Biological Conservation 249 (2020) 108634

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Urbanisation affects ecosystem functioning more than structure in tropical streams

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ARTICLE INFO

Keywords:
Anthropogenic stressors
Bacteriochlorophyll
Chlorophyll
Riparian
Stream health
Urban stream syndrome

ABSTRACT

Urbanisation poses a clear threat to tropical freshwater streams, yet fundamental knowledge gaps hinder our ability to effectively conserve stream biodiversity and preserve ecosystem functioning. Here, we studied the impact of urbanisation on structural and functional ecosystem responses in low-order streams in Singapore, a tropical city with a mosaic landscape of protected natural forests, managed buffer zones (between forest and open-country habitats), and built-up urban areas. We quantified an urbanisation gradient based on landscape, in-stream, and riparian conditions, and found an association between urbanisation and pollution-tolerant macroinvertebrates (e.g. freshwater snail and worm species) in litter bags. We also found greater macroinvertebrate abundance (mean individuals bag^{-1}; forest: 30.3, buffer: 70.1, urban: 109.0) and richness (mean taxa bag^{-1}; forest: 4.53, buffer: 4.75, urban: 7.50) in urban streams, but similar diversity across habitats. Higher levels of primary productivity (measured from algal accrual on ceramic tiles) and microbial decomposition (measured from litter-mass loss in mesh bags) at urban sites indicate rapid microbial activity at higher light, temperature, and nutrient levels. We found that urbanisation affected function 32% more than structure in the studied tropical streams, likely driven by greater algal growth in urban streams. These changes in ecological processes (i.e. ecosystem functioning) possibly lead to a loss of ecosystem services, which would negatively affect ecology, society, and economy. Our results point to possible management strategies (e.g. increasing vegetation density through buffer park creation) to reduce the impacts of urbanisation, restore vital ecosystem functions in tropical streams, and create habitat niches for native species.

1. Introduction

Habitat loss is increasing rapidly across the globe and represents one of the largest environmental threats to fresh waters and their biodiversity (Dudgeon et al., 2006; Vörösmarty et al., 2010). Streams are exceptionally vulnerable to environmental change as they are topographical low points that collect heat, sediment, and runoff (Nelson et al., 2009). The expanding human population as well as developments in infrastructure, agriculture, and industry threaten stream ecosystems by causing landscape modifications (channelisation of streams), pollution (surface runoff), and introduction of invasive species (Haddad et al., 2015; Pickett et al., 2011). These threats exert a disproportionately high impact on the native species within such waterways through reduction in available habitat niches, high nutrient loads, and simplified food webs, ultimately resulting in species loss and causing worldwide conservation issues (Peralta et al., 2019; Pickett et al., 2011). The interconnectivity of waterways can exacerbate such effects, or carry them to surrounding areas within the same hydrological basin. 90% of urban population growth over the next 30 years is projected to happen in Asia and Africa (United Nations, 2018), which include some of the most important biodiversity and endemism hotspots in the tropics. As such, there is an urgent need for more research on the effects of urbanisation on tropical stream ecosystems (Peralta et al., 2020; Yule et al., 2015), particularly its impact on ecosystem functions such as fluxes of energy and organic matter (Meyer et al., 2005; Yule et al., 2015). Intact lotic systems provide numerous benefits to society such as regulating (e.g. flood control), provisioning (e.g. drinking water), supporting (e.g. habitat), and cultural (e.g. recreation)

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https://doi.org/10.1016/j.biocon.2020.108634
Received 2 January 2020; Received in revised form 18 May 2020; Accepted 21 May 2020
Available online 13 August 2020
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ecosystem services (Millennium Ecosystem Assessment, 2005). The degradation of stream ecosystems could result in the loss of these services and therefore negatively affect both biodiversity and humans.

Delineating ecological effects of urban development on stream integrity requires moving beyond characterising the physico-chemical properties and biota of urban streams (Gessner and Chauvet, 2002; Paul and Meyer, 2001). Measuring both the structure (e.g. community composition) and function (e.g. process rates) of an ecosystem facilitates a more holistic understanding of its response to anthropogenic stressors, as these measures are indicators of ecological integrity (Bunn et al., 1999; Castela et al., 2008; Dale and Beyeler, 2001; Friberg et al., 2009; Harris, 1994; Matthews et al., 1982). For example, benthic macroinvertebrates are useful structural indicators as they perform numerous key roles in stream ecosystems (Wallace and Webster, 1996) and are generally ubiquitous and diverse (Blakely et al., 2014; Rosenberg and Resh, 1993). Similarly, leaf-litter breakdown and primary productivity assays are reliable, simple, and low-cost methods of assessing ecosystem functioning (Gessner and Chauvet, 2002). In order to capture the complexity of ecosystems, complementary information about both structural and functional responses is essential as they might present contrasting views (Bunn and Davies, 2000; Castela et al., 2008; Dale and Beyeler, 2001; Friberg et al., 2009). Despite declines in biodiversity, for instance, ecosystems can retain their functionality if several species perform the same function and at least some of those species persist (i.e. functional redundancy; Chua et al., 2019; Woodcock and Huryn, 2005). On the other hand, process rates might be altered even if community composition does not respond to environmental stressors, for example, by enhancing the efficiency of the community (e.g. by stimulating microbial or detritivore activity; McKie and Malmqvist, 2009).

Over the last two decades, our understanding of stream ecosystem structure and functioning has advanced substantially, and studies on urban streams have revealed several impacts of urbanisation (Booth et al., 2016; Chadwick et al., 2006; Liew et al., 2018; Ramírez et al., 2009; Yule et al., 2015). However, this understanding is largely based on research in the temperate zone (Ramírez et al., 2008; Wantzen et al., 2019). Studies in the tropics revealed that the factors driving ecological processes tend to be the same in temperate and tropical streams (Boulton et al., 2008), but that the impact of urbanisation on tropical streams differs from that described in temperate regions (Booth et al., 2016; Wantzen et al., 2019). Across biomes, structural assays revealed that macroinvertebrate abundance is decreased by toxins and siltation and increased by organic and inorganic nutrients; all of these factors can cause a decrease in macroinvertebrate diversity (Mackintosh et al., 2015; Paul and Meyer, 2001; Peralta et al., 2020). Functional measures identified eutrophication and loss of riparian vegetation (which leads to higher solar irradiation and temperatures) as key drivers of the green (autochthonous) pathway in urban streams by increasing primary productivity and oxygen production (Chauvet et al., 2016). Urbanisation also has the potential to increase the brown (allochthonous) pathway via greater microbial decomposition and macroinvertebrate consumption (McKie and Malmqvist, 2009; Ramírez et al., 2009). However, there have been contradicting observations of the relative importance of macroinvertebrate-driven decomposition in different ecoregions (Chauvet et al., 2016; Friberg et al., 2009; Graça, 2001; Graça et al., 2015). Given the increasing rates of urbanisation in the tropics (United Nations, 2018), coupled with the high conservation value of tropical fresh waters (Malmqvist and Rundle, 2002) and the importance of the ecosystem services they provide, a clear understanding of how urbanisation affects tropical lotic systems is crucial. Furthermore, previous studies failed to resolve the relative contribution of urbanisation to changes in stream ecosystem structure and functioning. While both structural and functional aspects are important for stream integrity and conservation, maintaining ecosystem functioning enables the provision of at least some ecosystem services. This indicates a need to understand the nuances of the impacts of urbanisation to maximise ecological, social, and economic benefits of management efforts.

To address the above knowledge gap, we aimed to investigate how structural and functional attributes of stream ecosystems responded to urbanisation in tropical Singapore, a city-state that possesses a mosaic of highly urbanised and protected forested habitats in close proximity, and that is representative of what might await other rapidly-urbanising tropical cities. We (1) calculated an urbanisation index based on both instream and landscape variables; (2) measured the structural responses of stream ecosystems to urbanisation; (3) measured the functional responses of stream ecosystems to urbanisation; and (4) determined the relationship between these three components of lotic systems. Our study contributes to determining strategies to mitigate urbanisation impacts and maintain ecosystem services in the face of rapidly advancing urbanisation.

2. Methods

2.1. Study sites and sampling strategy

The study was conducted from March until May 2019 in the city state of Singapore (1°18′ N, 103°50′ E), one of the world's most-densely populated and urbanised nations (United Nations, 2018) with just about 100 ha (0.16% of total land area) of primary rainforest left (Yee et al., 2011). Singapore's non-concrete stream habitats range from forest streams to rural (open-country) streams (Yeo and Lim, 2011). To capture an urbanisation gradient, we selected a total of 11 streams—four within forest reserves, three along the buffer zones between forest and open-country areas (National Parks Board, 2018, 2019), and four in open-country urban areas (Fig. 1A and Fig. A.1). We standardised sampling sites across the urbanisation gradient to include only low-order streams with natural substrate (lacking concretisation). The studied forest streams are small, shallow, slow-flowing, and well-shaded by the canopy (Fig. A.1A-D). Fine-grained substrate and an accumulation of leaf litter form the stream beds in the forest reserves and buffer zones. While trees dominate the riparian vegetation in the forest reserves, shrubs prevail along the buffer streams (Fig. A.1E-G). Urban streams selected are characterised by wide stream beds, a high proportion of gravel and concrete blocks, partially covered with a mat of algae, some macrophyte growth, and a lack of trees in the riparian vegetation (Fig. A.1H-K). In each stream, we established four sampling points over a reach of 20 m (Fig. 1B). At each of the 44 sampling points, biotic and abiotic parameters were measured and instream experimental units (one ceramic tile, one coarse-mesh leaf-litter bag, and one fine-mesh leaf-litter bag; see below for details) were fixed to the stream bed (midstream and parallel to the stream banks, dispersed over 0.5 m; Fig. 1C). All experimental units were retrieved after 21 days (incubation period determined by pilot studies; Choo, 2019; Wiederkehr, 2019).

