices (Table 1), for each season (pre-wet and post-wet) between the years 2002 and 2008, were used from 83 EHMP sites. Fish indices were not included.

Detailed methods of data collection for each of the indices can be found in Smith et al. (1999) and Bunn et al. (2010). In summary, aquatic macroinvertebrates were sampled using a pond net with a mesh size of 250 μm from both edge and

pool habitats, then live picked, counted, and identified to family level in accordance with standard Australian River Assessment System protocols (Davies et al. 2000). In this analysis, four measures from the macroinvertebrate dataset were used for each site as an estimate of river health, family richness, Plecoptera, Ephemeroptera and Trichoptera richness, and stream invertebrate grade number—average level score (Chessman 1995) (Table 1). Further, the family abundance by site matrix was used as the dataset for the analysis of macroinvertebrate assemblage composition.

To assess instream processes at a site as an indicator of overall river health, measures of benthic metabolism, gross

Table 1 The Ecosystem Health Monitoring Program annual score is based on 14 indices, which are normalised and aggregated into seasonal indicator scores. The five indicator scores at each site are averaged to derive a seasonal score for the site; the two seasonal scores

are then averaged to derive an annual score for each site. See also Bunn et al. (2010) and Sheldon et al. (2012). Data for the fish indices were not used in this analysis

| Measured index | Description | Indicator score (0–1) | Annual score (0–1) |
|--|--|-----------------------|--|
| Family richness | Number of taxa is a direct measure of taxa richness, which generally increases with ecological condition | Macroinvertebrates | Average of autumn score and spring score |
| SIGNAL score | SIGNAL is a simple scoring system for quantifying the ecological health of streams. It is based on the average sensitivity to disturbance of the aquatic macroinvertebrate taxa present in a sample | | |
| PET richness | PET richness refers to the number of families in a sample belonging to one of the three particularly sensitive orders of aquatic insects—Plecoptera (stoneflies), Ephemeroptera (mayflies) and Trichoptera (caddisflies) | | |
| Gross primary production | Benthic metabolism refers to the rates of respiration and primary production (i.e. photosynthesis) occurring at, and just below, the sediment–water interface of water bodies. Rates of instream respiration and production increase with anthropogenic disturbance | Ecosystem processes | |
| Benthic respiration | | | |
| Algal carbon isotope ($\delta^{13}\text{C}$) | The quantity $\delta^{13}\text{C}$ describes the ratio of ^{13}C to ^{12}C stable isotopes within a substance. Changes in the $\delta^{13}\text{C}$ of aquatic plants have been associated with high rates of primary production, respiration and methane production | | |
| 24-h Dissolved oxygen minimum and range | The lowest dissolved oxygen (DO) concentration (5th percentile) and change in DO concentration over a 24-h period | Water quality | |
| 24-h Temperature maximum and range | The highest (95th percentile) water temperature and change in water temperature over a 24-h period | | |
| Conductivity | Conductivity is commonly associated with minerals salts in the water; this index reflects salinity | | |
| pH | The concentration of free hydrogen ions [H^+] or the acidity of the water | | |
| Algal nitrogen isotope ($\delta^{15}\text{N}$) | The quantity $\delta^{15}\text{N}$ describes the ratio of ^{15}N to ^{14}N stable isotopes within a substance. This can be used to identify changes to the natural cycling of nitrogen in streams due to both point source and diffuse sources | Nutrients | |

primary production, and respiration were made over a 24-h period by determining the net change in dissolved oxygen within a dome-shaped perspex benthic chamber (see Fellows et al. 2006) (Table 1). Further assessments were conducted using the ratio of stable carbon isotopes ($^{13}\text{C}/^{12}\text{C}$) in the aquatic plants present at each site. Samples from submerged vascular macrophytes and filamentous algae were hand collected at each site, frozen, then processed for analysis with a continuous-flow ratio mass spectrometer (see Fellows et al. 2006) (Table 1). Nutrient processes at each site were assessed from the same samples by measuring the ratio of stable nitrogen isotopes ($^{15}\text{N}/^{14}\text{N}$) (see Udy et al. 2006) (Table 1).

The measurement of water quality as an indicator of river health included 24-h measures of temperature and dissolved oxygen made using loggers, where the 24-h range and maximum temperature (degrees Celsius) and 24-h range and minimum dissolved oxygen (percentage) were used as the measures of river health (see Bunn et al. 2010) (Table 1). Measures of conductivity and pH at each site were also made in situ using a handheld water quality meter (Bunn et al. 2010) (Table 1).

Classifying vegetation structure and composition

A previous study (Sheldon et al. 2012) identified that dense forest close to the survey site, medium dense forest in the hydrologically active near-stream areas of the catchment, urbanization in the riparian buffer, and tree cover at the reach scale were all significant in explaining river health, suggesting an overriding influence of forest cover, particularly that close to the stream. Therefore, to assess vegetation structure, four scales were assessed as viable for inclusion in the analysis. These scales included the catchment, riparian, reach, and site scale. Detailed methods used to calculate these variables can be found in Peterson et al. (2011) and Sheldon et al. (2012). In summary, measures at the catchment scale included a measure of upstream catchment dense forest weighted more heavily (inverse distance weighting) close to the sampling site, a measure of upstream catchment dense forest weighted more heavily (inverse distance weighting) closer to the upstream riparian zone, a measure of upstream catchment dense forest in the hydrologically active portion of the catchment weighted more heavily (inverse distance weighting) close to the sampling site, and a measure of upstream catchment mid-dense forest in the hydrologically active portion of the catchment weighted more heavily (inverse distance weighting) close to the riparian zone. Measures at the riparian scale included the percentage of dense and mid-dense woody vegetation in the 25-m riparian buffer throughout the upstream catchment from each site.

Measures at the reach scale included the percentage tree cover in the 1-km upstream reach. Finally, measures at the

site scale, which was defined as the 100-m section of stream upstream from each site, included canopy continuity (linear continuity) along the bank edge between points 0 m (downstream) to 100 m (upstream) classified into three categories (0–5%, 6–50% and 51–100% cover); riparian width, measured at the 0-, 50-, and 100-m points on both banks as the distance from the channel edge to the edge of the riparian zone, or to a maximum of 30 m, whichever came first, where the edge of the riparian zone was identified either by a change in vegetation type or a lack of canopy vegetation; foliage projective cover (canopy cover) approximated as a percentage from five readings using a sighting tube, which is a simple optical device designed to enable viewing of a standardised area of foliage vertically above the observer. Five readings were taken at the 0-, 25-, 50-, 75-, and 100-m points upstream from each site. The five readings, based on the Walker and Hopkins (1984) canopy cover descriptions, were taken on each corner of a 5×5 -m square with one reading in the middle, which were then averaged, and their variance was calculated.

Vegetation assemblage composition was measured by field observations only at the site scale, which represented a 100-m section of both the left and right banks of the river channel. The composition of the vegetation was assessed as the presence or absence of the five most dominant species (by cover and abundance) within the canopy, shrub layer, and groundcover at the 0-, 50- and 100-m points along the 100-m transect. Composition was further classified as native or non-native (Table S1).

Statistical methods

A correlation matrix using Pearson's correlation coefficient was created to assess collinearity between variables at the catchment and site scale (Fig. 3). Table 2 shows the selected catchment- and site-scale variables used for subsequent multivariate analyses. Variables were chosen based on degree of collinearity (less than or equal to 0.6) and ecological significance. This procedure helped reduce the variation inflation factor of the explanatory variables, increasing the accuracy of ordination results.

