

Invertebrate responses to land use in tropical streams: discrimination of impacts enhanced by analysis of discrete areas

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Abstract. We identified influences of land-use disturbances on invertebrate assemblages in streams draining eight areas of the Great Barrier Reef catchment in tropical Australia (~15.7–22°S), a region of high biodiversity. We used distance-based linear modelling (DistLM) to analyse assemblage data (103 taxa), richness and the SIGNAL2 taxon sensitivity index. DistLM of assemblages explained ~40% of variation across all samples and 7–54% of variation in individual areas. DistLM of richness and SIGNAL2 explained respectively 19–81 and 26–95% of variation. Explanatory variables were land use (especially cropping and grazing v. forest), riparian width, instream habitat, climate (drier south) and water quality (conductivity greater in south). Local impacts of activities such as mining were evident in models of individual areas. A detailed comparison of streams with contrasting riparian management demonstrated a 25% loss of richness, but no change in SIGNAL2 score. Accounting for local environmental gradients and using measures appropriate to the type of disturbance improved identification of impacts, and could form a framework for future regional monitoring of stream ecological condition. The impacts identified may be mitigated by remediation such as riparian rehabilitation, although management at catchment scales is required to be effective.

Additional keywords: disturbance, macroinvertebrate community, monitoring, riparian vegetation, river health.

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Introduction

Urban, industrial and agricultural developments degrade riparian zones and instream habitats, through vegetation clearing, weed infestation and increasing sediment and contaminant loads (Richards *et al.* 1993; Mažeika *et al.* 2004; Becker and Robson 2009; Dahm *et al.* 2013; Lorenz and Feld 2013), leading to lower biotic diversity than in undisturbed catchments (Lenat and Crawford 1994; Sponseller *et al.* 2001; Ferreira *et al.* 2014; Connolly *et al.* 2016). Impacts are superimposed on natural gradients and vary with local conditions, biota and the nature of the disturbance (Finn and Poff 2005; Maloney and Weller 2011; Clapcott *et al.* 2012; Clements *et al.* 2016; Connolly *et al.* 2016). In temperate zones, national river-health monitoring schemes involving large numbers of sites have greatly enhanced our knowledge of the anthropogenic factors that affect stream invertebrate assemblages, but studies in the tropics have generally been conducted at smaller scales (Pearson *et al.* 2017).

Regional studies aim to provide broad geographical understanding of ecological relationships and to generalise paradigms (Pearson *et al.* 2015). The small number of such studies in the tropics belies the large area of the tropics globally (~36% of the land surface), the increasing impact on streams in developing areas, and ecological differences between tropical and temperate systems (Pearson *et al.* 2015). Nevertheless, increasing numbers of tropical studies are improving our understanding of the factors that influence stream biodiversity. For example, in Brazil, physical-habitat variables had a greater influence on stream assemblages than did water quality in catchments dominated by agriculture or pasture (Ferreira *et al.* 2014); in Ecuador, forest streams showed a higher invertebrate diversity than did pasture streams, owing to the loss of riparian forest (Iñiguez-Armijos *et al.* 2018); and also in Ecuador, shading, substrate type and pH influenced invertebrate assemblages, but bioindicator metrics did not detect changes in assemblage structure between disturbed and forested streams (Bücker *et al.* 2010). In a

comparison of two small streams in the Australian Wet Tropics bioregion (hereafter, ‘Wet Tropics’), riparian vegetation was a key determinant of invertebrate diversity because of its supply of coarse particulate organic matter (CPOM), and *invertebrate* richness was a good indicator of stream biophysical condition (Connolly *et al.* 2016).

Most work on land-based impacts on Australian streams has been focused in the south-east of the continent, except for studies of intensive development in the tropical north, especially mining (e.g. Humphrey *et al.* 1995). North-eastern Australia is characterised by extensive rangelands, floodplains with intensive agriculture, and biomes of high biodiversity, including two World Heritage Areas, namely, the Great Barrier Reef (GBR) and Australian Wet Tropics (WTWHA). Although the freshwater systems of the region are important for their high diversity (Pusey *et al.* 2008; Pearson *et al.* 2015), most focus on water quality has been concerned with delivery of contaminants to the GBR from agricultural systems, with land-based pollution being a major stressor of coral-reef ecosystems (Fabricius 2005; Brodie and Pearson 2016). Water-quality stressors may occur at the catchment scale (e.g. in streams draining agricultural systems) or be more localised (e.g. cattle access, point-source discharges; Davis *et al.* 2017). Major contaminants are fertiliser-derived nitrate and herbicides from intensive agriculture, especially sugarcane and banana growing (Bainbridge *et al.* 2009; Kroon and Brodie 2009; Lewis *et al.* 2009), as well as nutrients and fine sediments from the grazing country and alluvial gullies in the rangelands (O’Reagain *et al.* 2005; Haynes *et al.* 2007). High contaminant loads in wet-season floods present the highest water-quality risk to marine ecosystems, but the greatest risk in streams is continuous input of contaminants over long periods of base flow (Davis *et al.* 2017). There are only a few published studies on within-catchment water quality and ecosystem health in the GBR region (Davis *et al.* 2017), including studies in the Wet Tropics (e.g. Pearson *et al.* 2013; Connolly *et al.* 2015, 2016) and wet-dry tropics (e.g. Perna and Burrows 2005; Preite and Pearson 2017).

Using a dataset derived from several studies, we investigated the effects of anthropogenic disturbance on invertebrate assemblages in coastal streams of the GBR catchment. Land-use change involved forest clearing for grazing, sugarcane production and urban development, associated reduction in extent of riparian vegetation, and alluvial mining. We compared invertebrate responses to measures of disturbance, including land-use area, riparian extent and water quality, across stream sites at regional and discrete (‘local’) scales, using distance-based linear modelling, taxonomic richness and the SIGNAL2 index, which provides a score for each sample according to sensitivity of taxa (Chessman 2003). We predicted that the composition of the invertebrate assemblage would be sensitive to disturbances, that responses would be consistent across scales and sampling areas, and that our different indicators would perform similarly. We investigated the effect of scale on our analysis by treating all samples as a whole, as northern and southern regions, and in individual sampling areas. We predicted that local-scale analysis would identify impacts that were hidden at a larger scale, although smaller sample sizes might obscure the result.