2.2. Urbanisation gradient: physico-chemical and landscape properties

We measured water temperature, pH, dissolved oxygen, conductivity, total dissolved solids, nitrate (YSI Pro Plus; Xylem Analytics), phosphate (Phosphate Checker® HC; Hanna Instruments), canopy cover (spherical densiometer), light intensity (LightScout Quantum Meter; Spectrum Technologies), and stream width at each sampling point. Water velocity (Flowatch®; JDC Electronics SA) and stream depth were measured at four intervals across the stream width at each sampling point and their average was recorded. In addition, two observers visually estimated the percentage of leaf-litter cover, macrophyte cover, and substrate composition (mud, sand, or gravel and concrete blocks) of the stream bed (five-metre stretch, entire width), and riparian vegetation (grass, shrub, or tree) along the stream banks (five-metre stretch, two metres on either side) at each sampling point (Wang et al., 1996). We calculated an urbanisation index as the proportion of urban (excluding open spaces, parks, reserve sites, and waterbodies) to total area

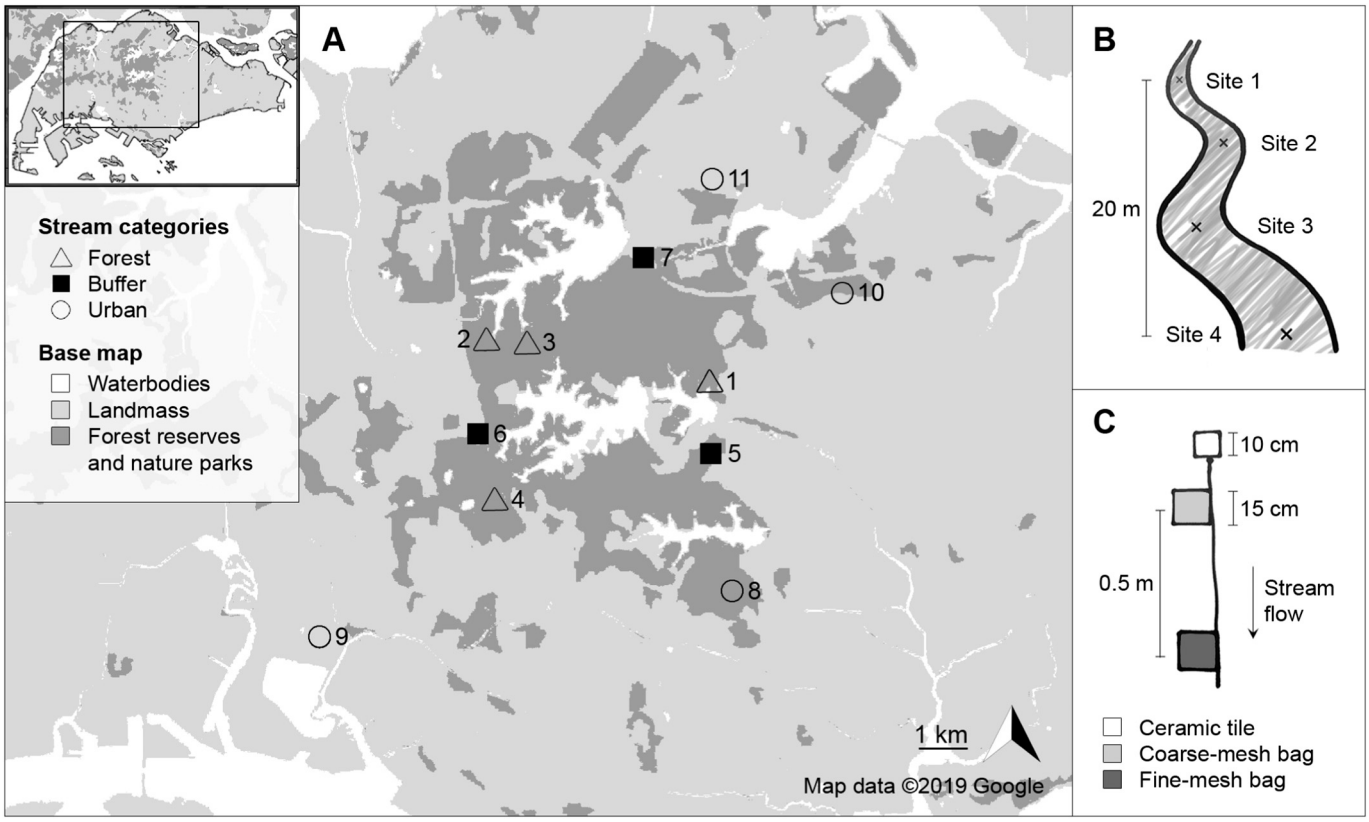

Fig. 1. Study design illustrated with (A) a map of the locations and categories of the 11 studied streams (numbers indicate the streams' position along the urbanisation gradient with 1 = least urbanised, 11 = most urbanised), (B) the distribution of the four sampling points within each stream, and (C) the experimental set-up (one ceramic tile, one coarse-mesh bag, one fine-mesh bag) at each sampling point.

using the open-source software QGIS 2.18.25 (QGIS Development Team, 2018), governmental land-use data (Urban Redevelopment Authority, 2017), and Google Maps in cases where there had been recent development in the catchment. We tested urbanisation indices calculated from areas with radii of 50, 100, 200, 500, and 1000 m around every sampling point for their correlation with all other variables to determine the appropriate urbanisation index for analysis.

2.3. Structural attributes: macroinvertebrate communities and stream health

Coarse-mesh bags (15 × 15 cm; pore size: 6 mm) containing leaf-litter discs (4.000 ± 0.040 g; diameter: 30 mm) of *Dillenia suffruticosa*, a common riparian plant that can be found across the range of habitats in this study, were used to quantify macroinvertebrate colonisation. While this sampling method is unlikely to reflect the entire macroinvertebrate community at a site (Yule et al., 2015), it serves as a proxy for the leaf-litter dwelling macroinvertebrates that colonised the chosen leaf-litter species. The animals were sorted from the leaf litter and accumulated sediment, preserved in 75% ethanol (Benstead, 1996), and identified to family level, except for the subclass Acari, orders Araneae, Collembola, and Isopoda, and infraorder Brachyura, using Blakely et al. (2010). We acknowledge that this does not capture the true diversity of species at each site, but remains a valid and consistent comparison of the diversity of the major macroinvertebrate taxonomic groups. We determined total macroinvertebrate abundance as the activity density (sensu Thiele, 1977) of each macroinvertebrate taxon after 21 days (individuals bag^{-1}), and estimated taxa diversity using Hill numbers of orders 0, 1, and 2 (Hill, 1973; Jost et al., 2011). The orders allow relative abundances to be weighted differently, with $q = 0$ equating to taxa richness, $q = 1$ weighting taxa by their relative abundances (exponential of Shannon's entropy index), and $q = 2$ emphasising abundant taxa (inverse of Simpson's concentration index). We examined the distribution of pollution-sensitive taxa using each taxon's tolerance score (Blakely et al., 2014). Stream health was determined by the SingScore, a biotic index specifically developed for Singapore's lotic ecosystems, which is calculated by summing the tolerance scores of the macroinvertebrate taxa present at a site, dividing this sum by the number of taxa present at a site, and multiplying the result by 20 (Blakely et al., 2014).

2.4. Functional attributes: primary productivity and leaf-litter decomposition

Primary productivity was quantified from biofilm growth on incubated 10 × 10 cm white glazed ceramic tiles, roughened with sand paper to remove the protective coating. Upon collection, the tiles were gently tilted in the stream water to wash off the accumulated fine sediment. The biofilm was scrubbed from the tiles using cotton swabs. Photosynthetic pigments were extracted in 2 ml of 96% ethanol following the methods described by Lawton et al. (1999). Chlorophyll *a* (photopigment of plants, algae, and cyanobacteria) and bacteriochlorophyll *a* (photopigment of anoxygenic photosynthetic bacteria) were used to quantify biofilm accumulation, which in turn served as a proxy for primary production (Lamberti et al., 2007). The concentrations of the photopigments (mg m^{-2}) after 21 days were estimated using a DU 730 Life Science UV/VIS Spectrophotometer and following the algorithms developed by Ritchie (2018).

Recently-senesced leaves of *D. suffruticosa* were collected, cut into discs (diameter: 30 mm) to generate leaf fragments of similar size and quality (by avoiding leaf stems), and oven-dried to a constant weight at 67 °C. Leaves were weighed (4.000 ± 0.040 g) using an analytical balance (Sartorius CP224S) and packed in 15 × 15 cm coarse-mesh (pore size: 6 mm; identical to the ones used to quantify

macroinvertebrate colonisation) and fine-mesh (pore size: 0.25 mm) bags. The coarse and fine mesh included and excluded macroinvertebrates, respectively, distinguishing macroinvertebrate-driven and microbial leaf-litter decomposition. At one stream, we used an additional four bags of both mesh sizes to estimate litter-mass loss due to handling (Benfield et al., 2017). After collecting the mesh bags, the remaining leaf litter was carefully rinsed before being oven-dried to a constant weight at 67 °C. Mass loss (g) over 21 days was determined. Macroinvertebrate-driven decomposition was derived from the difference between the lost litter mass in the coarse- and fine-mesh bags as described by Woodward et al. (2012).