To understand the direct and indirect influence of structure and/or composition of riparian vegetation on macroinvertebrate assemblage composition and water quality plus instream processes, a combination of unconstrained non-metric multidimensional scaling (NMDS) ordination and constrained redundancy analysis (RDA) with Euclidean distance matrices was used. Also, concordance between the multivariate datasets was examined using a symmetric Procrustes analysis, which allowed a direct assessment of the relationship between riparian vegetation structure and composition on macroinvertebrate assemblage composition and water quality plus instream processes. The difference

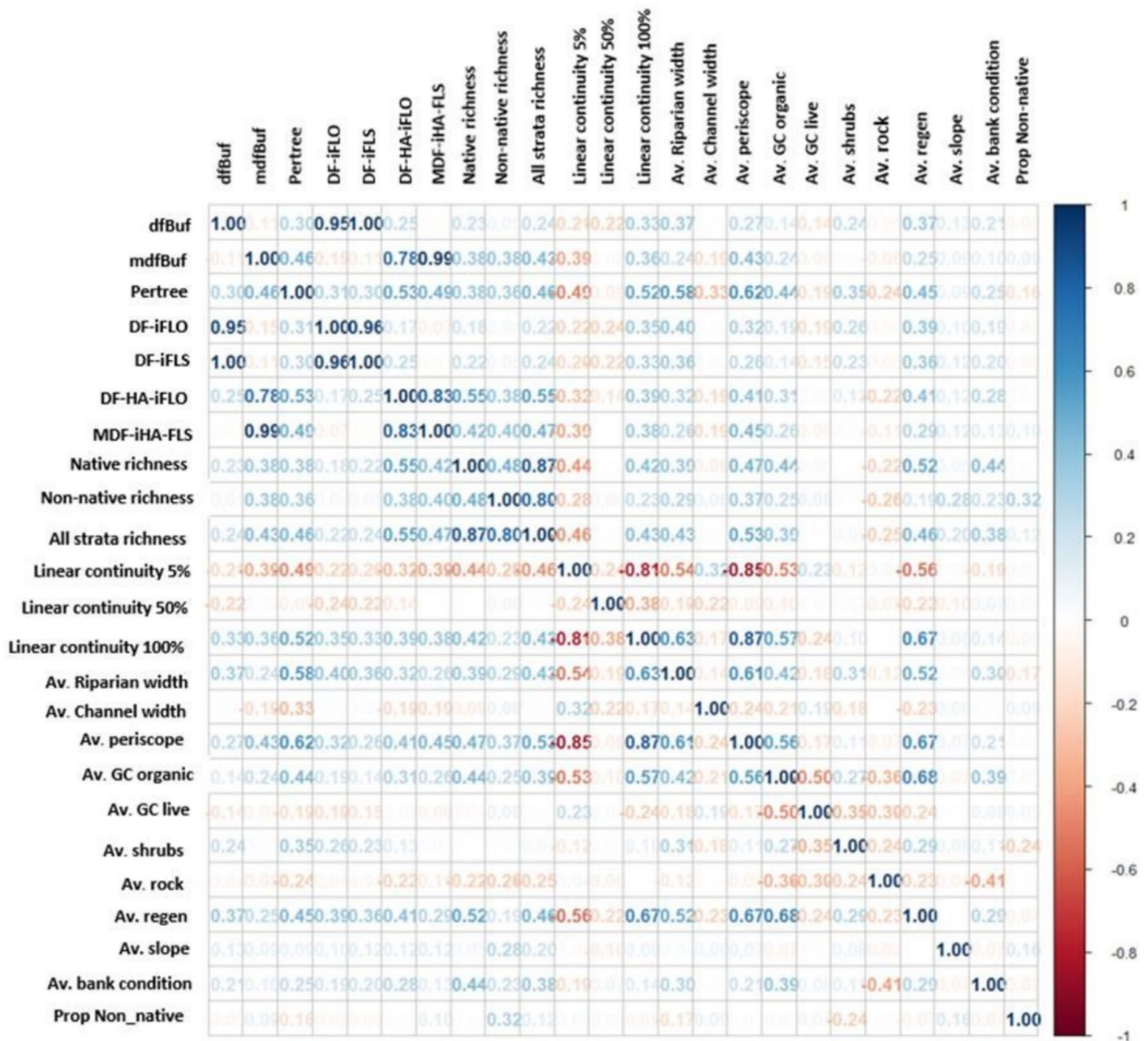


Fig. 3 Correlogram of catchment- and site-scale vegetation structural attributes. The size of the numbers indicates the strength of the pairwise relationship according to Pearson’s correlation coefficient. Blue values indicate a positive relationship, red values indicate a negative relationship

in riparian assemblage composition between stream classes was determined using an analysis of similarity (ANOSIM) based on a Jaccard dissimilarity matrix. A separate ANOSIM, based on a Bray Curtis dissimilarity matrix, was used to determine if macroinvertebrate community composition differed between stream classes. These analyses were performed using the vegan package in R (Oksanen et al. 2022).

To explore the influence of catchment-scale land use on site-scale riparian vegetation composition an NMDS ordination was used across the four different stream classes (upland, lowland, wallum, and coastal). Vegetation species

presence-absence data were Wisconsin transformed and assessed on a Jaccard dissimilarity matrix, as is commonly used for binary data (Legendre and De Cáceres 2013). An NMDS ordination was also used to explore how catchment-scale land use impacts site-scale macroinvertebrate assemblages. Multivariate analyses were carried out using the vegan package in R (Oksanen et al. 2022).

The relative influence of riparian vegetation and structure on macroinvertebrate assemblage composition and water quality plus instream processes at the site scale was assessed using RDA and a Euclidean distance matrix [vegan

Table 2 Environmental variables used to assess the relationship between riparian vegetation structural attributes and measures of nativeness and non-nativeness at multiple spatial scales and macroinvertebrate community composition

| Variable | Description | Reason for inclusion |
|--|---|---|
| Riparian dfBuf | Percentage dense woody vegetation in the 25-m upstream riparian buffer | Riparian vegetation cover throughout a catchment network has been shown to influence instream health metrics. It can also give an indication of the effect of DF-iFLO and DF-iFLS, as these variables are highly correlated |
| mdfBuf | Percentage mid-dense woody vegetation in the 25-m upstream riparian buffer | Riparian vegetation cover throughout a catchment network has been shown to influence instream health metrics. It can also indicate the effect of DFHA-iFLO and MDF-HA-iFLS, as these variables are highly correlated |
| PerTree | Percentage tree cover in the 1-km upstream reach | Local (reach) scale riparian vegetation cover has been shown to influence instream health metrics |
| Site | Avg. periscope Avg. bank condition | Site-scale canopy cover will influence instream health metrics Poor bank conditions including erosion can influence instream health. Poor bank conditions are associated with a lack of riparian vegetation |
| NN rich | A measure of non-nativeness—non-native species richness at a site across all strata (ground, shrub and canopy) | A measure of non-native richness across all strata (ground, shrub and canopy). The presence of non-native riparian vegetation may impact instream health metrics |
| Native richness | A measure of nativeness—native species richness at a site across all strata (ground, shrub and canopy) | The presence of native riparian vegetation may impact instream health metrics |
| Proportion of non-native canopy vegetation | A measure of non-nativeness—the metric was derived by determining the proportion of the canopy that comprises non-native species | Canopy vegetation is a source of allochthonous instream carbon; a high presence of non-native canopy vegetation may impact instream water quality and macroinvertebrate assemblages |
| Avg. shrubs | Average shrub coverage within a 5 × 5-m plot taken across five measurements | An indicator of the structural complexity of the riparian zone vegetation |
| Avg. riparian width | Average width of the riparian zone taken across five measurements | A measure of riparian zone structure; a narrow riparian zone may have a deleterious impact on instream health and be associated with less structural complexity |
| Avg. ground cover organic | Average organic ground cover (leaf litter, etc.) taken across five measurements | Measure of structural complexity of riparian zone; increased organic matter suggests increased vegetation cover |
| Avg. ground cover live | Average ground cover live (grasses, forbs etc.) taken across five measurements | A measure of riparian zone structural complexity |
| LC50% | Average measure of vegetation linear continuity, indicating that more than 50% of a 100-m reach consists of continuous vegetation cover | Riparian zones often act as corridors for the movement of biota and propagules; increased continuity suggests an intact riparian zone, which may positively impact instream health |

Variables were selected based on ecological relevance and degree of collinearity with other parameters (see Fig. 3)

DF-iFLO A measure of upstream catchment dense forest weighted more heavily (inverse distance weighting) close to the sampling site, *DF-iFLS* a measure of upstream catchment dense forest weighted more heavily (inverse distance weighting) closer to the upstream riparian zone, *MDF-HA-iFLS* a measure of upstream catchment mid-dense forest in the hydrologically active portion of the catchment weighted more heavily (inverse distance weighting) close to the riparian zone

package in R (Oksanen et al. 2022)]. RDA is a constrained form of ordination that explores the relationship between a response and explanatory matrix by combining regression and ordination techniques (Borcard et al. 2011). If the full RDA model was significant, an automatic stepwise model-building approach for constrained ordination based on the adjusted R^2 of the full model was then undertaken (Blanchet et al. 2008). The significance level at $p < 0.05$ of the final model and of each selected term was tested using a permutation ANOVA on 999 permutations; where required, all abundance data were Hellinger transformed, as recommended for constrained ordinations (Legendre and Anderson 1999) and constrained against range standardised environmental variables. RDAs were carried out at a regional scale, including all stream classes and in lowland sites only. This ensured that any observed patterns were not entirely explained by an upland to lowland gradient.