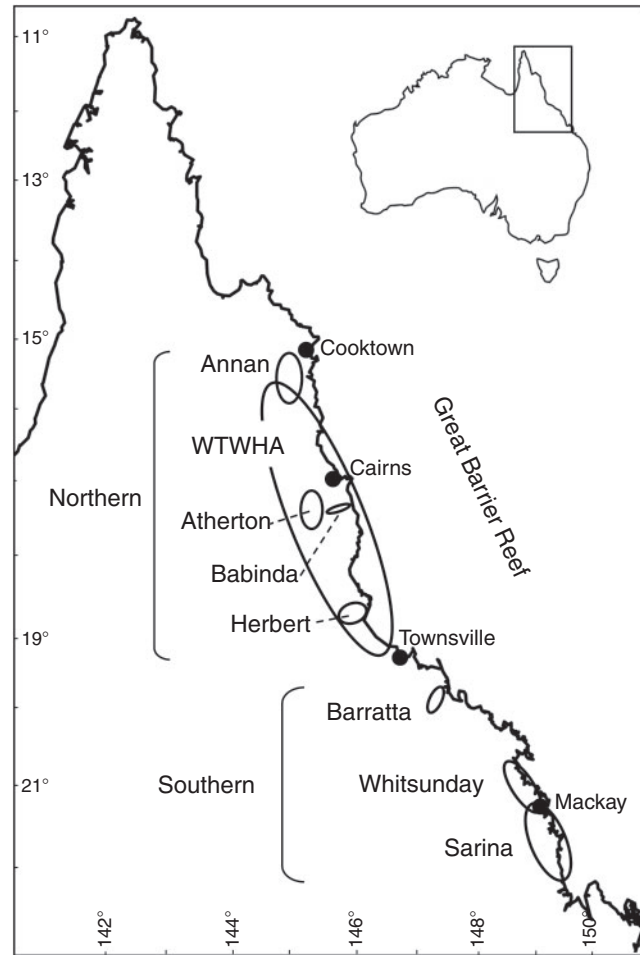


Fig. 1. Location of eight sampling areas in north-eastern Australia, with northern and southern regions indicated. WTWHA, Australian Wet Tropics World Heritage Area.

Materials and methods

Study region and sites

We selected 143 sampling sites from streams in eight sampling areas between 15.7 and 22°S (Fig. 1, Tables 1 and S1, the latter available as Supplementary material for this paper), representing ~50 000 km² (~13%) of the GBR catchment area. The climate of the region is seasonal tropical, with warm summers (November–March) and cooler winters (May–September), with rainfall concentrated in the summer, although more evenly distributed in the wetter areas (Table 1). Study streams (Orders 3–5) were flowing in the dry season, although not all are considered perennial on the basis of long-term flow records (Table 1; Kennard *et al.* 2010). Stream-flow classification correlated with annual rainfall, except in those areas where base flows were boosted by extensive basalt aquifers (Atherton streams), or by irrigation drainage (Barratta Creek, Sarina area). Background multi-year water-quality data for the study region were obtained from the Queensland Department of Natural Resources, Mines and Energy (<https://water-monitoring.information.qld.gov.au/>, accessed 16 January 2018).

Table 1. Characteristics of study areas

Ranges (min.–max.) across samples are given when appropriate, except for rainfall in areas where only single weather stations were available. Maximum riparian width was deemed to be 100 m. Flow classes follow Kennard *et al.* (2010), and include the following: 3, stable summer baseflow (perennial); 7, unpredictable intermittent; 11, unpredictable summer highly intermittent. Data-source abbreviations: BOM, Australian Bureau of Meteorology; GE, Google Earth; GPS, global positioning system at site. WTWHA, Australian Wet Tropics World Heritage Area

Variable	Source	Study area							
		Annan	WTWHA	Babinda	Atherton	Herbert	Barratta	Whitsunday	Sarina
Number of sites, samples		16, 22	20, 38	19, 19	29, 29	26, 26	9, 9	13, 24	25, 36
Latitude (°S)	GPS & GE	15.6–15.8	15.7–18.4	17.1–17.4	17.2–17.6	18.5–18.8	19.6–19.8	20.6–21.3	21.2–21.9
Altitude (m)	GPS & GE	49–235	12–620	10–143	630–940	6–23	10–33	20–141	13–74
Flow class	Kennard	3	3	3	3	3	11 ^A	7	11 ^A
Annual rainfall (mm)	BOM	1979	1268–4264	4264	1268–2619	2072	1043	1402–1742	1402–1754
Monthly rainfall variation (maximum : minimum ratio)	BOM	17.4	6.9–18.1	7.1	7.4–17.7	12.6	17.9	12.6–18.7	12.5–15.1
Gradient (%)	GE	2.6–15.6	0.7–31.3	4.9–14.2	0.7–7.2	0.01–19	0.1–2.0	0.8–12	0.1–6.6
Riparian width (site) (m)	GE	10–100	70–100	3–100	0–100	0–90	0–70	0–100	0–60
Catchment area (km ²)	GE	1.6–276	0.6–374	1.5–106	0.1–127	1.7–115	3.5–498	2.5–1223	3.5–300
Forest percentage area	GE	35–100	80–100	80–100	0–100	0–89	0–50	27–100	0–85
Grazing percentage area	GE	0–63	0–10	0–1.4	0–100	0–20	0–78	0–73	9–89
Cropping percentage area	GE	0–0.2	0	0–20	0–100	6–100	0–68	0–28	0–86
Urban percentage area	GE	0–2.4	0	0–1.7	0–17	0–13	0	0–0.2	0–12
Conductivity (µS cm ⁻¹)	Field data	46–115	20–111	21–32	27–213	50–160	250–454	69–817	45–1167
pH	Field data	5.0–6.2	5.2–7.2	5.5–6.4	6.2–7.7	6.4–6.8	5.8–9	6.8–9.3	5.9–8.5
Number of taxa (total)	Field data	21	65	45	63	16	57	48	63
Number of taxa/sample	Field data	14.6±0.88	23.1±1.24	18.4±0.97	21.4±1.11	10.8±0.31	31.1±2.58	16.2±0.82	19.4±0.92

^AFlow was supplemented by irrigation tailwater at some Barratta Creek and Sarina sites.