2.5. Statistical analysis

Principal component analysis (PCA) based on a correlation matrix was used to explain the variation in stream properties among sampling points and to compute an urbanisation gradient. The urbanisation indices derived from the different areas (radius: 50, 100, 200, 500, and 1000 m) were correlated with the measured environmental variables. We considered the urbanisation index with the weakest average correlation with all other variables to be most appropriate for including in the PCA. The measurements of total dissolved solids and conductivity were strongly correlated (Pearson correlation coefficients, $r = 0.999$), so conductivity was excluded for the final PCA. The values from the first principal component axis were used as a measure of urbanisation, with low and high values representing natural and urbanised habitats, respectively.

Generalised linear mixed-effects models (GLMM) were used to test whether structural and functional variables were significantly correlated to the urbanisation gradient. Models were fitted to the data using maximum likelihood (ML) estimation, with stream as a random effect to account for the spatial autocorrelation of sampling points within streams. Macroinvertebrate abundance and taxa richness calculated with $q = 0$ were modelled using Poisson errors, whereas taxa diversities estimated with $q = 1$ and $q = 2$, SingScore, chlorophyll *a* and bacteriochlorophyll *a* concentrations, and loss of leaf-litter mass due to microbial and macroinvertebrate-driven decomposition were modelled using a Gaussian error distribution. Photopigment concentrations were square-root-transformed and taxa diversities were $\log_e$-transformed to meet the assumptions of normality and heterogeneity of variance. Models with an urbanisation gradient were compared to null models, and likelihood-ratio tests were used to determine parameter significance. The similarity between macroinvertebrate communities was assessed using non-metric multidimensional scaling (NMDS) with Raup-Crick distance calculations to include rare taxa (Peralta et al., 2019; Pos et al., 2014; Raup and Crick, 1979).

We used structural equation modelling (SEM) to understand the linkages between structural and functional attributes that were significantly correlated to the urbanisation gradient using GLMM. Here, we evaluated models with three latent factors representing urbanisation, ecosystem structure, and ecosystem functioning in an information-theoretic approach (Burnham and Anderson, 2002). We fixed the variances of all three latent factors to unity, allowing free estimation of all measured-variable loadings. We used robust ML estimations to offset any bias introduced by non-normal distribution on z-score normalised variables with full information ML (FIML) for missing data, and compared the model predictions to those estimated by robust ML without FIML, and ML with and without FIML to determine their reliability. We determined the relative effect of urbanisation on function versus structure by dividing their standardised regression coefficients.

All statistical analyses were performed using the open-source software R 3.6.0 (R Core Team, 2019). Diversity indices were estimated using the package "vegetarian" (Charney and Record, 2012), GLMMs were fitted and compared using the packages "lme4" (Bates et al., 2015) and "MuMIn" (Barton, 2019), NMDS was run with the package "vegan" (Oksanen et al., 2019), and SEM was performed using the package "lavaan" (Rosseel, 2012).

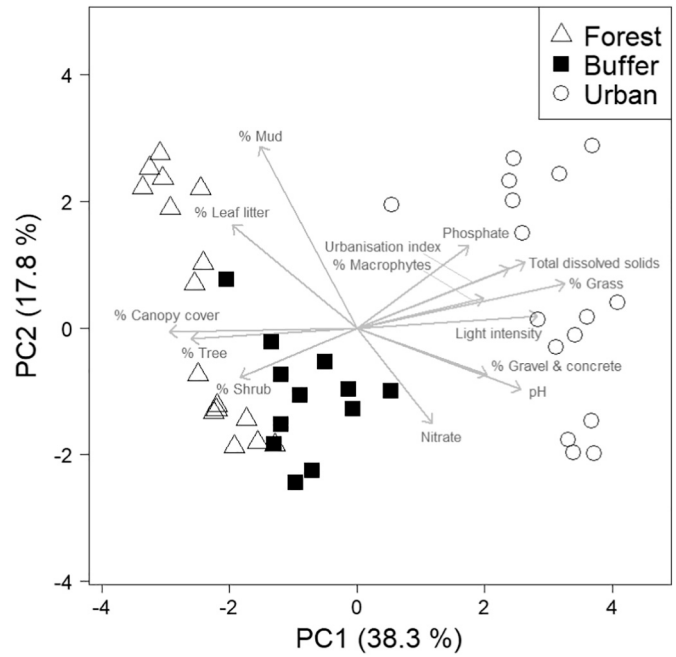

Fig. 2. Principal component analysis (PCA) of environmental stream properties in the 44 sampling points. The direction and magnitude of environmental variables that are significantly correlated with PC1 ($p < 0.05$) are displayed.

3. Results

3.1. Urbanisation gradient: physico-chemical and landscape properties

To calculate an urbanisation index, we chose an area with a radius of 500 m around every sampling point (Table A.1). The PCA clearly separated forest, buffer, and urban sites along axis 1 (PC1), which explained 38.3% of the variation found among sites and was most strongly associated with riparian vegetation, canopy cover, light intensity, total dissolved solids, and pH (Fig. 2; variable loadings on PC1 are reported in Table A.2). Principal component axis 2 (PC2) explained a further 17.8% of the variation, which was found mostly within categories, and was associated with high mud, low dissolved oxygen, and low sand contents. Urban streams scored highest in all measured chemical variables except for dissolved oxygen, and showed a high level of variance in most chemical properties, while low values and little variation were recorded at forest sites. Canopy cover decreased substantially from 90 to 100% in forest sites to 10 to 30% in urban sites (except for one urban site with steep banks), whereas light intensity increased with degree of urbanisation. Riparian vegetation was dominated by trees in forest, shrubs in buffer, and grass in urban streams (Fig. A.2 and Table A.3).

3.2. Structural attributes: macroinvertebrate communities and stream health

A total of 3085 macroinvertebrates from 38 taxa were collected. Activity densities of colonising macroinvertebrates per leaf-litter bag ranged from 4 individuals in a forest stream to 284 individuals in an urban stream. Chironomidae was the most abundant family, contributing 40 to 89% of recorded individuals per site. Total macroinvertebrate abundance and taxa richness ($q = 0$) increased with increasing urbanisation (likelihood-ratio test, $\chi^2_{(1)} = 55.389$, $p < 0.001$; Fig. 3A and Table A.4A; and likelihood-ratio test, $\chi^2_{(1)} = 8.280$, $p =$

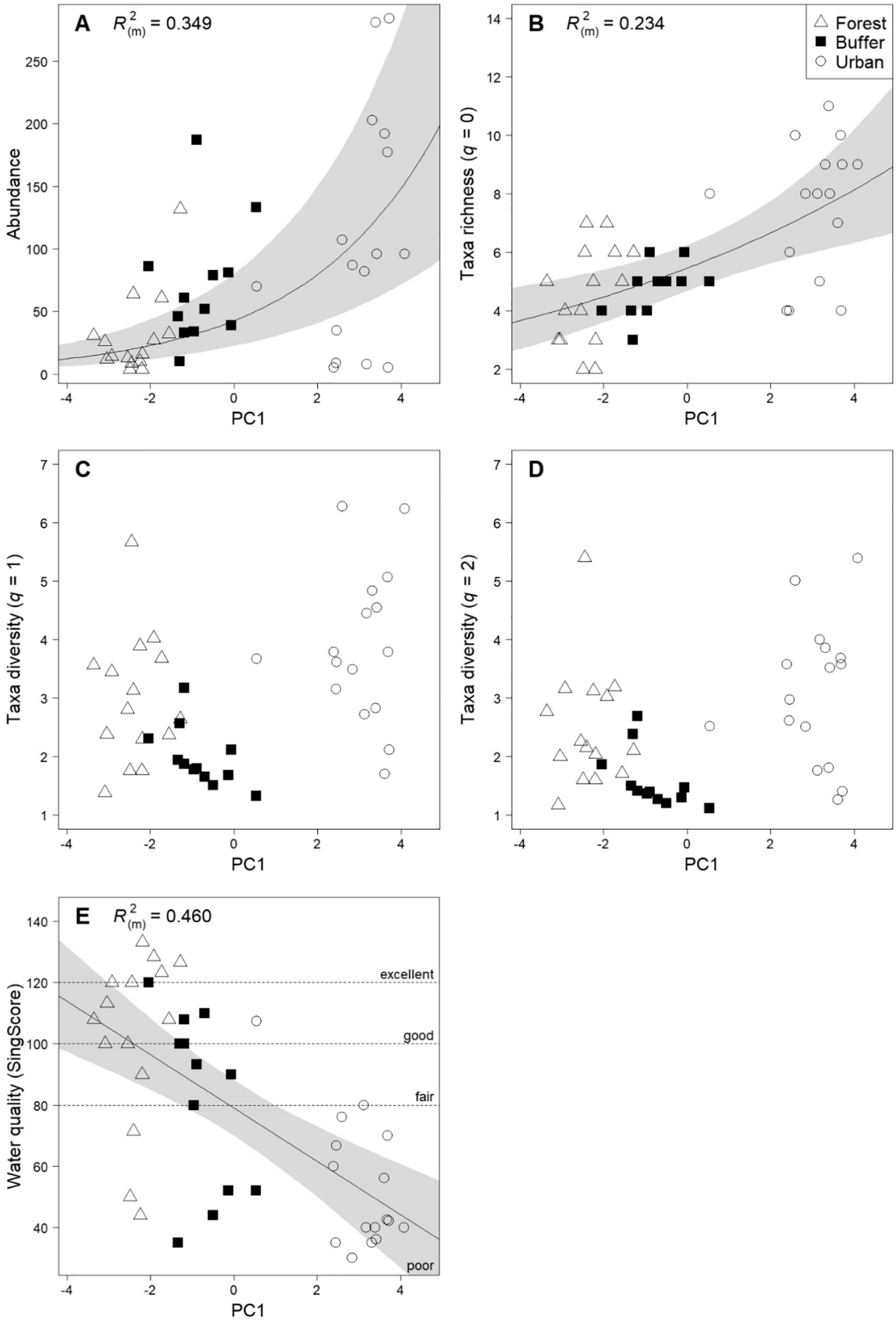

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Fig. 3. Relationship between the urbanisation gradient (PC1; higher values indicate higher degree of urbanisation) and (A) macroinvertebrate abundance, (B) taxa richness calculated with $q = 0$, (C) community diversity estimated with $q = 1$, (D) community diversity estimated with $q = 2$, and (E) water quality measured using the macroinvertebrate biotic index SingScore (Blakely et al., 2014). Regression lines (solid line; predicted by GLMM) and their predicted 95% CI (shaded area; obtained through bootstrapping) visualise the magnitude and uncertainty of significant relationships.