The first RDA explored the relationship between riparian vegetation attributes, including measures of structure and non-nativeness (Table 2), and macroinvertebrate assemblage composition. The second RDA explored the relationship between riparian vegetation attributes, including measures of structure and non-nativeness (Table 2), and water quality and instream process measurements. Subsequent RDAs were performed that assessed these relationships while controlling for the potential effect of stream class.

Procrustes rotation analyses were then performed to examine the relative impact of riparian vegetation assemblages and measures of riparian vegetation structure on macroinvertebrate assemblages and water quality plus instream processes. Procrustes analysis maximizes the fit between two ordination configurations by scaling, rotating, and dilating the solution of one matrix and overlaying it over another. Four pairwise Procrustes analyses were performed; the first examined the concordance between riparian vegetation assemblages and macroinvertebrate assemblages, the second examined the concordance between riparian vegetation structural attributes and macroinvertebrate assemblages, the third assessed the concordance between riparian vegetation assemblage composition and measures of water quality and instream processes, while the fourth assessed the concordance between riparian vegetation structural attributes and measures of water quality and instream processes. Each of the four multivariate datasets—macroinvertebrate assemblage composition, riparian structure, riparian vegetation assemblage composition, and water quality plus instream processes—was analysed using RDA, then Procrustes rotations were performed on pairs of principal component analyses (PCAs) to determine their level of concordance. The vegan package in R (Oksanen et al. 2022) was used to carry out the protest function with 4999 permutations to determine the significance of any concordance between a pair of PCA ordinations (Fig. 4).

Results

How does catchment-scale land use influence site-scale riparian vegetation composition?

To understand how catchment-scale land use influences riparian vegetation assemblage composition, an NMDS ordination was overlain with intrinsic (riparian vegetation species identity) and extrinsic (structural catchment attributes) vectors (Fig. 5a). Lowland sites tended to cluster separately from other site types (coastal, wallum, and upland), with ANOSIM suggesting significant differences between all the stream classes ($R = 0.313$, $p = 0.001$).

Vector fitting suggested lowland sites were characterised by the canopy presence of the natives *Callistemon* sp., *Melaleuca* sp. and *Acacia* sp. and the non-native *Celtis sinensis* (Chinese elm). Grasses in the riparian zone also typified lowland sites. Native rainforest canopy species *Elaeocarpus angustifolius* (blue quandong) and *Syzygium* spp. (lillipilli) were associated with the other stream classes. This separation of lowland sites from other stream classes also reflected land use, with upstream, coastal, and wallum sites being associated with dense woody vegetation (dfBuf) and mid-dense woody vegetation (mdfBuf) in the 25-m upstream riparian buffer throughout the catchment network. Lowland sites were not associated with riparian vegetation cover throughout the catchment (Fig. 5a).

How does catchment-scale land use influence site-scale macroinvertebrate assemblage composition?

To understand how catchment-scale land use influences macroinvertebrate assemblage composition, an NMDS ordination was overlain with intrinsic (macroinvertebrate taxa) and extrinsic (structural catchment attributes) vectors (Fig. 5b). An upland to lowland gradient is evident, with upland sites clustering together lower on NMDS axis 1 compared to lowland sites, which clustered higher on NMDS axis 1 (Fig. 5b). The NMDS biplot suggests that the macroinvertebrate assemblage patterns are driven by dense forest in the riparian buffer at the catchment scale, with upland sites typified by high dense forest cover, while lowland sites have low dense forest cover in the riparian buffer at the catchment scale. Mid-dense forest (mdfBuf) in the riparian buffer was associated with coastal and wallum sites (Fig. 5b). Upland, high cover sites were associated with macroinvertebrate taxa deemed to be comparatively sensitive (see Chessman 1995), including the ephemeropteran family Leptophlebiidae and the trichopteran family Leptoceridae. In comparison, lowland, low cover sites were associated with generalist taxa including Belostomatidae, copepods, and

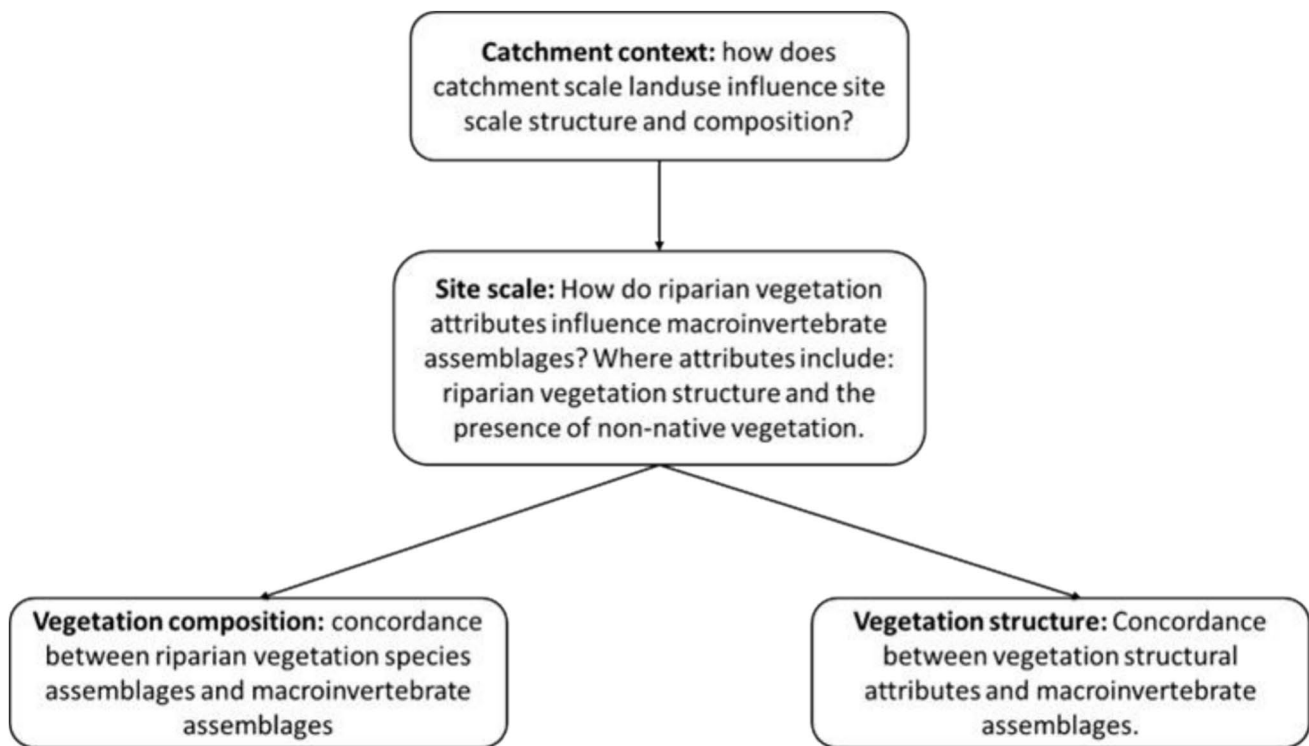


Fig. 4 Flow chart illustrating how different spatial scales and attributes are examined to determine the relative influence of riparian vegetation composition and structure on macroinvertebrate assemblages

Nematoda (Fig. 5b). ANOSIM suggested significant differences between all the stream classes ($R=0.362$, $p=0.001$).

How do site-scale riparian vegetation attributes influence macroinvertebrate assemblages?