Sampling sites included streams that were undisturbed and streams draining anthropologically disturbed catchments. Streams of the Annan area originated in forested mountains in the northern Wet Tropics bioregion; mid- and lower reaches of the catchments transitioned into woodland, retaining riparian vegetation. Land use included grazing and alluvial tin mining, which caused the deposition of fine sediments in some streams (Hortle and Pearson 1990). WTWHA sites were undisturbed streams located from uplands to lowlands and were a subset of those described by Pearson *et al.* (2017). Within the Wet Tropics, we sampled three smaller areas that were subject to anthropogenic disturbance, namely, the Atherton, Babinda and Herbert areas. The Atherton streams were located on the Atherton Tableland, a plateau to the west of the main mountain range, much of which was used for grazing and cropping, often with limited remnant riparian vegetation. Streams in the Herbert area drained forested escarpments and the Herbert River floodplain, mostly through sugarcane plantations with limited riparian vegetation (Pearson *et al.* 2003). Streams in the Babinda area drained the highest Wet Tropics mountains through a coastal floodplain, which was almost entirely devoted to sugarcane growing, with riparian condition differing between the two study streams: forest vegetation was largely intact along Behana Creek, whereas, along Babinda Creek, it was highly disturbed and dominated by invasive grasses and weeds (Connolly *et al.* 2015, 2016).

Barratta Creek drained low wooded hills and the floodplain to the north of the Burdekin River, fed by heavy wet-season rains, over-bank flooding of the Burdekin River, and irrigation tailwater from sugarcane plantations, which covered much of the floodplain. Streams in the Whitsunday area drained the forested mountain range and floodplains, which were used for grazing and sugarcane growing. Riparian vegetation was generally sparse on the floodplain. Streams in the Sarina area were similar to the Whitsunday streams, except that for many of them adjacent sugarcane was fertilised with dunder, a waste product from the Sarina distillery containing high concentrations of dissolved organic material and plant nutrients.

Sampling

Samples were mostly collected in the mid-dry season, with additional late dry-season samples being collected for some sites, giving a total of 203 pooled samples for the analysis, each of which comprised several replicates. Benthic invertebrates were collected from the predominant substratum at each site (stones, sand, plants or leaf litter) by using a dip net (210- μ m mesh), upstream of which patches of stream bed of ~ 0.1 m² were scoured by hand, causing invertebrates to be washed into the net. Samples were preserved in 80% ethanol and returned to the laboratory, where invertebrates were identified and counted. Taxa were grouped by family or higher to standardise taxonomic resolution across regions. Family-level identification is typically adequate for discriminating among sites (Chessman *et al.* 2007; Heino 2008; Connolly *et al.* 2016).

For each site, we recorded geomorphological features of the landscape, stream dimensions (catchment area; distance and gradient from source), predominant in-stream habitat, riparian width, areas of different land uses and water quality (Table 2).

For the Babinda sites, we measured sediment size for each invertebrate sample by sieving sediment samples and weighing size categories.

Analysis

Principal-component analysis of normalised data (PCA, in Primer, ver. 6.1.2, PRIMER-E Ltd, Plymouth, UK) was used to investigate background water-quality gradients across the study region, from more than 2000 Queensland Government samples. PCA was also used to investigate gradients in environmental and land-use variables for the study sites. Correlations among landscape, disturbance and water-quality measures were calculated in Statistix (ver. 10, Analytical Software, Tallahassee, FL, USA).

Twenty-four invertebrate taxa that each contributed more than 0.5% of overall abundance were included in multivariate analyses. Data were square-root transformed and standardised by the sample total prior to generating Bray–Curtis resemblance matrices. The combined influence of the selected variables on the invertebrate assemblages, taxonomic richness and the SIGNAL2 index (presence–absence and weighted by abundance, following fourth-root transformation and standardisation of data; Chessman 2003) was investigated with distance-based linear modelling (DistLM) in Permanova+ (ver. 1.0.2, in the Primer package), using forward selection and Akaike information criterion adjusted for small sample sizes (AICc) as the selection criterion, for all samples, northern and southern regions and individual areas. DistLM seeks the most significant relationships between a similarity matrix and environmental variables by progressively modelling the matrix against the most influential variable, taking the residuals of that relationship, modelling the next most influential variable, and so on. Correlations among variables are, thus, accounted for. However, as reduction of highly correlated variables ($r = \sim 0.95$) is recommended (Anderson *et al.* 2008), we removed one of each pair of variables with $r > 0.94$ (Table 2). Following inspection of initial draughtsman plots, we log-transformed some environmental variables to improve linear relationships, as recommended (Table 2). Relationships among sample areas, environmental data and invertebrates were illustrated in ordination space using redundancy analysis (RDA, part of the DistLM procedure). Relationships between environmental variables and taxonomic richness and SIGNAL2 scores were illustrated by scatterplots and analysed using linear regression. We used ANCOVA in Statistix to compare richness and SIGNAL2 scores between streams in the Babinda area, taking into account sediment size at each site.

Results

Streams from the different sample areas varied in landscape metrics, rainfall and flow, proportions of land under different uses, water quality and the number of taxa collected (Table 1). PCA of the Queensland Government water-quality data demonstrated differences among regions mainly because of (1) gradients in major ions, conductivity and associated variables, which correlated with latitude (Axis 1, 42% of the variation, $r = 0.829$, $P = 0.006$), with higher conductivity and ionic concentrations in the southern streams and, (2) concentrations of

Table 2. Environmental variables recorded for each site and used in or excluded from analyses
 'log' indicates log₁₀ transformation applied prior to analysis (see text)

Variable	Definition	Reason for exclusion
Climate		
RainTot ^A	log(mean annual rainfall)	
RainMax ^A	Mean monthly maximum rainfall	<i>r</i> with RainTot (0.983)
RainMin ^A	Mean monthly minimum rainfall	<i>r</i> with RainTot (0.979)
RainVar ^A	Rainfall variation: monthly maximum : minimum ratio	
Season	Season: mid- or late dry season	
Landscape		
Lat	Latitude	
Long	Longitude	Not relevant
Alt	log altitude (elevation)	
Catch	log catchment area upstream of site	
Length	log stream length upstream of site	
Grad	log stream gradient upstream of site	
Land use		
Forest	Proportion of forest or woodland in catchment	
Grazing	log proportion of catchment under grazing	
Crops	log proportion of catchment under cropping	
Urban	log proportion of catchment urbanised	
Mining	Instream sedimentation from mines (1–4 scale)	
Dunder	Dunder (distillery waste) applied to agricultural land upstream of site (1–2 scale)	
Riparian		
Rip site	Riparian width at site (maximum 100 m)	
Rip upstream	Mean riparian width within 10 km upstream of site	
Habitat		
Stones	Dominant habitat stones	
Sand	Dominant habitat sand	<i>r</i> with stones (–0.946)
Plants	Dominant habitat macrophytes	
Litter	Dominant habitat leaf litter	
Water quality		
Conduct	Log electrical conductivity at time of sampling	
pH	pH at time of sampling	