0.004; Fig. 3B and Table A.4B). Taxa diversity was similar between all sites along the urbanisation gradient whether taxa were weighted by their relative frequencies ($q = 1$; likelihood-ratio test, $\chi^2_{(1)} = 3.446$, $p = 0.063$; Fig. 3C and Table A.4C) or whether emphasising abundant taxa ($q = 2$; likelihood-ratio test, $\chi^2_{(1)} = 2.133$, $p = 0.144$; Fig. 3D and Table A.4D).

There was a significant reduction in SingScores with increasing urbanisation (likelihood-ratio test, $\chi^2_{(1)} = 12.666$, $p < 0.001$; Fig. 3E and Table A.4E), indicating that macroinvertebrate communities changed from being dominated by pollution-sensitive to pollution-tolerant taxa. The NMDS further supported this community shift by showing that proportionally more pollution-sensitive taxa, such as Coleoptera, Decapoda, Ephemeroptera, Odonata, Plecoptera, and Trichoptera (Blakely et al., 2014), were associated with forest sites, while urban sites tended to be most strongly associated with Hirudinea and Gastropoda (the latter were found in the five most-urbanised streams only; Fig. A.3 and Table A.5). Water quality ranged from good (SingScore: 110–119) in forest streams to poor (SingScore: < 80) in urban streams (Fig. 3E).

3.3. Functional attributes: primary productivity and leaf-litter decomposition

Tiles to measure algal growth were successfully retrieved from 42 out of the 44 sampling points. At urban sites, microscopic unicellular and filamentous green algae could be detected in a fine organic mat on the tiles, while only unicellular growth was visible at forest and buffer sites. Chlorophyll *a* and bacteriochlorophyll *a* concentrations increased significantly with increasing urbanisation (likelihood-ratio test, $\chi^2_{(1)} = 17.709$, $p < 0.001$; Fig. 4A and Table A.6A; and likelihood-ratio test, $\chi^2_{(1)} = 10.936$, $p < 0.001$; Fig. 4B and Table A.6B).

In total, 43 coarse- and 44 fine-mesh leaf-litter bags were retrieved. Leaf-litter mass loss due to microbial decomposition increased with increasing urbanisation (fine mesh; likelihood-ratio test, $\chi^2_{(1)} = 6.586$, $p = 0.010$; Fig. 4C and Table A.6C). There was no significant contribution of macroinvertebrates to overall decomposition (coarse-mesh; GLMM, $t = 0.772$), and no evidence that urbanisation had an influence on macroinvertebrate-driven decomposition (likelihood-ratio test, $\chi^2_{(1)} = 0.428$, $p = 0.512$; Fig. 4D and Table A.6D).

3.4. Linkages between structural and functional responses to urbanisation

The best-supported structural equation model (Fig. 5) excluded SingScore and leaf-litter mass loss (a full list of models, underlying hypotheses, associated performances and fit are reported in Table A.7). The model predicted the effect of urbanisation on ecosystem functioning (SEM, $\beta = 1.00$, $p < 0.001$) to be 32% stronger than on ecosystem structure (SEM, $\beta = 0.76$, $p < 0.001$). The indirect effect of urbanisation on ecosystem functioning via structure was found to be non-significant (SEM, $p = 0.226$). Riparian grass cover, canopy cover, light intensity, and riparian tree cover were significantly correlated with urbanisation (SEM, $p < 0.001$). All measured structural and functional variables were highly correlated with their respective latent factor (abundance with structure: SEM, $\beta = 0.77$, $p < 0.001$; taxa richness with structure: SEM, $\beta = 0.95$, $p < 0.001$; chlorophyll *a* with functioning: SEM, $\beta = 0.93$, $p < 0.001$; bacteriochlorophyll *a* with functioning: SEM, $\beta = 0.86$, $p < 0.001$).

4. Discussion

Urbanisation had a clear effect on the sampled streams, characterised by higher dissolved solid and nutrient concentrations, altered hydrology, and increased water temperature, conductivity, and pH. The degraded riparian vegetation also allowed more light to reach stream beds and enabled macrophyte growth, similar to other tropical streams and to the temperate regions (urban stream syndrome; e.g. Booth et al., 2016; Peralta et al., 2020; Pickett et al., 2011; Walsh et al., 2005; Wantzen et al., 2019). This led to significant changes in the measures of ecosystem structure and functioning, thereby affecting the ecological integrity of the streams.

4.1. Structural attributes

The urban streams of this study possessed significantly greater macroinvertebrate abundance (Fig. 3A) and taxa richness (Fig. 3B) than forest streams, yet diversity was similar across sites (Fig. 3C,D). These findings are contrary to previous temperate studies, which have suggested that urbanisation should lead to declines in total macroinvertebrate abundance, taxa richness as well as diversity, albeit acknowledging that the nature of urbanisation (e.g. extent of impervious surface, amount of residential and industrial discharge, height and nature of riparian vegetation) varies with climate, culture, and history (Del Arco et al., 2012; Mackintosh et al., 2015; Meyer et al., 2005; Paul and Meyer, 2001). In the temperate zone, stream macroinvertebrates are thought to derive the majority of their energy from allochthonous sources, particularly in shaded headwater streams (Vannote et al., 1980). Cyanobacteria appear to be unpalatable to temperate grazing macroinvertebrates (O'Gorman et al., 2017). Tropical macroinvertebrates, however, are suggested to primarily rely on autochthonous resources such as microalgae and cyanobacteria (Lau et al., 2009; Mantel et al., 2004), the production of which is greater in urban habitats due to elevated temperature and nutrient levels (Friberg et al., 2009). This suggests that in contrast to their temperate counterparts, tropical macroinvertebrates profit from the increased availability of autochthonous resources in urban streams, which may have contributed to the observed increase in abundance. In addition, macrophytes provide macroinvertebrates with habitat, shelter, and food resources; their presence in urban streams therefore has the potential to support larger numbers of macroinvertebrates (Walker et al., 2013). However, urban streams were dominated by a completely different fauna, including introduced snails and leeches that were absent from forest streams (reflecting patterns found in Malaysian streams; Yule et al., 2015). While other tropical studies have also reported an increase in macroinvertebrate abundance with urbanisation (Peralta et al., 2020; Yule et al., 2015), they found a decrease in taxa richness, which is in contrast to the findings of this study. Past habitat fragmentation and disturbance events likely resulted in depauperate communities in Singapore's forest streams compared to e.g. Malaysian forest streams (Castelletta et al., 2005; Corlett, 1992), which may make Singapore's urban streams seem more favourable in comparison. Alternatively, as a forerunner in sustainable urban water management (Liu and Jensen, 2018), Singapore's urban streams may provide sufficient habitat and water quality for some native species, thus resulting in the observed increases in taxa richness. Furthermore, Singapore is relatively small, and so macroinvertebrates could spread easily across its watersheds through dispersal agents (e.g. mammals and birds) or on their own if they have