There was a significant relationship between aquatic macroinvertebrate assemblage composition and the full riparian vegetation structure model ($p=0.001$), with the first RDA axis (RDA1) being significant ($p=0.001$). In the full model, riparian vegetation structure explained ~26% of the constrained variation in macroinvertebrate assemblage composition. An automatic stepwise model based on the adjusted R^2 of the full RDA model for macroinvertebrate assemblage composition revealed that average periscope, average ground cover organic, average ground cover live, and linear continuity (50%) were the best predictors of macroinvertebrate assemblage composition (Table 3; Fig. 6a). The reduced model of riparian vegetation structure was significant ($p=0.001$) and explained ~18% of the variation in macroinvertebrate assemblage composition, with the first three RDA axes being significant (RDA1, $p=0.001$; RDA2, $p=0.022$; RDA3, $p=0.029$).

A gradient of riparian zone structural complexity and associated macroinvertebrate sensitivity to disturbance was observed along RDA1. Structurally complex sites were

associated with macroinvertebrate taxa deemed to be comparatively sensitive (see Chessman 1995), including the ephemeropteran family Leptophlebiidae and the trichopteran family Leptoceridae. These sites tended to belong to upland, wallum and coastal stream classes. In comparison, sites with low structural complexity were associated with generalist taxa including chironomids and copepods (Fig. 6a). These sites tended to belong to the lowland stream class and were associated with high amounts of live ground cover as opposed to woody vegetation structural attributes such as canopy cover. Lowland sites that did have a riparian canopy appeared to have a large proportion of the canopy made up of non-native vegetation.

To ensure the observed patterns at a regional scale were not entirely associated with the different stream classes, an RDA that assessed the relationship between macroinvertebrate assemblages and riparian structural attributes in lowland sites only was performed (Fig. 6b). There was a significant relationship between aquatic macroinvertebrate assemblage composition in lowland sites and the full riparian vegetation structure model ($p=0.003$), with the first RDA axis being significant ($p=0.04$). In the full lowland model, riparian vegetation structure explained 31% of the constrained variation in macroinvertebrate assemblage. An automatic stepwise model based on the R^2 of the full RDA lowland model for macroinvertebrate assemblage

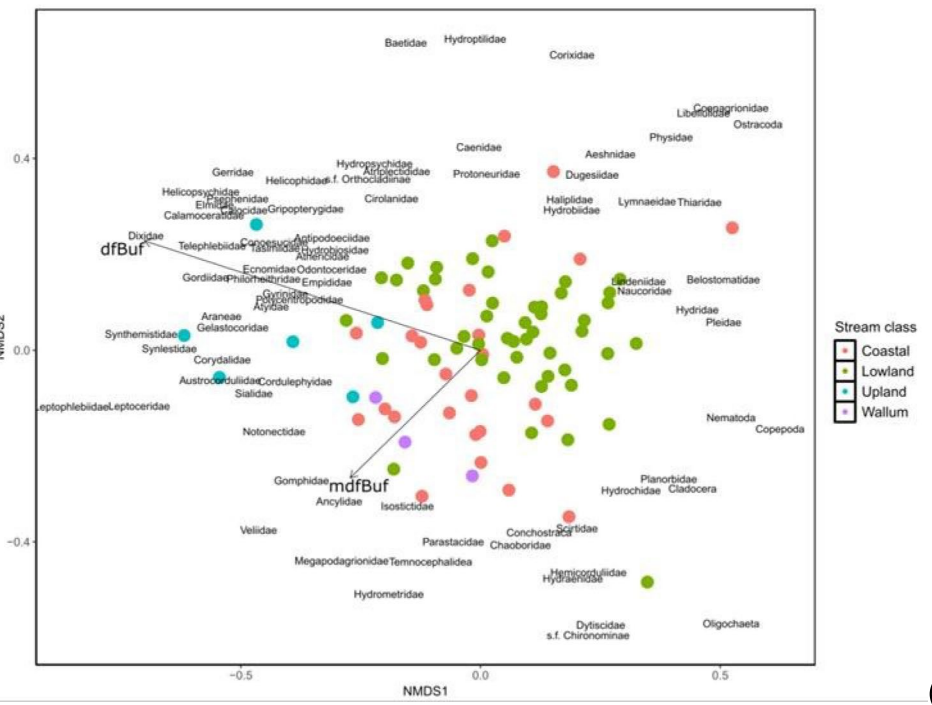
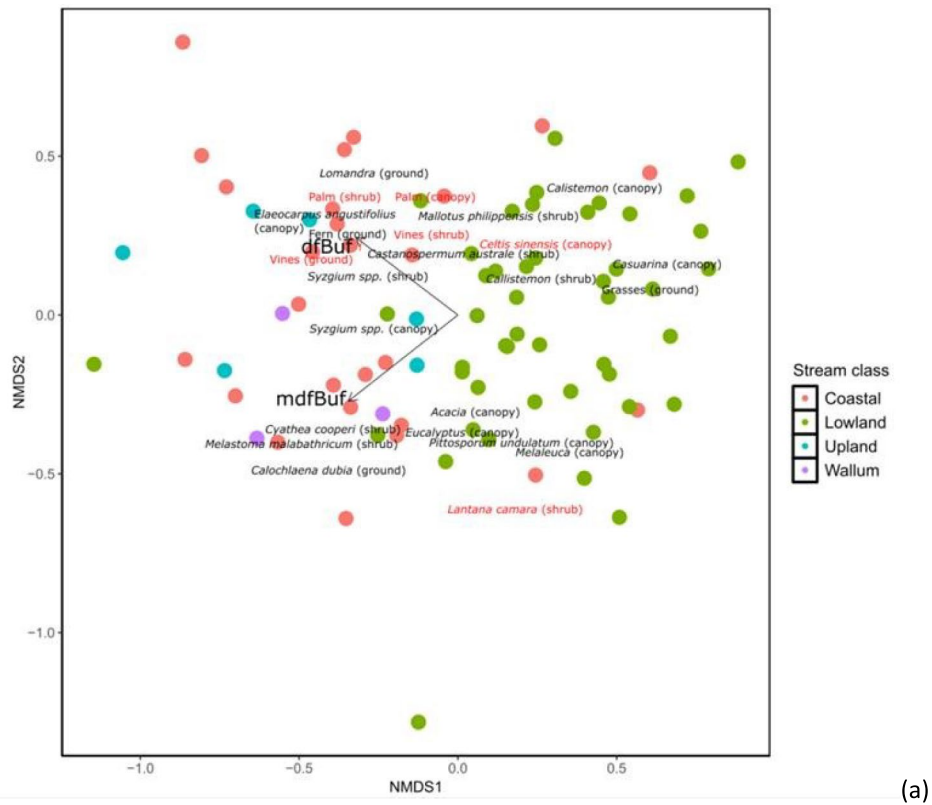


Fig. 5 Non-metric multidimensional scaling (NMDS) biplot of **a** Wisconsin transformed riparian vegetation assemblage composition based on presence-absence data on a Jaccard dissimilarity matrix ($k=3$, stress=0.169). The locations of significant vegetation species ($p < 0.01$) in multidimensional space are shown; non-native species are shown in red, native species are in black. The extrinsic vector represents the direction of significant catchment woody vegetation cover-

age ($p < 0.01$). **b** NMDS biplot of Hellinger transformed macroinvertebrate assemblage composition on a Bray–Curtis dissimilarity matrix ($k=2$, stress=0.18). The locations of significant macroinvertebrate taxa ($p < 0.01$) in multidimensional space are shown. The extrinsic vector represents the direction of significant catchment woody vegetation coverage ($p < 0.01$)

Table 3 Best predictor variables of macroinvertebrate community composition as suggested by an automatic stepwise model building approach based on the adjusted R^2 ($Adj. R^2$) of the full distance-based redundancy analysis model

| Model | Predictor variable | Adj. R^2 | AIC | $F[Pr(>)]$ |
|-------------------------------------|---------------------------|------------|---------|------------|
| Regional model (all stream classes) | Avg. periscope | 0.097 | -139.05 | 0.002 |
| | Avg. ground cover organic | 0.117 | -139.96 | 0.006 |
| | Avg. ground cover live | 0.13 | -140.17 | 0.004 |
| | Linear continuity 50% | 0.14 | -140.06 | 0.036 |
| Lowland model | Pertree | 0.052 | -83.780 | 0.002 |
| | Avg. ground cover organic | 0.077 | -84.080 | 0.006 |
| | Avg. periscope | 0.092 | -83.928 | 0.048 |

AIC Akaike information criterion

composition revealed that average organic ground cover, percentage tree cover in the 1-km upstream reach, and average periscope were the best predictors of macroinvertebrate assemblage composition in lowland sites (Table 3). The reduced model of lowland riparian structure was significant ($p=0.001$) and explained 15% of the variation in lowland macroinvertebrate assemblage composition, with the first two RDA axis being significant (RDA1, $p=0.001$; RDA2, $p=0.016$). A similar pattern emerged for the lowland sites to that observed for the regional analysis, where pollution-sensitive macroinvertebrate taxa were associated with structurally complex riparian zones and high levels of organic ground cover (Fig. 6b). Comparatively, generalist taxa were associated with open canopy sites with higher levels of live ground cover.