^ARainfall data from the nearest station of Bureau of Meteorology (<http://www.bom.gov.au/climate/data/>, accessed 10 January 2018).

dissolved oxygen and several metal ions, suspended solids and colour, which correlated with rainfall variation (Axis 2, 17% of the variation, $r = -0.914$, $P < 0.001$; Fig. S1, available as Supplementary material for this paper). PCA of the environmental data recorded at each site also demonstrated correlation between water quality and latitude, negative correlation between variables representing intact landscapes (forest, riparian width) and disturbed landscapes (crops, grazing) and contrasts in rainfall measures and habitats (Fig. 2).

In total, 103 taxa of invertebrates (family or higher) were recognised, 55 of which occurred in less than 10% of samples and 13 of which occurred in more than 50% of samples; these 13 were, in order of ubiquity, Chironomidae, Baetidae, Leptophlebiidae, Caenidae, Hydropsychidae, Elmidae, Simuliidae, Lep-toceridae, Philopotomidae, Psephenidae, Tipulidae, Ceratopogonidae and Oligochaeta (Table S2, available as Supplementary material for this paper).

The DistLM model for all sites produced a solution that explained ~40% of the total variation (Table 3), with 27% of the variation explained by the first two RDA axes (Fig. 3a–c). Most influential variables were land use (cropping v. forest), latitude, habitat (litter) and riparian site width. Northern and southern

sites separated clearly on Axis 2. Lower disturbance (to the left of Axis 1) related to the presence of stoneflies, leptophlebiid mayflies, caddis larvae and elmids; greater disturbance (to the right of Axis 1) related to the presence of oligochaetes, microcrustaceans, caenid mayflies and chironomids.

The separate DistLM models for northern and southern sites produced solutions that explained respectively ~47 and 40% of the total variation (Table 3), with 35 and 34% of the variation being explained by the first two RDA axes. For northern sites (Fig. 3d–f), the most influential variables were land use (cropping v. forest) and riparian site width. Lower disturbance (to the left of Axis 1) again related to presence of stoneflies, leptophlebiid mayflies, caddis larvae and elmids; greater disturbance (to the right of Axis 1) related to presence of nematodes, oligochaetes, planorbid snails, microcrustaceans, caenid mayflies and leptocerids. For southern sites (Fig. 3g–i), the most influential variables were season and dunder. Lower disturbance (to the right of Axis 1) related to the presence of leptophlebiid and baetid mayflies, caddis larvae, pyralids and psephenids; greater disturbance (to the left of Axis 1) related to the presence of oligochaetes, thiarid snails, atyid shrimps, caenid mayflies and ceratopogonids.

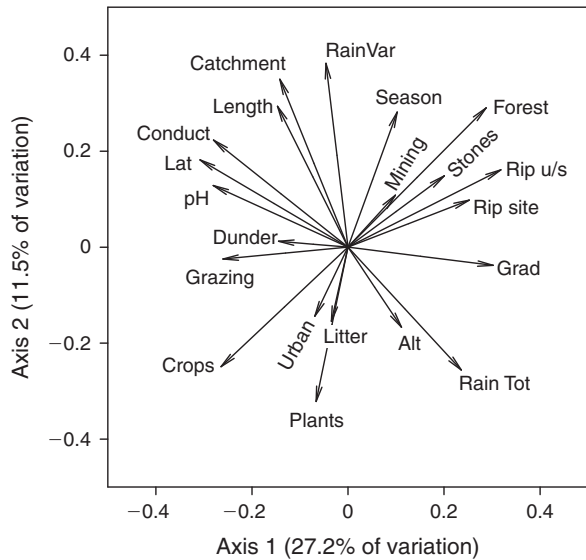


Fig. 2. First two axes of a principal-component analysis (PCA) of environmental data recorded for each site, showing vectors for each variable. Proportion of variation explained by each axis indicated. The variables are defined in Table 2.

The DistLM models of assemblage data for individual areas produced solutions that explained 7–54% of the total variation (Table 3), with most of the variation being accommodated in the first two RDA axes (Fig. 4). The number of samples had no bearing on the variation explained by the models ($r = 0.191$, $P = 0.651$). Important variables differed among models, but disturbance variables figured in most of them, and all except the WTWHA and Atherton models included variables that explained more than 10% of the variation. For the WTWHA, which had no major human disturbance, influences were mainly season and conductivity, with altitude and catchment area explaining a small amount of the variation. Abundant taxa positively related with season; that is, they were more abundant as the dry season progressed. For other areas, land use (mainly cropping v. forest, and urbanisation in three areas) and other impacts (especially mining in the Annan area and dunder in the Sarina area) were important in the models. Riparian width (at the site or upstream) was important in several models. Habitat variables were important in some models, such as, for example, stones in the Babinda area, in which there was a gradient from stones to sand, and in the Herbert area, contrasting with litter as an alternative habitat. The suite of invertebrate taxa correlating with more disturbed and less disturbed environments was similar to that in the broader-scale analyses.