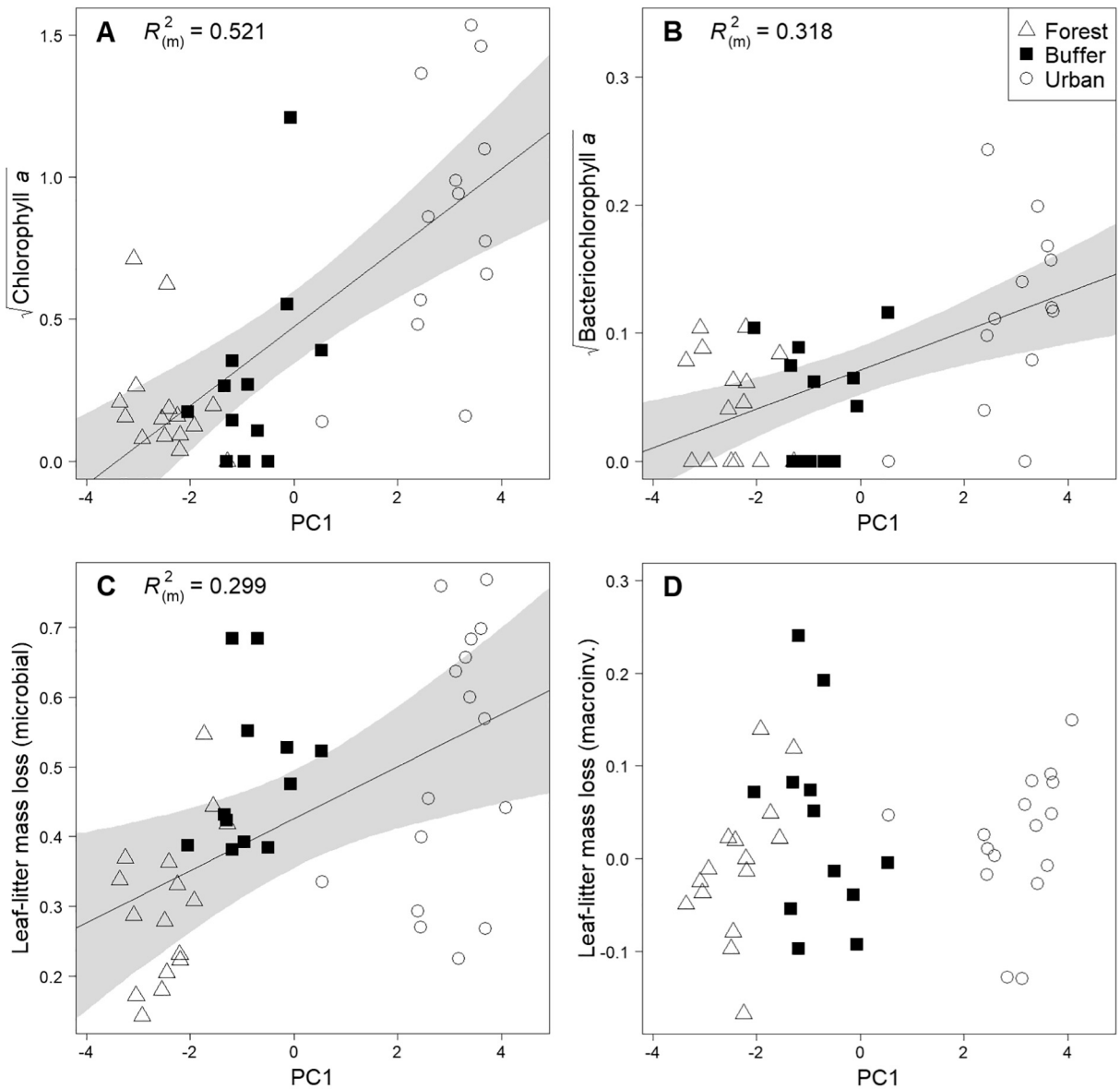

Fig. 4. Relationship between the urbanisation gradient (PC1) and concentrations of (A) chlorophyll *a* and (B) bacteriochlorophyll *a*, and leaf-litter mass loss due to (C) microbial decomposition and (D) macroinvertebrate-driven decomposition. Regression lines (solid line; predicted by GLMM) and their predicted 95% CI (shaded area; obtained through bootstrapping) visualise the magnitude and uncertainty of significant relationships.

flying adult stages (Dodds et al., 2015), which might account for the discrepancies compared to other tropical studies. Even though we recorded more taxa at urban sites, there was no effect on overall diversity as taxa evenness was reduced. Buffer streams had particularly low macroinvertebrate diversity, indicating that their communities were dominated by a few abundant taxa. Singapore's buffer parks have been developed relatively recently (National Parks Board, 2017) and might not yet have attracted the same diversity of macroinvertebrates as the older forest and urban habitats. Alternatively, the higher water velocity recorded in buffer streams (Table A.3) might also present unfavourable habitats to some benthic macroinvertebrates (Wallace and Webster, 1996), thereby resulting in low diversity.

The decreases in water quality and stream health with increasing urbanisation (SingScore; Fig. 3E) are reflective of the marked changes in physico-chemical properties along the urbanisation gradient and appear to be a universal phenomenon (e.g. Blakely et al., 2014; Othman et al., 2012; Ramírez et al., 2009; Walsh et al., 2005). As a result of their poor water quality, urban streams had macroinvertebrate communities that were dominated by local pollution-tolerant taxa (e.g. among Hirudinea and Gastropoda), which is in line with the findings of previous temperate and tropical studies (e.g. Al-Shami et al., 2011; Del Arco et al., 2012; Yule et al., 2015). The dominance of gastropods in urban streams is most likely a result of the increased availability of algae and macrophytes for snails to graze on. Gastropods can only survive there, however, because of their pollution tolerance and the availability of high concentrations of calcium carbonate (which they need to build their shells; White et al., 2007). Even though the taxa Ephemeroptera, Odonata, and Trichoptera (generally pollution-sensitive according to Singapore-specific tolerance scores; Blakely et al., 2014) were mostly associated with less disturbed habitats, members of these groups were also present in urban streams. This could partly be attributed to the relatively compressed scale and connectedness of freshwater habitats in Singapore, or to the high biodiversity typically associated with tropical fresh waters and the physiological tolerance of tropical macroinvertebrates (Schowalter, 2016; Yule et al., 2010). Despite their low diversity, the communities in Singapore's buffer streams reflected on average fair water quality (compared to poor in urban and good in forest streams), indicating that the buffer parks are to an extent

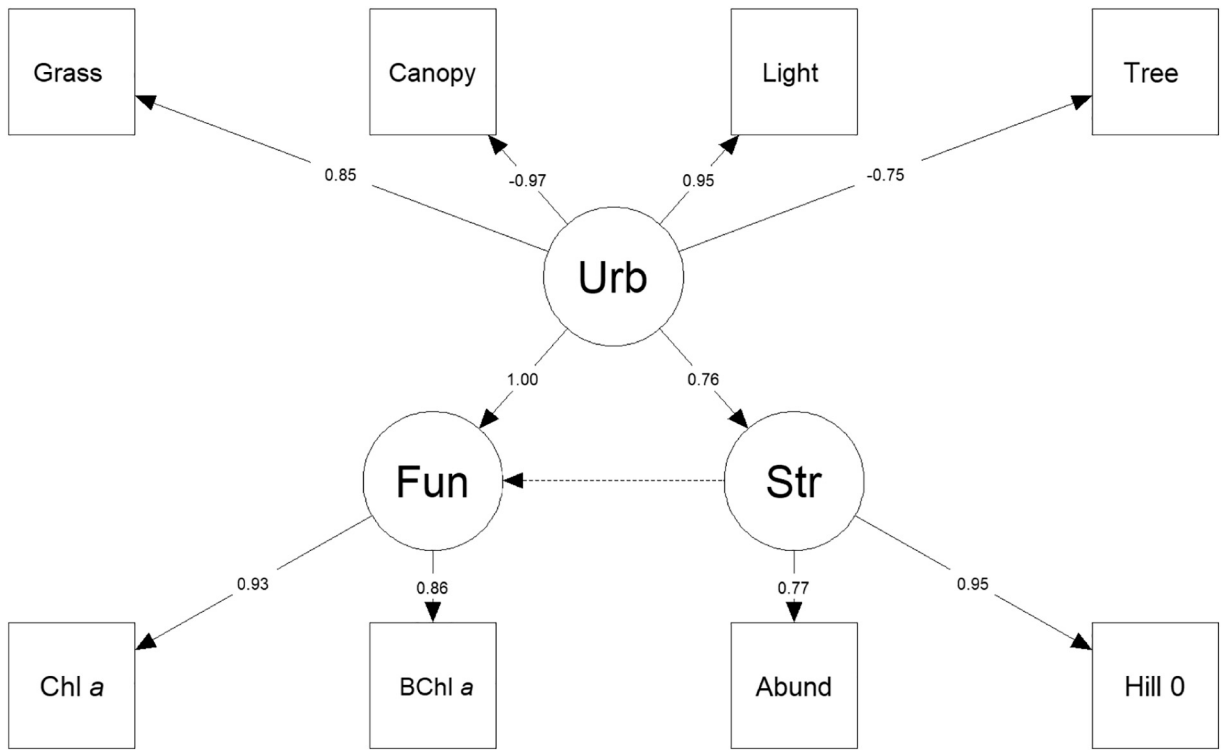

Fig. 5. Graphical representation of the best-supported structural equation model. Latent variables (circles; Urb = urbanisation, Fun = ecosystem functioning, Str = ecosystem structure) are indicated by observed variables (boxes; Chl *a* = chlorophyll *a*, BChl *a* = bacteriochlorophyll *a*, Abund = macroinvertebrate abundance, Hill 0 = taxa richness, Grass = riparian grass cover, Canopy = canopy cover, Light = light intensity, Tree = riparian tree cover). Values are standardised regression coefficients (β). Solid arrows represent significant ($p < 0.05$), dashed arrows non-significant correlations. Covariances are not displayed. Fit indices are reported in Table A.7A (Model 3).

carrying out their function as alternative nature venues. In urbanised and densely-populated areas, stream water of adequate quality is essential for the use of residents, irrigation, and industries (Kido et al., 2009). Thus targeted water quality enhancements in urbanised landscapes through environmental preservation and proactive policies are of great socio-economic importance (Othman et al., 2012).

4.2. Functional attributes

Ecosystem functioning related to microbial activity (primary productivity and leaf-litter decomposition) increased along the urbanisation gradient (Fig. 4A–C). Higher levels of nutrients, temperature, and irradiation due to forest clear-cutting have all been found to fuel microbial activity, periphyton growth rates, and consequently primary production in both temperate and tropical streams (Chauvet et al., 2016; Friberg et al., 2009; Ramírez et al., 2009). Likewise, they have been reported to promote microbial decomposition of leaf litter across the different climate zones (Friberg et al., 2009; Imberger et al., 2008; Yule et al., 2015). The higher water temperatures and phosphate concentrations we recorded in the urban streams are thus likely key drivers of the increased primary productivity and microbial leaf-litter decomposition.