How do site-scale riparian vegetation attributes influence measures of water quality and instream processes?

There was a significant relationship between measures of water quality and instream processes and the full riparian vegetation structure model ($p=0.001$) with the first RDA axis being significant ($p=0.001$). In the full model, riparian vegetation structure explained ~29% of the constrained variation in measures of water quality and instream processes (Fig. 7a). An automatic stepwise model based on the adjusted R^2 of the full RDA model for measures of water quality and instream processes revealed that average periscope was the best predictor (Table 4). The reduced model of riparian vegetation structure was significant ($p=0.001$) and explained ~17% of the variation in measures of water quality and instream processes. Sites with high structural complexity, including high canopy cover, were associated with increased metabolism (gross primary production and respiration over a 24-h period) and higher variations in temperature. Sites with low structural complexity were associated with higher nutrient concentrations ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) and high pH levels (Fig. 7a).

To ensure the observed patterns were not entirely associated with stream class, an RDA that assessed the relationship

between measures of water quality and instream processes and riparian structural attributes in lowland sites only was also performed (Fig. 7b). There was a significant relationship between measures of water quality and instream processes and the full lowland riparian structure model ($p=0.002$), with the first RDA axis being significant ($p=0.002$). In the full lowland model, riparian vegetation structure explained ~34% of the constrained variation in measures of water quality and instream processes. An automatic stepwise model based on the R^2 of the full RDA lowland model for measures of water quality and instream processes revealed average periscope was the best predictor (Table 4). The reduced model of lowland riparian vegetation structure was significant ($p=0.002$) and explained ~7% of the variation in measures of water quality and instream processes. A similar pattern emerged for lowland sites only, whereby sites with low structural complexity were associated with higher values for measures of algal metabolism and nutrient processing, as measured by stable isotope ratios of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$), while sites with high structural complexity were associated with increased metabolism and increased temperature variation (Fig. 7b).

Concordance between measures of vegetation structure and composition and macroinvertebrate composition at the site scale

Procrustes analysis indicated that the fit of the macroinvertebrate assemblage PCA (dependent ordination) to the riparian vegetation assemblage PCA (independent ordination) was significantly concordant ($M2=0.78$, $p=<0.001$ after 4999 permutations), with a symmetric correlation value of 0.46. A plot of the Procrustes errors (Fig. 8a) suggested that there was a greater difference between the macroinvertebrate dataset and the vegetation dataset in lowland sites compared to sites belonging to the other stream classes. When the PCA for riparian vegetation structure (independent variable) was assessed against the macroinvertebrate PCA (dependent variable), the two were also more concordant than could be obtained by chance ($M2=0.74$, $p=<0.001$ after 4999 permutations), with a symmetric correlation value of 0.51

(Fig. 8a). The Procrustes error plots suggested a closer association between riparian vegetation species assemblages and macroinvertebrate assemblages than between riparian vegetation structural attributes and macroinvertebrate assemblages (Fig. 8a, b), although both were statistically significant.

Concordance between the water quality and instream process dataset (dependent ordination) and riparian vegetation assemblage dataset (independent ordination) was greater than could be obtained by chance ($M2 = 0.84$, $p = < 0.001$ after 4999 permutations), with a symmetric correlation value of 0.4. A plot of the Procrustes errors (Fig. 8c) suggested the difference between the water quality and instream processes dataset and the vegetation assemblage dataset was greater in lowland sites compared with upland, coastal or wallum sites. The concordance between riparian vegetation structure (independent variable) and the measures of water quality and instream processes (dependent variable) was also greater than could be obtained by chance ($M2 = 0.9$, $p = < 0.001$ after 4999 permutations), with a symmetric correlation value of 0.31 (Fig. 8d).

The Procrustes error plots suggested a closer association between riparian vegetation species assemblages and water quality plus instream processes than between riparian vegetation structural attributes and water quality (Fig. 8a, b), although both were statistically significant.

Discussion

Riparian vegetation structure at all spatial scales can influence macroinvertebrate assemblage composition and measures of water quality and instream processes (Sheldon et al. 2012; Stoll et al. 2016; Jonsson et al. 2017). Our results suggest lowland sites in SEQ are associated with low levels of woody vegetation (mdfBuf and dfBuf) in the riparian buffer at a catchment scale. In comparison, coastal and wallum sites are associated with mid-dense forest in the riparian buffer (mdfBuf) and upland sites are associated with dense forest in the riparian buffer (dfBuf). When assessed at a site scale, this catchment-scale pattern translated into low riparian zone structural complexity in lowland sites. For instance, we found that lowland sites were associated with low canopy cover, mostly consisting of non-native species and ground cover dominated by live grasses. In comparison, upland, coastal, and wallum sites were associated with high structural complexity, typified by wide riparian zones with high canopy cover, high vegetation species richness (both native and non-native), good bank condition, and organic matter (leaf litter and woody debris) in the ground cover.

The observed upland to lowland gradient of structural complexity was associated with a gradient of macroinvertebrate sensitivity to disturbance, where sensitive taxa

were associated with structurally complex upland sites. A gradient of water quality and instream processes was also observed, where high nutrient turnover, as measured by $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and high pH, were associated with lowland sites with low structural complexity. These patterns also held when assessed in lowland sites only, suggesting that regional stream class patterns are not the primary driving force behind the observed results, but rather riparian zone structural complexity at the site and catchment scale.

To unpick the relative effect of riparian zone structure and vegetation species assemblages on macroinvertebrate community composition and measures of water quality and instream processes, the variables native richness (across all strata), non-native richness (across all strata), and proportion of non-native canopy vegetation were included in the constrained ordination models. The results suggested that measures of vegetation cover, most notably canopy cover, were stronger predictors of macroinvertebrate assemblage composition and water quality and instream process metrics than measures of vegetation richness and density (native or non-native). This was true at a regional scale and when assessed in lowland sites only. These results suggested that novel riparian vegetation assemblages may support detrital food webs and function as suitable habitat for macroinvertebrates, at least when observed across coarse taxonomic and spatial scales. This was further supported by the finding that high organic matter in the riparian ground cover was an important predictor of macroinvertebrate community assemblages, highlighting the importance of allochthonous carbon to support macroinvertebrate nutrition, with subsequent effects for higher trophic orders (LeRoy and Marks 2006; Jonsson and Sponseller 2021; Oester et al. 2023).

At the family level macroinvertebrate assemblages showed a clear spatial separation between lowland and other site types (upland, wallum, and coastal). Constrained ordination plots revealed a change in macroinvertebrate assemblage composition that corresponded to a continuum of human activity and vegetation cover, including canopy cover and linear continuity. For instance, vegetated upland, coastal, and wallum streams were typified by sensitive macroinvertebrate families belonging to the shredder functional feeding groups (Leptophlebiidae in the order Ephemeroptera and Leptoceridae in the order Trichoptera). These sensitive taxa, in the orders Ephemeroptera, Trichoptera and Plecoptera, are reliant on coarse particulate organic matter inputs from riparian vegetation and are, therefore, associated with densely vegetated riparian zones (dos Reis Oliveira et al. 2020). These taxa have a short-lived terrestrial adult stage, which functions primarily as a means of reproduction and dispersal. Consequently, a lack of riparian connectivity throughout a catchment will increase dispersal costs and limit the arrival of these taxa in new environments (Leps et al. 2015; O'Toole et al. 2017).