Table 3. Summary of results of distance-based linear modelling (DistLM)

Results are shown for assemblages, richness and SIGNAL2 scores across all sites (All), all northern sites (All north), all southern sites (All south) and individual study areas (see Fig. 1). For each model, percentage variation in the dataset explained by the model (Model%) and individual variables contributing >10% of the data variation (Var%) with $P < 0.05$ are shown. Directionality of relationships can be seen in Fig. 3–5. Individual variables are defined in Table 2. Statistical details are shown in Tables S2 and S3. WTWHA, Australian Wet Tropics World Heritage Area

AREA	Assemblage similarity			Richness			SIGNAL2		
	Model%	Variable	Var%	Model%	Variable	Var%	Model%	Variable	Var%
All	40.3	Crops	11	38.4			61.8	Forest	33
								Litter	10.8
All north	46.8	Crops	17.1	48	Altitude	18.9	70.5	Crops	39.7
All south	39.4	Season	15.3	55.1	Season	29.2	72.7	Season	26.7
		Dunder	10.6		RainTot	13.1		Conduct	19.2
								RainTot	14.4
Annan	22.9	Mining	22.9	80.5	Mining	34.7	25.9	Conduct	15.5
					Length	16.4		Rip u/s	10.3
					Latitude	25.3			
WTWHA	29.2			54.8	Season	31.6	40	Lat	22.4
					RainTot	18.1		Season	11.6
Babinda	43.9	Forest	33.3	51.6	Rip u/s	51.6	42.9	Forest	42.9
		Stones	10.6						
Atherton	6.8			19	Stones	10.1	49.7	Rip site	12.8
								Stones	19.6
								Lat	11.2
Herbert	54.3	Litter	30.7	49.6	Plants	32.5	75.4	pH	41.7
		Altitude	16					Stones	11.1
								Alt	12.3
Barratta	28.5	Rip site	28.5	14.5			94.6	Catch	54.2
								pH	31.2
Whitsunday	34.7	Season	18	70	Grazing	21.8	45.7	Lat	20.4
		Urban	16.7		Length	29.6		Forest	16.3
Sarina	25.1	Dunder	15.8	33	Season	33	77.3	Conduct	36.4
								Season	18.1

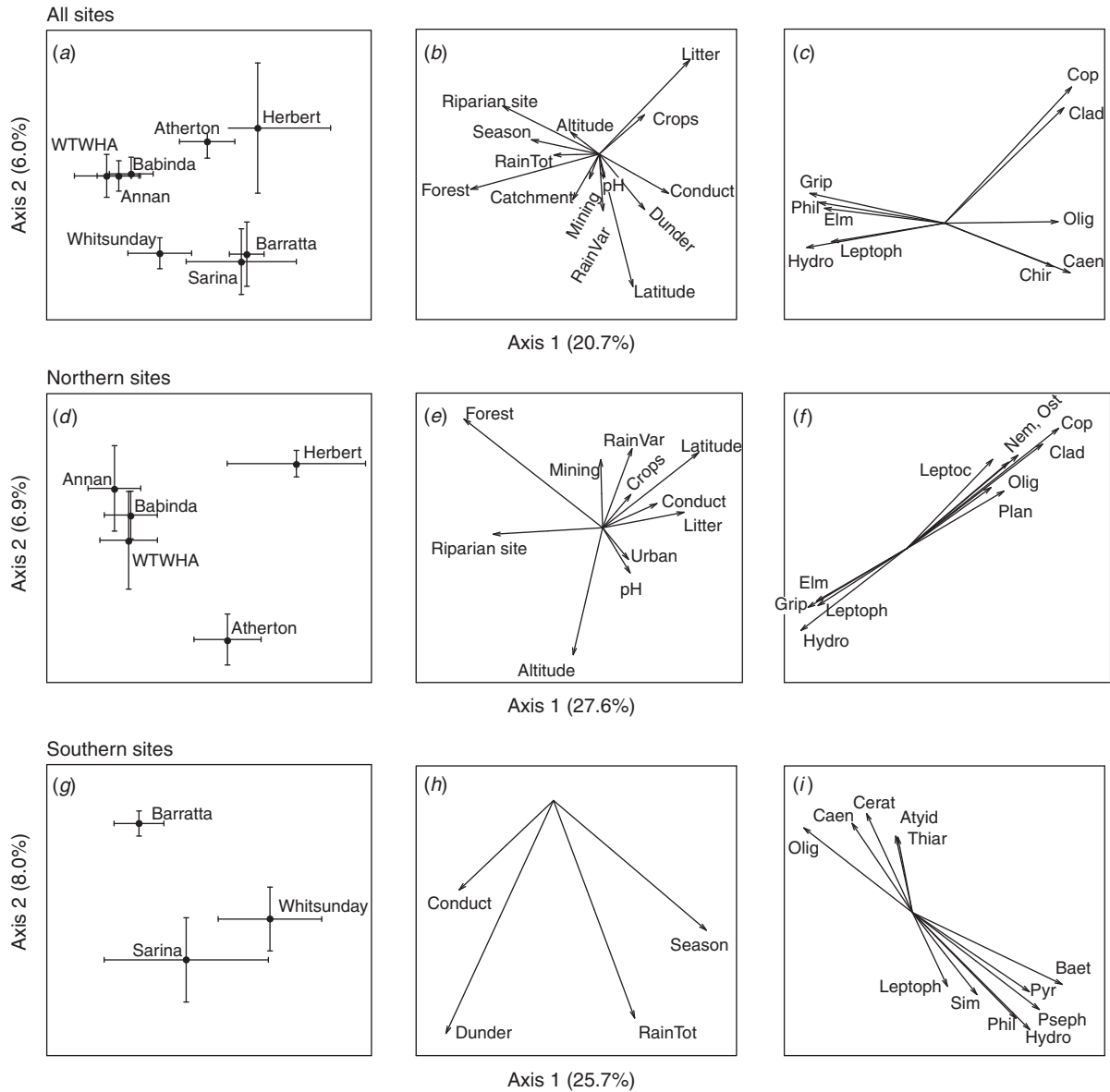


Fig. 3. Redundancy analysis (RDA) plots from distance-based linear modelling (DistLM) analysis of (a–c) all, (d–f) northern and (g–i) southern sites (see Fig 1). Ordinations are of sites (left panels; centroids \pm s.d.), environmental vectors (central panels) and invertebrate vectors (right panels). Relative importance of axes (percentage of variation explained) is indicated. Environmental variables are defined in Table 2. Invertebrate abbreviations: Atyid, Atyidae; Baet, Baetidae; Caen, Caenidae; Cerat, Ceratopogonidae; Chir, Chironomidae; Clad, Cladocera; Cop, Copepoda; Elm, Elmidae; Grip, Griptopterygidae; Hydro, Hydropsychidae; Leptoc, Leptoceridae; Leptoph, Leptophlebiidae; Nem, Nematoda; Olig, Oligochaeta; Ost, Ostracoda; Phil, Philopotomidae; Plan, Planorbidae; Pseph, Psephenidae; Pyr, Pyralidae; Sim, Simuliidae; Thiar, Thiaridae. WTWHA, Australian Wet Tropics World Heritage Area.