In contrast to findings in the temperate zone, however, we did not detect any evidence of macroinvertebrate-driven decomposition, suggesting that leaf-litter breakdown is primarily mediated through microbial activity in these tropical streams (Fig. 4D). Negative values for macroinvertebrate-driven leaf-litter mass loss indicated that more leaf-litter mass was lost in fine-mesh than in coarse-mesh bags. A possible explanation is that in coarse-mesh bags, macroinvertebrate grazers were feeding on the microbial biomass that accumulated on the leaf litter (Feminella et al., 1989; Gessner and Chauvet, 1994), thereby reducing microbial decomposer activity in coarse-mesh compared to fine-mesh bags. The lack of macroinvertebrate-driven decomposition might be linked to the discussed lack of significant difference between the macroinvertebrate communities of the different habitats in our study, or it could be due to the often-cited lower diversity and trophic contribution of shredders in the tropics (Dobson et al., 2002; Graça et al., 2015; Irons III et al., 1994; Lau et al., 2009; Rosemond et al., 1998; but see Benstead, 1996; Wright and Covich, 2005). Singapore's forest streams might be lacking the abundance of shredders found in much larger, more pristine forest streams in Malaysia due to the ecological transformation of Singapore over the past two centuries. Furthermore, as macroinvertebrate shredders (e.g. crabs) in tropical lowland streams are typically relatively large (Yule et al., 2009), such individuals might have been excluded from the coarse-mesh bags (pore size: 6 mm), the shredding activity of which would therefore not have been measured in this study. In contrast to their tropical counterparts, temperate macroinvertebrates were generally found to contribute greatly to the decomposition of leaf litter, particularly in shaded forest streams, where leaf detritus is the major energy source (river continuum concept; Chauvet et al., 2016; Lau et al., 2009; Vannote et al., 1980). Irrespective of whether leaves are broken down by shredders or microbes, other macroinvertebrates (e.g. collector-gatherers and collector-filterers) possibly still derive much of their energy from leaves as they feed on fine leaf detritus. Nevertheless, the lack of macroinvertebrate-driven decomposition might suggest a fundamental difference at the base of the food web (at least in allochthonous pathways) across climate zones. From these discrepancies between temperate and tropical lotic systems, it follows that well-established temperate solutions to urbanisation are not inevitably successful in the tropics.

4.3. Ecosystem linkages

Although urbanisation exerted a considerable influence on all aspects of the studied stream ecosystems, we found that it affected ecosystem functioning more than structure. This might be linked to the enhanced microbial activity in urban habitats that accelerated ecosystem process rates related to microbes. We found that the structural changes (i.e. shift in macroinvertebrate community composition) did not affect ecosystem functioning significantly, thus the functional attributes appear to respond directly to urbanisation. Structural responses were presumably not only influenced by those habitat characteristics captured by the urbanisation gradient, but by other factors such as differing dispersal ability of macroinvertebrates or frequency and intensity of flood events as well (Clarke et al., 2008; Friberg et al., 2009; Osmundson et al., 2002). Ecosystem functioning increased with both primary production and decomposition, but its effect on the latter was inconsequential, such that removing decomposition improved the model fit substantially (Table A.7). This indicates that urbanisation promoted the green (autochthonous) pathway more strongly than the brown (allochthonous), with a dramatic increase in algae and cyanobacteria in urban streams. Thus, ecosystem functioning should be dominated by autochthony in the open, warm, nutrient-rich urban streams (i.e. algae fed upon by grazers) compared to allochthony in the cooler, shaded forest streams (i.e. leaf litter broken down by microbes, macroinvertebrate shredders, or physical abrasion, and fed upon by collector-gatherers and collector-filterers; Chauvet et al., 2016; Vannote et al., 1980). However, the apparent lack of macroinvertebrate decomposition in the studied streams supports the idea that tropical lotic ecosystems derive the majority of their energy from autochthonous rather than allochthonous sources (Lau et al., 2009). As very few macroinvertebrates in these tropical streams seem to be capable of using the brown pathway, primary production could be the primary driver of the observed patterns in macroinvertebrate abundance and richness, thus explaining the high abundance and taxa richness of macroinvertebrate communities observed in the urban streams.

4.4. Conservation implications

Urban ecosystems play a pivotal role in increasing the health and resilience of cities by providing many services, including habitat provision, culture, recreation, pollution reduction, potable water, and microclimate regulation (Elmqvist et al., 2015). Riparian buffers and forests can provide a cooling effect through shading and reduce the risk of flooding by intercepting rainfall (Pataki et al., 2011). Urban areas create a mosaic of habitats that support a high diversity of fauna and flora. Mitigating the loss of biodiversity also has important benefits for citizens, cultures, and governments by enhancing human well-being (Elmqvist et al., 2015). Ecosystem functioning influences and is influenced by community composition, which is in turn shaped by habitat, other environmental characteristics, and human disturbances (Frainer, 2013). In the studied streams, ecosystem processes such as leaf-litter breakdown and algal production were found to be largely controlled by microbial consumers and producers, which were the basic food source for aquatic macroinvertebrates. Singapore's forest streams have few exotic species and so are safe havens for the native freshwater diversity (Kwik and Yeo, 2015; Ng et al., 1993), whereas its urban streams facilitate the establishment of invasive species, e.g. some of the snails found in this study (see also Kwik et al., 2013; Yeo and Lim, 2011). The studied urban communities were dominated by a small subset of taxa that were indicative of a polluted environment and thus not desirable for a natural habitat. Urbanisation is not purely categorical, however, and even urban streams can provide suitable habitats for some native species (Ng et al., 1993). Well-managed urban streams, and specifically buffer streams, are therefore essential for maintaining freshwater communities or species of conservation significance.

Information from this study on the structural and functional changes associated with urbanisation is a fundamental step towards maximising the conservation and ecosystem management success in tropical streams. We identified riparian grass cover and light intensity (positively correlated to urbanisation), as well as riparian tree cover and canopy cover (negatively correlated to urbanisation), as the major factors associated with the urbanisation-induced changes in both ecosystem structure and functioning. Based on these findings, we recommend that urban stream restoration or rehabilitation projects directly address the above environmental factors in order to create naturalised stream environments that restore ecological processes, functions, and services. The potential of habitat restoration/rehabilitation (e.g. by incorporating woody tree species that increase shading along urban stream banks) to not only protect existing core forested areas, but also to limit the impacts of urbanisation on stream ecosystem structure and functioning is exemplified in the performance of Singapore's green buffer parks (Fig. 3 and Fig. 4). This enhanced understanding is ecologically, socially, and economically advantageous by enabling (at least partial) restoration of highly urbanised streams to promote more natural and diverse (i.e. healthy) ecosystems that maintain regulating and provisioning services, offer recreational areas for the public, create habitat niches for native species (thereby encouraging re-colonisation and increasing biodiversity), and improve the resilience of these urban ecosystems to other threats such as climate change or invasive species.

5. Conclusion

Overall, most of the extensively-described manifestations of the urban stream syndrome were reflected in our urbanisation gradient (e.g. high nutrient loading, high pH and water temperature, degradation of riparian vegetation). These similarities likely influenced most structural and functional responses of the studied tropical stream ecosystems to urbanisation to be like those found in temperate and other tropical regions, i.e. pollution-tolerant macroinvertebrate taxa dominate, and primary productivity and microbial leaf-litter decomposition are increased. Nevertheless, there are important differences in lotic systems between the climate zones that primarily relate to the community composition and role of stream macroinvertebrates (i.e. abundance, decomposer activity), and even within the tropical zone (i.e. taxa richness). These differences make research in tropical regions essential, despite the existing body of temperate work. Our study adds to the growing research examining urbanisation impacts on both the structure and functioning of ecosystems, and expands our general understanding of the stability of stream ecosystems in response to anthropogenic disturbances. Ecosystem functioning, particularly the autochthonous pathway, was most strongly affected by urbanisation. The important downstream challenge is to integrate these findings into the development of effective and targeted ecosystem management strategies to maintain urban ecosystem services (i.e. recreational green parks, local pollution removal, habitat provision to reduce biodiversity loss) that are ecologically, socially, and economically advantageous, and to mitigate or even reverse urbanisation-induced effects. We suggest that by restoring dense riparian canopies, the intensity of the incoming light might be reduced, thereby attenuating many effects of urbanisation on ecological processes in streams and creating additional green spaces in urban areas for the enjoyment of the public.

CRediT authorship contribution statement

Fabienne Wiederkehr: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft. **Clare L. Wilkinson**: Methodology, Investigation, Writing - review &

editing. **Yiwen Zeng**: Methodology, Formal analysis, Writing - review & editing. **Darren C.J. Yeo**: Methodology, Writing - review & editing. **Robert M. Ewers**: Formal analysis, Writing - review & editing. **Eoin J. O'Gorman**: Methodology, Writing - review & editing.

Acknowledgements

We thank Movin Nyanasengeran, Bastian Morath, and the Freshwater and Invasion Biology Lab, National University of Singapore (NUS), for excellent field and laboratory assistance, and National Parks Board (NParks), Singapore, for support and permission to conduct research. This work was funded by a project grant from Imperial College London's MRes Tropical Forest Ecology, a National Parks Board Grant, Singapore (NUS Grant No. R-154-000-A88-490), and NERC (NE/L011840/1).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A

Table A.1
Correlation of urbanisation indices calculated from areas with radii of 50, 100, 200, 500, and 1000 m around every sampling point with all other environmental variables.

Urbanisation index	50 m	100 m	200 m	500 m	1000 m
50 m	1.000	0.954	0.784	0.586	0.376
100 m		1.000	0.919	0.730	0.448
200 m			1.000	0.875	0.535
500 m				1.000	0.826
1000 m					1.000
pH	-0.017	0.171	0.286	0.422	0.467
Dissolved oxygen	-0.135	-0.186	-0.372	-0.375	-0.293
TDS	-0.034	0.183	0.495	0.607	0.533
Nitrate	-0.187	0.033	0.185	0.168	0.035
Phosphate	-0.082	0.150	0.493	0.551	0.357
Light intensity	0.528	0.535	0.476	0.490	0.583
% Macrophyte	0.490	0.429	0.390	0.392	0.472
% Canopy cover	-0.516	-0.514	-0.468	-0.459	-0.542
% Leaf litter	-0.133	-0.187	-0.258	-0.299	-0.206
% Grass	0.391	0.498	0.550	0.601	0.683
% Shrub	-0.082	-0.184	-0.225	-0.245	-0.303
% Tree	-0.455	-0.498	-0.526	-0.577	-0.612
% Mud	-0.005	-0.028	-0.051	-0.113	-0.036
% Sand	0.079	0.078	0.105	0.101	-0.135
% Gravel and concrete	-0.108	-0.071	-0.077	0.023	0.255

Table A.2
Importance of principal components 1–4 and variable loadings on each component.