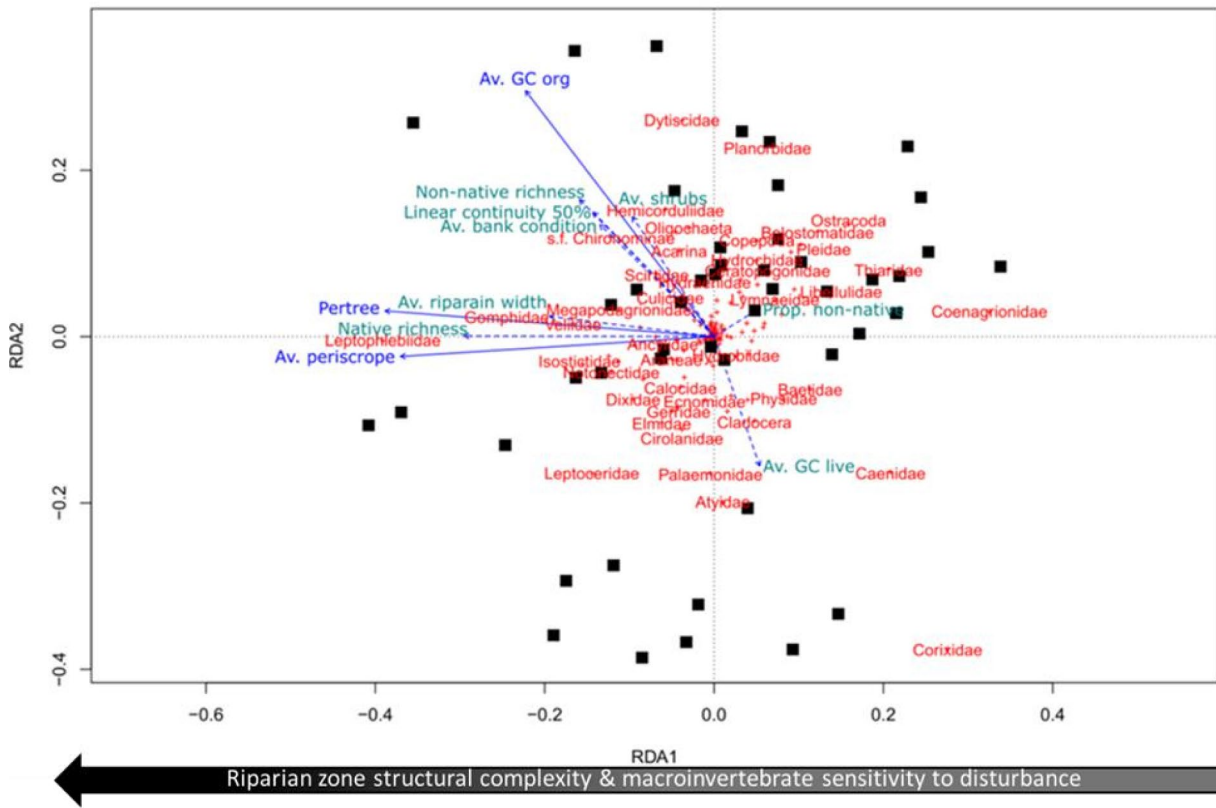
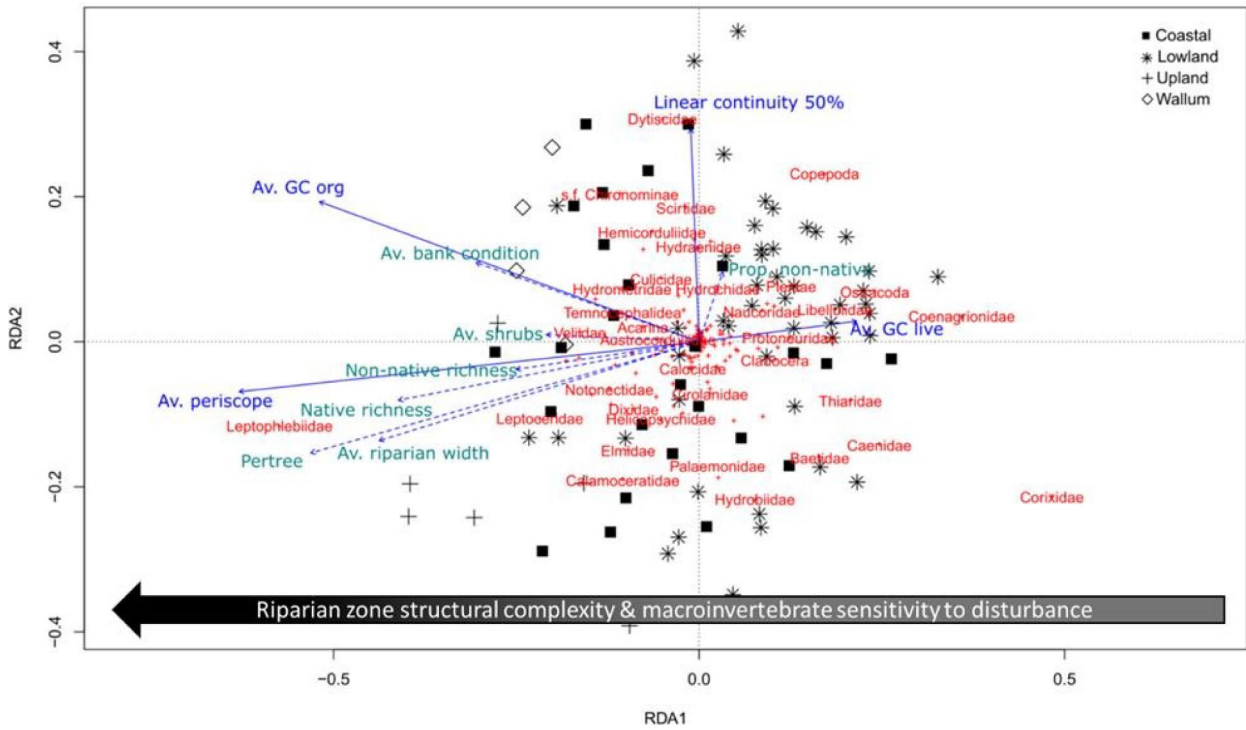


Fig. 6 Symmetrically scaled redundancy analysis (RDA) triplot illustrating **a** the relationship between attributes of physical riparian structure and macroinvertebrate assemblage composition ($p=0.001$). The significant variables ($p<0.05$) identified through the stepwise model building process are depicted as *solid blue arrows* and *dark blue text*. Symmetrically scaled RDA triplot illustrating **b** the relationship between attributes of physical riparian structure and macroinvertebrate assemblage composition in lowland sites ($p=0.001$). The significant variables ($p<0.05$) identified through the stepwise model building process are depicted as *solid blue arrows* and *dark blue text*. *Red crosses* denote the location of macroinvertebrate species. Only the names of the species most strongly influenced by the physical riparian attributes are shown. An *arrow* depicting a gradient of increased riparian zone structural complexity and macroinvertebrate sensitivity to disturbance has been superimposed on the plot