Richness of taxa varied from 16 to 65, weighted SIGNAL2 scores varied from 4.6 to 8.7, and presence–absence SIGNAL2 scores varied from 2.6 to 6.7 among sites. As presence–absence and weighted scores were closely related ($F_{1,201} = 5409.3$, $P < 0.0001$; $r^2 = 0.964$), only the weighted score was used for further analysis. Richness and SIGNAL2 scores did not correlate ($r^2 < 0.001$, $P = 0.923$). The DistLM models for richness explained 19–81% of variation in the data, and for SIGNAL2 explained 26–95% of the variation (Table 3). Important environmental variables in the richness models included

mainly climate and landscape variables, except that mining was important in the Annan area, riparian width in the Babinda area and grazing in the Whitsunday area (Fig. 5). Important variables in the SIGNAL2 models included disturbance-related land-use, riparian or water-quality variables in all models apart from the WTWHA model. Particularly strong relationships were evident between SIGNAL2 and forest area overall and in the Babinda area, cropping in the northern region, catchment size in the Barratta area, and conductivity and dunder application in the Sarina area (Fig. 5).

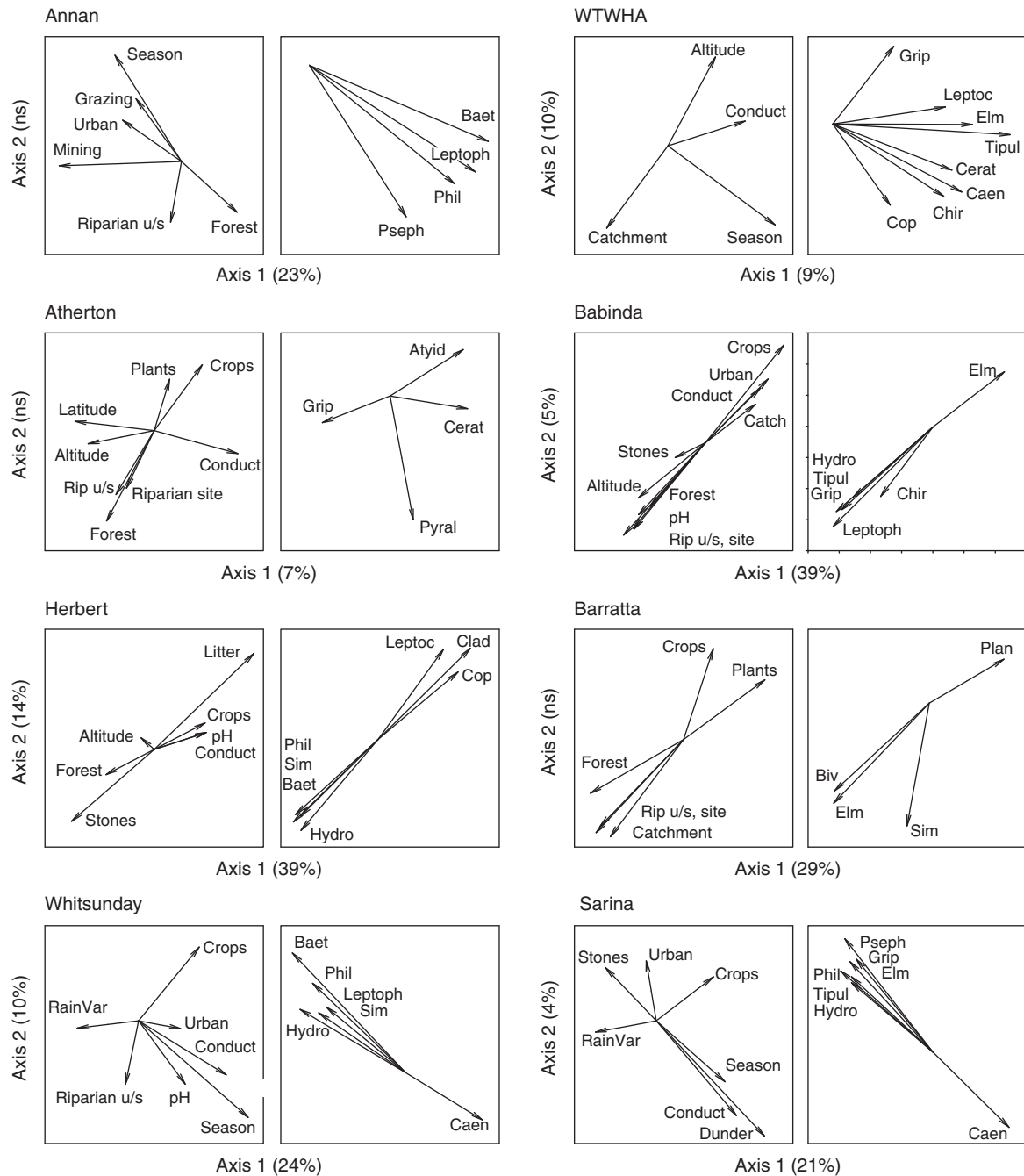


Fig. 4. Redundancy analysis (RDA) plots from distance-based linear modelling (DistLM) analysis of individual areas. Each pair of panels shows environmental vectors (left panels) and invertebrate vectors (right panels) for each area. Relative importance of axes (percentage of variation explained) is indicated. Environmental variables are defined in Table 2. Invertebrate abbreviations are as in Fig. 3; and Biv, Bivalvia; and Tip, Tipulidae. WTWHA, Australian Wet Tropics World Heritage Area.

Invertebrate assemblages in Babinda and Behana creeks showed substantial declines in richness and SIGNAL2 with sediment size (Fig. S2, available as Supplementary material for this paper). However, accounting for sediment size, ANCOVA showed a strong contrast between streams in richness, with ~25% fewer taxa in Babinda Creek ($F = 21.0$, $P < 0.001$), but no such contrast in SIGNAL2 scores ($F = 0.6$, $P = 0.47$).