Principal components	PC1	PC2	PC3	PC4
% Variance	38.32	17.82	14.41	12.07
% Cumulative var.	38.32	56.15	70.55	82.63

Loadings				
Urbanisation index	0.273	0.160		0.293
pH	0.296	-0.164	0.303	-0.157
Dissolved oxygen		-0.511		-0.306
TDS	0.304	0.175	0.283	0.194
Nitrate	0.136	-0.255	0.473	
Phosphate	0.202	0.221	0.395	0.286
Light intensity	0.326		-0.278	-0.154
% Macrophyte	0.228		-0.413	0.110
% Canopy cover	-0.340		0.297	0.129
% Leaf litter	-0.225	0.275		-0.256
% Grass	0.375	0.118		-0.141
% Shrub	-0.211	-0.130	-0.202	0.327
% Tree	-0.300		0.247	-0.141
% Mud	-0.174	0.486		-0.157
% Sand		-0.419		0.451
% Gravel and concrete	0.235	-0.125		-0.428

Table A.3
Location and mean ± SE of recorded environmental variables in the 11 studied streams.

	Forest				Buffer			Urban			
Site	1	2	3	4	5	6	7	8	9	10	11
Latitude (N)	1°22'30.6"	1°22'59.7"	1°22'56.6"	1°21'03.9"	1°21'38.4"	1°21'52.7"	1°24'0.7"	1°19'59.3"	1°19'26.1"	1°23'34.6"	1°24'56.4"
Longitude (E)	103°49'28.2"	103°46'46.9"	103°47'14.6"	103°46'53.8"	103°49'28.2"	103°46'41.5"	103°48'40.0"	103°49'44.0"	103°44'47.8"	103°51'02.9"	103°49'30.4"
Urbanisation index	0.092 ± 0.005	0.062 ± 0.003	0.000 ± 0.000	0.078 ± 0.003	0.459 ± 0.002	0.351 ± 0.006	0.344 ± 0.002	0.693 ± 0.009	0.707 ± 0.001	0.321 ± 0.003	0.321 ± 0.005
Mean stream width (m)	1.50 ± 0.38	1.86 ± 0.11	1.00 ± 0.02	1.02 ± 0.17	1.65 ± 0.47	1.31 ± 0.19	1.08 ± 0.11	1.04 ± 0.06	0.87 ± 0.09	1.71 ± 0.34	1.85 ± 0.30
Mean water depth (cm)	9.38 ± 1.72	24.94 ± 3.35	5.81 ± 0.58	7.50 ± 1.62	10.75 ± 3.10	4.06 ± 0.62	19.56 ± 2.90	23.13 ± 4.88	16.94 ± 3.68	16.75 ± 1.90	13.69 ± 2.13
Mean velocity (cm s^{-1})	1 ± 1	0 ± 0	4 ± 1	14 ± 3	7 ± 3	16 ± 2	8 ± 2	9 ± 3	2 ± 1	4 ± 2	6 ± 2
Water temperature (°C)	27.6 ± 0.4	26.2 ± 0.0	26.2 ± 0.0	25.8 ± 0.0	25.4 ± 0.0	26.8 ± 0.0	26.2 ± 0.0	27.9 ± 0.4	27.6 ± 0.3	31.8 ± 0.1	30.0 ± 0.1
pH	5.78 ± 0.14	5.50 ± 0.01	5.46 ± 0.03	6.47 ± 0.29	6.30 ± 0.01	6.71 ± 0.11	5.84 ± 0.05	6.30 ± 0.07	7.05 ± 0.01	8.31 ± 0.02	6.74 ± 0.02
Dissolved oxygen (mg L^{-1})	3.61 ± 0.74	3.38 ± 0.26	5.13 ± 0.23	6.30 ± 0.26	4.74 ± 0.12	6.85 ± 0.05	4.84 ± 0.12	3.55 ± 0.97	0.30 ± 0.09	7.82 ± 0.15	4.26 ± 0.33
Conductivity (μS cm^{-1})	24.2 ± 1.5	20.0 ± 0.3	17.2 ± 0.1	43.8 ± 1.3	64.3 ± 0.2	62.6 ± 0.9	57.2 ± 0.5	94.4 ± 2.2	586.0 ± 3.3	273.4 ± 29.1	305.9 ± 20.8
Total dissolved solids (g L^{-1})	0.015 ± 0.001	0.013 ± 0.000	0.011 ± 0.000	0.028 ± 0.001	0.039 ± 0.003	0.039 ± 0.000	0.036 ± 0.000	0.058 ± 0.001	0.362 ± 0.002	0.157 ± 0.017	0.181 ± 0.013
Nitrate (mg L^{-1})	0.10 ± 0.03	0.08 ± 0.00	0.09 ± 0.01	1.57 ± 0.06	0.07 ± 0.01	2.02 ± 0.09	0.11 ± 0.03	0.28 ± 0.02	1.39 ± 0.23	1.87 ± 0.20	0.43 ± 0.04
Phosphate (ppm)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.02 ± 0.01	0.02 ± 0.01	0.06 ± 0.04	0.00 ± 0.00	0.01 ± 0.01	0.77 ± 0.05	0.11 ± 0.04	0.13 ± 0.08
Light intensity (μmol m^{-2} s^{-1})	84 ± 27	223 ± 203	39 ± 8	93 ± 56	230 ± 129	37 ± 9	834 ± 171	1439 ± 393	574 ± 202	1250 ± 134	1320 ± 179
% Macrophyte	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	38 ± 3	43 ± 8	14 ± 6	5 ± 0	60 ± 18
% Canopy cover	95 ± 1	92 ± 7	96 ± 1	95 ± 1	96 ± 2	95 ± 1	34 ± 7	28 ± 11	66 ± 13	26 ± 3	12 ± 3
% Leaf litter	64 ± 19	55 ± 13	14 ± 3	20 ± 5	26 ± 18	23 ± 4	19 ± 9	21 ± 11	12 ± 2	11 ± 2	6 ± 1
% Grass	0 ± 0	1 ± 1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	4 ± 2	95 ± 5	72 ± 8	92 ± 3	98 ± 3
% Shrub	11 ± 7	75 ± 11	49 ± 6	29 ± 7	69 ± 7	48 ± 8	91 ± 4	3 ± 3	17 ± 6	8 ± 3	0 ± 0
% Tree	89 ± 7	24 ± 11	51 ± 6	71 ± 7	31 ± 7	52 ± 8	5 ± 5	2 ± 2	11 ± 7	0 ± 0	2 ± 2
% Mud	85 ± 5	80 ± 7	15 ± 5	20 ± 5	29 ± 7	15 ± 5	9 ± 1	49 ± 12	42 ± 3	5 ± 2	9 ± 4
% Sand	15 ± 5	20 ± 7	85 ± 5	80 ± 5	71 ± 7	85 ± 5	90 ± 2	51 ± 12	58 ± 3	49 ± 4	56 ± 17
% Gravel and concrete	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1 ± 1	0 ± 0	0 ± 0	46 ± 5	35 ± 19
Photo in Fig. A.1	A	B	C	D	E	F	G	H	I	J	K

Table A.4
Generalised linear mixed-effects models testing for the effects of urbanisation on five structural attributes of macroinvertebrate community composition: (A) abundance, (B) taxa richness ($q = 0$), (C) taxa diversity ($q = 1$), (D) taxa diversity ($q = 2$), and (E) SingScore. Fixed effects *b*: mean intercepts and slopes [and their 95 % CI] with significant parameters ($p < 0.05$) highlighted in bold.

Structural attribute:	A Abundance Poisson mixed model (log link)		B $q = 0$ Poisson mixed model (log link)		C $\log_e$ ($q = 1$) Gaussian mixed model		D $\log_e$ ($q = 2$) Gaussian mixed model		E SingScore Gaussian mixed model	
Model name	Null model	Full model	Null model	Full model	Null model	Full model	Null model	Full model	Null model	Full model
Fixed effects	*b* [95 % CI]	*b* [95 % CI]	*b* [95 % CI]	*b* [95 % CI]	*b* [95 % CI]	*b* [95 % CI]	*b* [95 % CI]	*b* [95 % CI]	*b* [95 % CI]	*b* [95 % CI]
Intercept	**3.76 [3.12, 4.41]**	**3.75 [3.13, 4.38]**	**1.70 [1.50, 1.91]**	**1.70 [1.55, 1.84]**	**1.03 [0.86, 1.19]**	**1.02 [0.88, 1.16]**	**0.80 [0.63, 0.97]**	**0.80 [0.64, 0.95]**	**78.8 [63.0, 94.6]**	**79.1 [70.0, 88.2]**
PC1	-	**0.31 [0.23, 0.40]**	-	**0.10 [0.04, 0.16]**	-	0.06 [0.00, 0.12]	-	0.05 [-0.01, 0.11]	-	**-8.86 [-12.5, -5.23]**
Random effects	VC	VC	VC	VC	VC	VC	VC	VC	VC	VC
Stream (Intercept)	1.184	1.111	0.070	0.010	0.050	0.026	0.048	0.032	598.0	121.3
Residuals	-	-	-	-	0.121	0.123	0.145	0.146	454.8	447.9
AIC_C	783.32	730.25	185.04	179.07	48.53	47.52	54.82	55.13	411.74	401.51
$R^2_{(m)}$	-	0.349	-	0.234	-	0.127	-	0.077	-	0.460
$R^2_{(c)}$	0.989	0.993	0.268	0.271	0.291	0.282	0.249	0.245	0.568	0.575

VC = variance components of random effects; AIC_C = Akaike Information Criterion corrected for small sample sizes; $R^2_{(m)}$ = proportion of variance explained by fixed effects; $R^2_{(c)}$ = proportion of variance explained by fixed plus random effects.