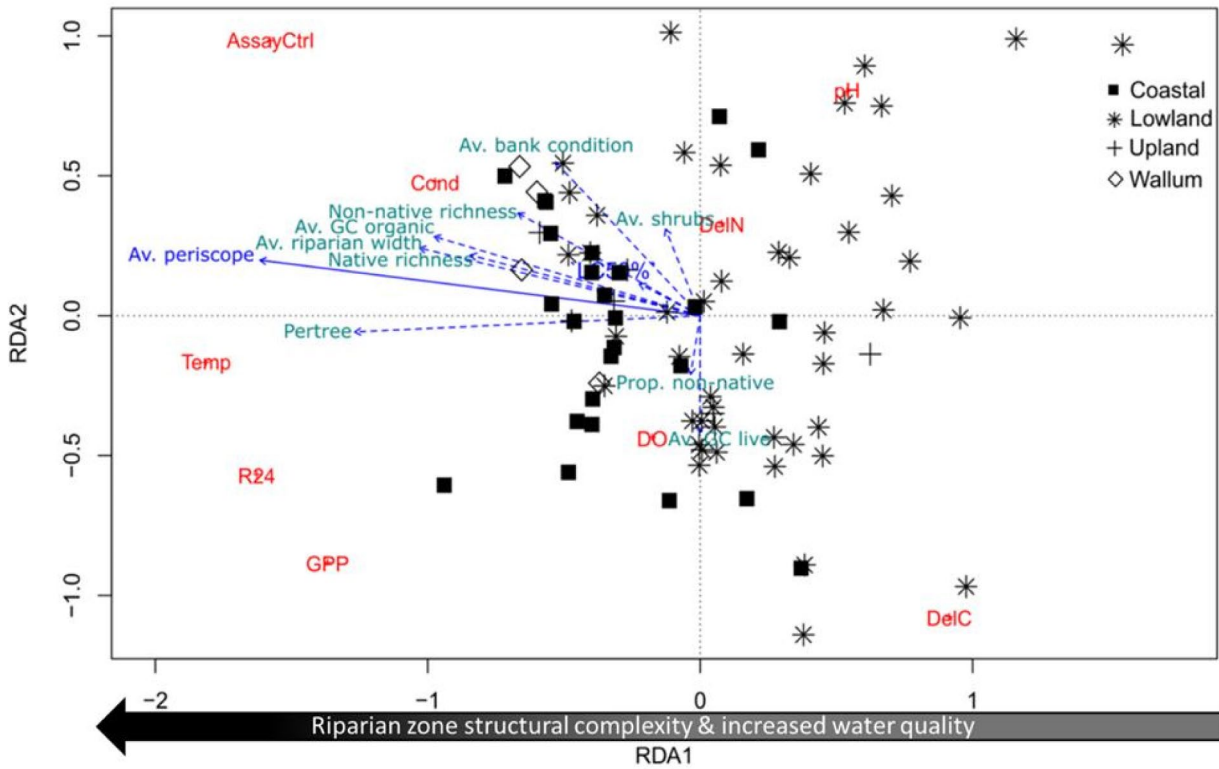
At the other end of the spectrum, sparsely vegetated lowland areas which experience a large degree of human activity were represented by generalist taxa such as cladocerans and chironomids. These generalist taxa were associated with limited riparian vegetation cover, both at the site and catchment scale. An abundance of generalist taxa has often been described for lowland areas which experience high anthropogenic stress (Johnson and Angeler 2014; Mondy and Usseglio-Polatera 2014; Leps et al. 2015; Harvey and Altermatt 2019). Non-native trees (*Celtis sinensis*) and shrubs (*Lantana camara*) also appeared to be common in lowland areas. However, as no clear impact of non-native canopy vegetation was detected on macroinvertebrate assemblages, we suggest that the presence of non-native vegetation in lowland areas is a symptom of broadscale anthropogenic disturbance and not necessarily a cause of instream degradation (MacDougall and Turkington 2005). This suggestion is supported by the Procrustes results which indicate that riparian features have less influence on macroinvertebrate assemblage composition and water quality at lowland sites compared to sites within the other stream classes. This suggests that other factors, possibly anthropogenic ones, may overshadow the effects of riparian zone attributes on instream ecosystem health metrics within lowland sites.

Our results suggest that site-based macroinvertebrate assemblage composition is structured by taxon-dependent dispersal ability combined with vegetation cover and connectivity at catchment and site scales. These results highlight the interdependence between catchment- and site-scale land use in structuring biotic assemblages (Jonsson et al. 2017; dos Reis Oliveira et al. 2020; Ma et al. 2023). The results also suggest that site-scale riparian vegetation species identity is not a primary driver of macroinvertebrate family assemblage composition, despite its potential influence on the quantity and quality of food availability and instream water quality and processes (Franklin et al. 2020a, 2020b). Rather, the physical effects of vegetation cover at site and catchment scales may interact to spatially influence macroinvertebrate assemblages, likely through mediating water

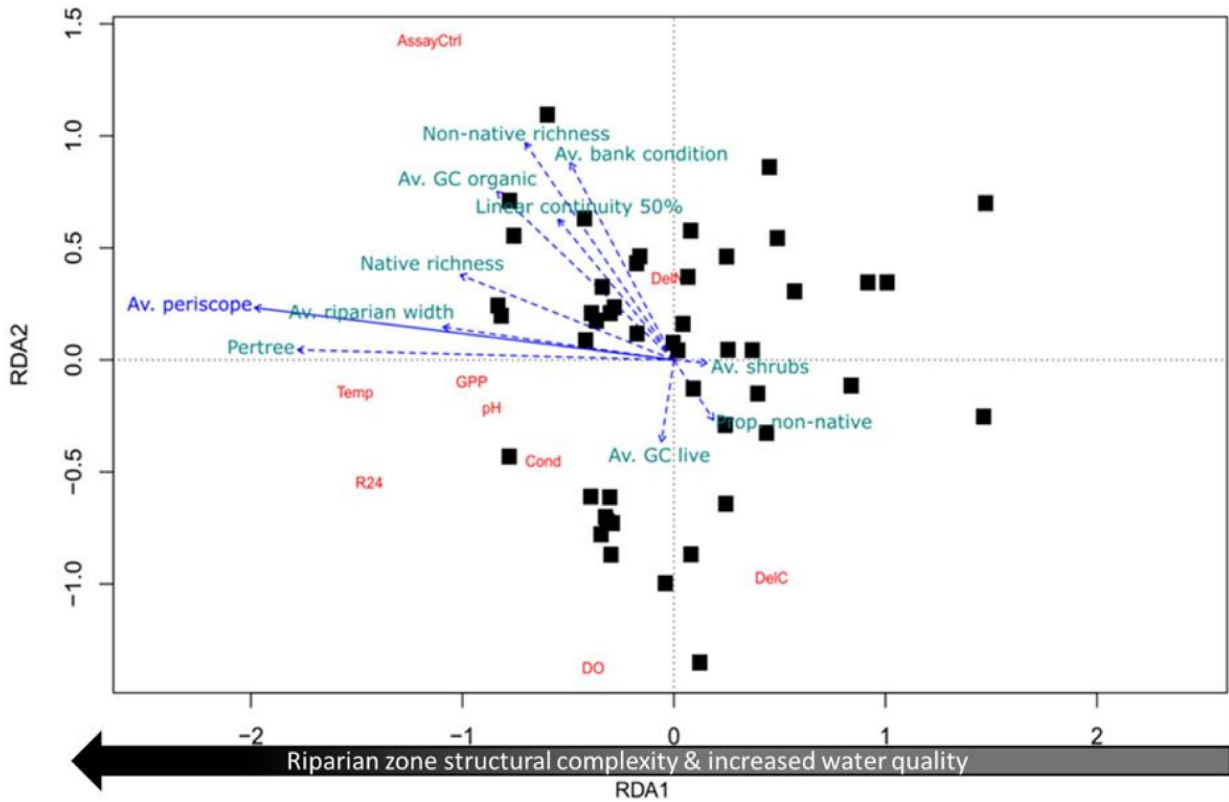
quality through the control of light and temperature regimes (Fellows et al. 2006; Gjerløv and Richardson 2010; Guo et al. 2016) and buffering sediments and associated pollutants and nutrients before they reach the instream environment (Wilkes et al. 2019; Smith et al. 2021). This notion is supported by our finding that improved water quality was associated with high catchment- and site-scale riparian vegetation cover.

When assessed broadly using attributes of riparian zone structural complexity, we found that the proportion of non-native vegetation in the riparian canopy had little impact on measures of macroinvertebrate assemblage composition or water quality and instream processes. However, when vegetation assemblage composition across all vegetation strata (ground cover, shrub layer, and canopy) was assessed against macroinvertebrate assemblages, water quality, and instream processes, associations between the multivariate matrices were revealed. A link between riparian vegetation composition and macroinvertebrate assemblage composition may suggest that different species of riparian vegetation have a differential effect on instream processes and site-scale water quality. This effect may be indirect, via an influence on water quality (Neilen et al. 2019), or it may be via a direct impact on nutrient and habitat availability through changes in leaf litter dynamics (Franklin et al. 2020a, b). However, these results may also reflect interactions between attributes of physical structure and different vegetation assemblages that exist along a gradient of land use (Jonsson et al. 2017). For instance, grass species were associated with lowland areas and low riparian vegetation cover both at the site scale and throughout the catchment network. These vegetation attributes were associated with generalist macroinvertebrates and poor water quality. In contrast, upland areas were typified by complex assemblages of tree and shrub species and high riparian canopy cover at the catchment and site scale. Upland areas were also characterised by sensitive macroinvertebrate taxa and good water quality metrics.