Discussion

The stream invertebrate assemblages reflected land-use disturbances as expected (e.g. Clapcott *et al.* 2012; Connolly *et al.* 2016), although most streams supported a fauna that was not restricted to disturbance-tolerant taxa. The regional stream fauna is resilient to moderate natural disturbance (Rosser and

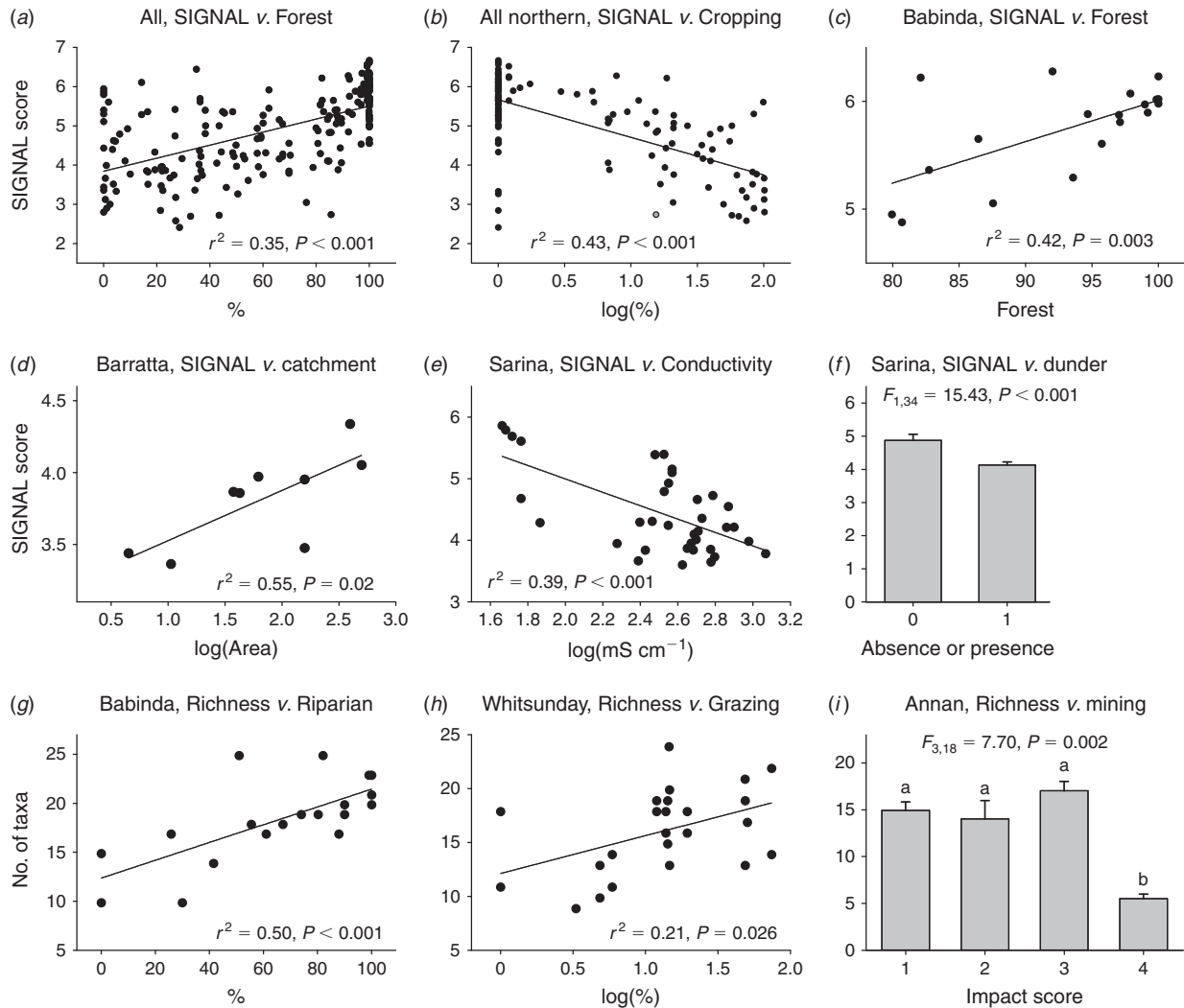


Fig. 5. Plots of selected ($r^2 > 0.20$) relationships between environmental variables and SIGNAL2 scores and taxonomic richness. (a–e, g, h) Scatterplots of linear regressions, with values of r^2 and P ; (f, i) histograms of categorical variables, with ANOVA results (F and P) shown; in i, different letters above the treatment bars indicate a significant difference between the treatments (Tukey test, $P < 0.05$).

Pearson 2018) but sensitive to major flood or drought (Pearson 2014); however, there was no evidence of either occurring prior to our sampling periods in the present study. Land use and other disturbances were identified by linear modelling, taxonomic richness and SIGNAL2 as influential factors across the study region (except in the WTWHA sites), along with several other environmental variables. These included latitude, reflecting the gradient of water physico-chemistry demonstrated by the Queensland Government data and our field data and probably relating to the more consistent flows in the north (Kennard *et al.* 2010), enhancing water quality through dilution of natural and anthropogenic contaminants (Connolly *et al.* 2015; Davis *et al.* 2017). Gradients in water quality may also relate to the longitudinal position of sites across the landscape, because solutes tend to increase in concentration in a downstream direction through natural processes and through increased run-off from disturbed landscapes (Connolly *et al.* 2015). Increase in fine sediment

may also occur as a result of altered land use, although this appeared to be a major influence only in the Annan area, as a result of alluvial mining.

The proportion of overall variation explained by the DistLM models for assemblage similarity, richness and SIGNAL2 for all samples (40, 38 and 62% respectively) suggested reasonably robust models, given the variation in the geographic, geological, geomorphological, vegetation and anthropogenic variables affecting streams across the study region. In contrast, in a comparable study in Britain, modelling explained only 26% of variation (Murphy and Davy-Bowker 2005). The proportion of variation explained ranged from low (7%) to high, particularly for some richness (up to 81%) and SIGNAL2 (up to 95%) models. Our identification of disturbance at the broad scale is noteworthy, because habitat features, such as substrate and water quality, are typically the greatest predictors of local invertebrate assemblages (e.g. in Europe, Lammert and Allan 1999; Brazil, Ferreira *et al.* 2014; the Wet Tropics, Pearson *et al.*

2017), although landscape-scale changes can affect variables at the local scale (Johnson *et al.* 2007).

DistLM models for the northern and southern regions highlighted the latitudinal differences, with climate features (seasonality and rainfall) being important in the south. Division into the two regions, thus, facilitated identification of relationships. DistLM models for individual areas further emphasised important variables, with higher levels of variation being explained by particular variables. For example, specific influences such as mining in the Annan area, grazing in the Whitsunday area and application of dunder in the Sarina area were clearer when these areas were separated from the overall data. The greater influence of grazing in the Whitsunday model may be due to the greater extent of grazing in that area and bank and stream-bed disturbance by cattle (cf. Quinn *et al.* 1992; Niyogi *et al.* 2007). Both grazing and sugarcane production may cause deterioration of the riparian zone and the main difference between these two stressors is the input of agrichemicals from sugarcane (Bramley and Roth 2002), which were not greatly implicated in our study (see below). However, despite the greater resolution of specific impacts at smaller scales, few sites were as disturbed as those suffering point-source pollution from a sugar mill on Babinda Creek (subsequently decommissioned), which had a severe impact on invertebrate assemblages (Pearson and Penridge 1987).

SIGNAL2 scores showed strong relationships with conductivity and pH, as expected of an index focussed on water quality (Chessman 2003; Chessman *et al.* 2007). Differences in SIGNAL2 scores among categories were generally not high, partly because moderate mean scores masked occasional low-scoring sites. The accuracy of disturbance indices depends on the correct allocation of scores to regional taxa and their relevance to the type of disturbance, so the indication of disturbance measures as important factors in our study indicated the efficacy of SIGNAL2 at regional and local scales. Influence of disturbances on richness and SIGNAL2 varied among areas. In the overall analyses, taxonomic richness related to several environmental variables, but not disturbance. Conversely, although both richness and SIGNAL2 declined with sediment size in Babinda and Behana creeks, only richness discriminated between streams when sediment size was accounted for. As the main difference between these streams was the amount of organic material in the substratum (Connolly *et al.* 2016), it is not surprising that SIGNAL2 did not pick up the contrast, although its sensitivity to the habitat gradient highlights the need to compare sites that are similar or take account of such gradients. Our results showed that accurately identifying impact over broad regions may be hampered by differences in local conditions and types of impact. Not surprisingly, analyses of data from within our predefined local sampling areas, using local criteria and taking into account environmental gradients, were better able to identify important disturbances. Similarly, in Europe, monitoring datasets detected major trends of impact, but identifying the effects of local-scale stressors required locally specific approaches (Dahm *et al.* 2013).

Our measures of land-use area were sufficient to indicate impacts on the invertebrate assemblages whether by influence on habitat, water quality or their interactions, but mostly could

not discriminate precise causes or interactions, only correlating variables. For example, we did not include concentrations of nutrients, dissolved oxygen (DO) or pesticides in our analyses because suitable data were unavailable for some or all sites. The effects of nutrients on the study region's assemblages are expected to be indirect, mediated by microbial or plant productivity, but not reducing invertebrate richness (Pearson and Connolly 2000; Connolly and Pearson 2013; Connolly *et al.* 2016). Pronounced hypoxia leads to a loss of sensitive taxa (Connolly *et al.* 2004); however, there was no evidence of hypoxia being a major impact in the samples, in contrast to situations downstream of point-source pollution (Pearson and Penridge 1987), or where flow is very low in the dry season (Pearson *et al.* 2003; Connolly *et al.* 2004). Although land-based pesticides have been implicated in deterioration of GBR ecosystems (Bainbridge *et al.* 2009; Lewis *et al.* 2009; Smith *et al.* 2012), there was no evidence of deleterious effect of pesticides in well-flushed Wet Tropics lagoons (Pearson *et al.* 2013) and the same may apply in perennial streams. Deposition of fine sediment typically leads to reduction in abundance of most taxa and, consequently, to reduction in sample diversity (Connolly and Pearson 2007), as occurred in the Annan system. There was no evidence of excessive sedimentation at other sites. Nevertheless, these and other variables may be components of the land-use impacts we describe, which could be identified only by more detailed studies (e.g. Connolly *et al.* 2016).

Conclusions

Our results supported the prediction that invertebrate assemblages would be sensitive to disturbance, but not that responses would be consistent across scales and sampling areas, or that our different indicators would perform similarly. As expected, natural landscape and habitat factors influenced the assemblages (e.g. Marchant *et al.* 1994, 1999; Schröder *et al.* 2013; Pearson *et al.* 2017), whereas changes in land use had a substantial impact, with different variables being important in different areas (cf. Richards *et al.* 1993; Stendera *et al.* 2012). Individual sites may exhibit greater stress than reported here in the close vicinity of point sources of contaminants, such as cane-field drains (Pearson *et al.* 2003), sugar mills (Pearson and Penridge 1987) or waste-treatment plants (e.g. Atherton, R. G. Pearson, unpubl. data). However, continuous stream flows probably mitigate adverse water-quality impacts across much of the study region (Pearson *et al.* 2013; Connolly *et al.* 2016; Davis *et al.* 2017), except in more seasonal systems such as lagoons on the Herbert floodplain (Pearson *et al.* 2003) and, perhaps, the more southerly streams of the present study. Nevertheless, the loss of 25% of taxa in a stream mostly influenced by riparian disturbance indicates that disturbances must be taken very seriously. In particular, despite conservation protection of forested upland streams in the study region, lowland and tableland streams are largely unprotected, despite being important contributors to the overall biodiversity (Januchowski-Hartley *et al.* 2011).

Land-use change that occurred across the study region was readily identified by our analyses of the invertebrate assemblages but masked the impact of disturbance that occurred at smaller scales (within a particular study area). Broad-scale studies can, thus, be inadequate for identifying local impacts

and their causes (Lammert and Allan 1999; Johnson *et al.* 2007). Regional monitoring programs can be improved by accounting for local-scale environmental gradients, thereby clarifying relationships with land-use effects on biotic assemblages (Blanchette and Pearson 2012, 2013; Ferreira *et al.* 2014; Connolly *et al.* 2016; Davis *et al.* 2017; Pearson *et al.* 2017) within a hierarchical spatial framework (Johnson *et al.* 2007). The degree of impact we identified in the study region is such that simple remediation may be sufficient for mitigation; for example, in the Wet Tropics, current rehabilitation of riparian zones will be beneficial and may be the best approach to restoring and maintaining the diverse assemblages in streams of the GBR catchment (Lorion and Kennedy 2009; Ferreira *et al.* 2012; Aguiar *et al.* 2015; Connolly *et al.* 2015, 2016; Hunt *et al.* 2017). Nevertheless, site-scale restoration measures are unlikely to be effective if the habitat upstream is degraded (Lorenz and Feld 2013), and so, catchment-wide management is required to mitigate impacts (Magierowski *et al.* 2012).

Conflicts of interest

The authors declare that they have no conflicts of interest.

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