These results suggest that the association between riparian vegetation species composition and macroinvertebrate composition may have more to do with the structural attributes of different vegetation communities and less with species identity and endemism. A study of streamside boreal forests by Jonsson et al. (2017) suggested that macroinvertebrate assemblage composition was linked to the successional changes of terrestrial vegetation, with the macroinvertebrate assemblage differing predictably between grassed, young logged, and old logged catchments. The results in the present study, and those of Jonsson et al. (2017), highlight the importance of riparian vegetation successional trajectories and how they influence the instream environment. The results of the present study also suggested that low canopy cover sites were dominated by woody non-native canopy



(a)



(b)

Fig. 7 Symmetrically scaled RDA triplot illustrating **a** the relationship between attributes of physical riparian structure and water quality ($p=0.001$) and **b** the relationship between attributes of physical riparian structure and water quality in lowland sites ($p=0.002$). The significant variables ($p<0.05$) identified through the stepwise model building process are depicted as *solid blue arrows* and *dark blue text*. An *arrow* depicting a gradient of increased riparian zone structural complexity and increased water quality has been superimposed on the plot

Table 4 Best predictor variables of instream health as suggested by an automatic stepwise model building approach based on the Adj. R^2 of the full distance-based RDA model

| Model | Predictor variable | Adj. R^2 | AIC | $F[\text{Pr}(>)]$ |
|--|--------------------|------------|--------|-------------------|
| Regional model (all stream classes) | Avg. periscope | 0.16 | 169.38 | 0.002 |
| Lowland model | Avg. periscope | 0.11 | 99.8 | 0.002 |

vegetation along with grass in the ground cover strata and that these sites were typical of lowland areas.

These findings suggest that the vegetation of many lowland riparian areas may comprise pioneer communities, where non-native species are establishing after anthropogenic disturbance. The link between successional changes on land and instream biological communities and water quality is significant and needs to be considered when designing restoration programs. During the process of riparian restoration, significant riparian structural change will occur which may have an impact on macroinvertebrate assemblage composition, hindering ecological recovery (Samways et al. 2011; Moreno-Mateos et al. 2017). Adaptive management may be an option in low cover sites dominated by non-native canopy vegetation, where native assemblages are restored alongside the pioneer non-native canopy to maintain a level

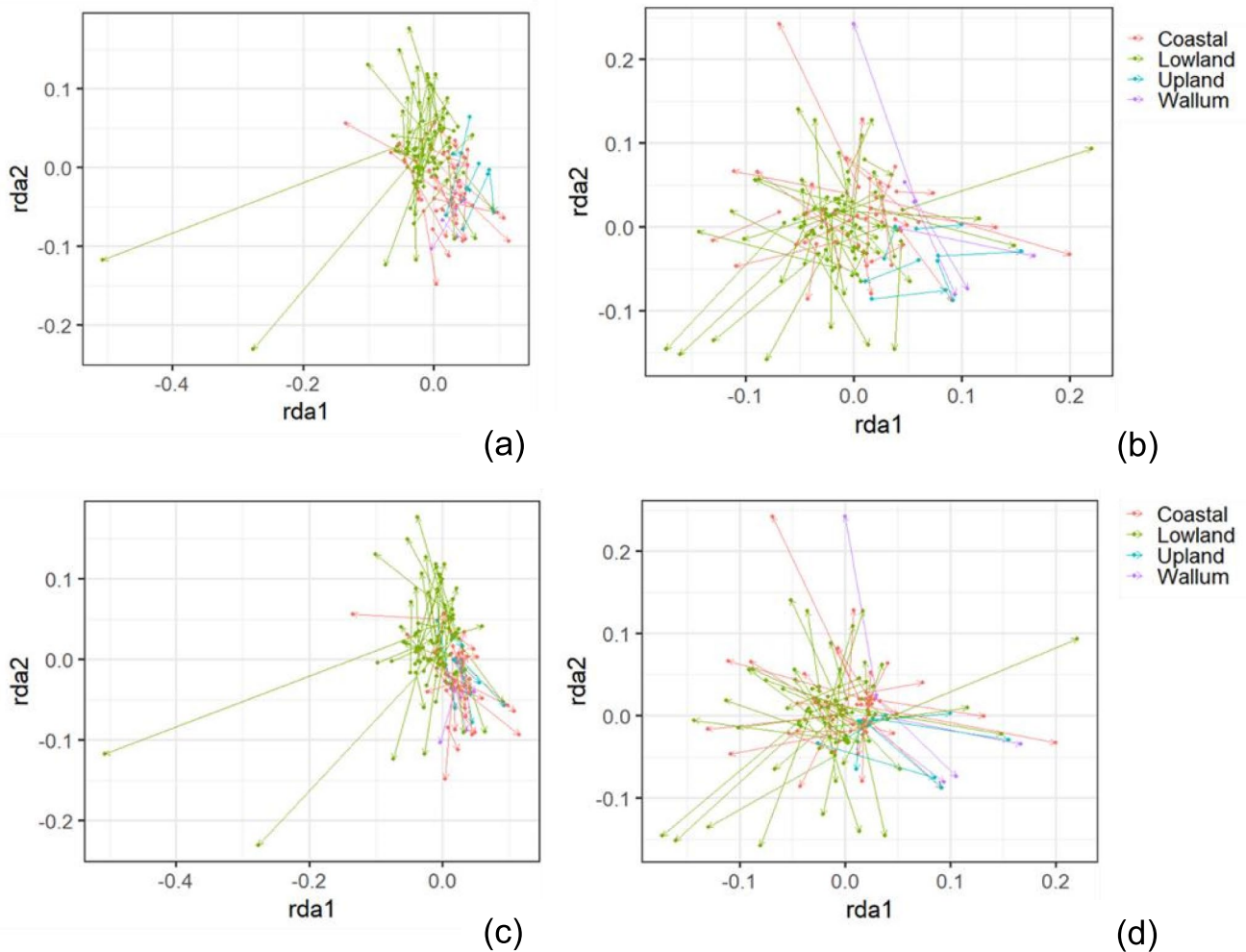


Fig. 8 Procrustes plots comparing the principal component analysis ordinations of **a** vegetation assemblages and macroinvertebrate assemblages, **b** macroinvertebrate assemblages and vegetation structural attributes, **c** vegetation assemblages and water quality, and **d**

vegetation structural attributes and water quality. A longer arrow indicates a greater difference between the two multivariate analyses. Each Procrustes fit is more concordant than could be obtained by chance ($p<0.001$)

of structural complexity during the restoration process (Samways et al. 2011).

This study provides a spatially expansive overview of the association between riparian vegetation cover (at multiple spatial scales) and macroinvertebrate community composition, water quality, and instream processes. The results suggest that the geographic origin of riparian vegetation is secondary to structural riparian vegetation attributes when explaining spatial variation in macroinvertebrate assemblages, water quality, and instream processes. Findings such as these are significant, considering the labour and financial costs involved in clearing established non-native woody vegetation from riparian zones. However, when making management decisions at the site scale it is important to consider other factors, such as the invasiveness of the species present at a site and the impact they may have on the surrounding landscape. This study highlights the need to consider ecological trade-offs between a loss of riparian vegetation structure and the impact that non-native vegetation has on attributes of instream health. A compromise between riparian vegetation structure and species assemblage will be particularly relevant in catchments that are heavily influenced by anthropogenic activities.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00027-025-01236-5>.

Acknowledgements The authors thank Healthy Land and Water for the use of the EHMP data. The authors also acknowledge the traditional custodians of the lands on which the data were collected, the peoples of the Yuggera, Gubbi Gubi and Bundjalung Nations, and recognise their enduring connection to land and water.

Author contributions LG made substantial contributions to the analyses and interpretation of the data and wrote the main text of the manuscript. FS revised the work critically, provided feedback and aided with formatting and organizing the manuscript content. HF revised the work critically and provided feedback.

Funding The initial analysis of land use data was funded under an Australian Research Council Linkage Grant (LP0668369), with additional funding provided by the Commonwealth Scientific and Industrial Research Organisation Water for a Healthy Country Flagship and the Healthy Waterways Partnership. LG was supported by an Australian Postgraduate Research Award.

Data availability Data are provided in the article and the supplementary information file.

Declarations

Conflict of interest The authors declare no competing interests.

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