Table A.5
List of identified macroinvertebrate taxa and their mean abundance per site. Taxa in bold are referred to in the text.

Phylum / Class / Subclass / Order / Suborder / Family	Mean abundance										
	Forest				Buffer			Urban			
	1	2	3	4	5	6	7	8	9	10	11
Platyhelminthes											
Tricladida											
Dugesiidae	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Annelida											
Clitellata											
Tubificidae	0.7	0.0	0.3	0.0	0.0	0.0	0.5	0.0	1.5	0.0	0.0
Hirudinea											
Erpobdellidae	0.0	0.0	0.3	0.0	1.5	0.0	1.0	1.5	0.0	4.3	21.0
Glossiphoniidae	0.3	0.0	0.0	0.0	0.3	0.3	0.8	2.5	0.3	1.3	9.8
Mollusca											
Gastropoda											
Physidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	16.0	4.5
Ancylidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.8	0.3
Lymnaeidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0
Planorbidae	0.0	0.0	0.0	0.0	0.5	0.0	0.5	6.5	0.5	12.3	0.3
Bulinidae	0.0	0.0	0.0	0.0	0.0	0.0	0.5	4.3	0.3	33.3	0.0
Neritidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.8
Viviparidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.3
Thiaridae	0.0	0.0	0.0	0.0	0.0	0.0	1.5	1.0	0.3	8.8	10.5
Arthropoda											
Arachnida											
Araneae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0
Acari	0.0	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.3	0.0
Malacostraca											
Isopoda	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0
Decapoda											
Atyidae	0.0	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Brachyura	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0.0	0.0	0.0	0.0
Entognatha											
Collembola	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.5	0.0	0.0
Insecta											
Odonata											
Anisoptera											
Aeshnidae	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Corduliidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.0	0.0	1.5	0.0
Libellulidae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0
Zygoptera											
Coenagrionidae	2.3	0.8	0.0	0.3	0.0	0.0	0.0	0.0	0.3	0.8	0.3
Ephemeroptera											
Baetidae	0.0	0.0	0.3	1.8	0.3	0.5	0.0	1.0	0.0	0.0	0.0
Leptophlebiidae	0.0	0.0	0.0	4.3	0.0	5.0	0.0	0.5	0.0	0.0	0.0
Caenidae	4.3	1.3	0.0	5.0	0.5	0.8	1.0	14.8	0.0	0.0	0.0
Plecoptera											
Perlidae	0.0	0.3	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Hemiptera											
Hebridae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
Hydrometridae	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0
Coleoptera											
Dytiscidae	0.0	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Scirtidae	0.0	0.0	0.0	23.8	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Trichoptera											
Ecnomidae	4.0	0.0	0.0	0.0	11.3	0.0	0.8	0.3	0.0	0.0	1.3
Polycentropodidae	0.7	1.8	0.3	0.5	3.8	0.0	0.0	1.0	0.0	0.0	0.0
Lepidoptera											
Crambidae	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Diptera											
Tipulidae	0.0	0.0	0.3	0.0	0.0	0.3	0.0	0.0	0.0	0.0	0.0
Ceratopogonidae	0.3	0.0	0.3	0.3	0.5	1.3	0.3	0.0	0.0	0.0	0.0
Chironomidae	27.7	5.8	4.5	25.5	76.3	23.3	75.3	37.8	2.8	151.3	65.0
Athericidae	0.0	0.0	0.0	0.0	0.0	0.0	0.3	0.0	0.0	0.0	0.0

Table A.6
Generalised linear mixed-effects models testing for the effects of urbanisation on four functional attributes of ecosystems: (A) chlorophyll *a* and (B) bacteriochlorophyll *a* concentrations, (C) microbial and (D) macroinvertebrate-driven leaf-litter mass loss. Fixed effects *b*: mean intercepts and slopes [and their 95 % CI] with significant parameters ($p < 0.05$) highlighted in bold.

Functional attribute:	A √(Chlorophyll *a*) Gaussian mixed model		B √(Bacteriochlorophyll *a*) Gaussian mixed model		C Microbial decomposition Gaussian mixed model		D Macroinvertebrate decomposition Gaussian mixed model	
Model name	Null model	Full model	Null model	Full model	Null model	Full model	Null model	Full model
Fixed effects	*b* [95 % CI]	*b* [95 % CI]	*b* [95 % CI]	*b* [95 % CI]	*b* [95 % CI]	*b* [95 % CI]	*b* [95 % CI]	*b* [95 % CI]
Intercept	**0.47 [0.25, 0.70]**	**0.47 [0.35, 0.60]**	**0.07 [0.04, 0.10]**	**0.07 [0.05, 0.09]**	**0.43 [0.34, 0.51]**	**0.43 [0.36, 0.50]**	0.01 [-0.02, 0.05]	0.01 [-0.02, 0.05]
PC1	-	**0.14 [0.09, 0.19]**	-	**0.01 [0.01, 0.02]**	-	**0.04 [0.01, 0.06]**	-	0.00 [-0.01, 0.02]
Random effects	VC	VC	VC	VC	VC	VC	VC	VC
Stream (Intercept)	0.119	0.025	0.001	0.000	0.019	0.012	0.003	0.002
Residuals	0.091	0.076	0.003	0.002	0.009	0.008	0.004	0.004
AIC_C	43.36	28.13	-106.62	-115.08	-52.18	-56.34	-91.14	-89.13
$R^2_{(m)}$	-	0.521	-	0.318	-	0.299	-	0.019
$R^2_{(c)}$	0.568	0.639	0.317	0.412	0.692	0.719	0.363	0.366

VC = variance components of random effects; AIC_C = Akaike Information Criterion corrected for small sample sizes; $R^2_{(m)}$ = proportion of variance explained by fixed effects; $R^2_{(c)}$ = proportion of variance explained by fixed plus random effects.

Table A.7
Structural equation model testing for direct and indirect effects of urbanisation on ecosystem structure and functioning using estimations by (A) robust ML and full information maximum likelihood (FIML) for missing data, (B) robust ML, (C) ML and FIML, and (D) ML. Hypotheses: Model 1: All urbanisation-correlated ecological indicators (determined by GLMM) are useful predictors of urbanisation effects on ecological integrity; Model 2: Due to the low taxonomic resolution of the SingScore and the presence of taxa without an attributed tolerance score, this biotic index may not reflect the entire diversity of ecological sensitivity at species level and is therefore a less useful predictor of urbanisation effects on ecological integrity; Model 3: As autochthonous dominate over allochthonous pathways in tropical streams, mass loss is a less useful predictor of urbanisation effects on ecological integrity. Standardised regression coefficients β [and their 95 % CI] with significant parameters ($p < 0.05$) highlighted in bold.

A	Model 1	Model 2	Model 3
Index	full	excl. SingScore	excl. SingScore, mass loss
	β [95 % CI]	β [95 % CI]	β [95 % CI]
Function ~			
Urbanisation	**1.04 [0.54, 1.53]**	**0.94 [0.60, 1.28]**	**1.00 [0.64, 1.36]**
Structure	-0.29 [-0.91, 0.32]	-0.19 [-0.63, 0.26]	-0.29 [-0.75, 0.18]
Structure ~			
Urbanisation	**0.81 [0.65, 0.97]**	**0.75 [0.61, 0.90]**	**0.76 [0.62, 0.90]**
χ^2 (df)	79.205 (32)	54.019 (24)	18.219 (17)
P	0.000	0.000	0.375
n	44	44	44
RMSEA [90 % CI]	0.183 [0.128, 0.240]	0.169 [0.104, 0.234]	0.040 [0.000, 0.147]
SRMR	0.117	0.101	0.035
CFI	0.860	0.900	0.995
TLI	0.803	0.850	0.992
NFI	0.792	0.839	0.933
AIC	954.589	836.839	715.650
ECVI	2.981	2.417	1.627

(*continued on next page*)

Table A.7 (*continued*)

B	Model 1	Model 2	Model 3
Index	full	excl. SingScore	excl. SingScore, mass loss
	β [95 % CI]	β [95 % CI]	β [95 % CI]
Function ~			
Urbanisation	**1.10 [0.58, 1.61]**	**0.99 [0.63, 1.36]**	**1.03 [0.63, 1.42]**
Structure	-0.39 [-1.00, 0.23]	-0.28 [-0.74, 0.19]	-0.34 [-0.82, 0.15]
Structure ~			
Urbanisation	**0.82 [0.66, 0.99]**	**0.77 [0.61, 0.93]**	**0.77 [0.61, 0.93]**
χ^2 (df)	75.506 (32)	55.537 (24)	18.513 (17)
P	0.000	0.000	0.357
n	39	39	39
RMSEA [90 % CI]	0.187 [0.127, 0.247]	0.184 [0.116, 0.252]	0.048 [0.000, 0.158]
SRMR	0.131	0.122	0.041
CFI	0.850	0.879	0.993
TLI	0.789	0.818	0.988
NFI	0.774	0.813	0.922
AIC	850.433	746.230	640.302
ECVI	2.782	2.306	1.433

C	Model 1	Model 2	Model 3
Index	full	excl. SingScore	excl. SingScore, mass loss
	β [95 % CI]	β [95 % CI]	β [95 % CI]
Function ~			
Urbanisation	**0.91 [0.63, 1.19]**	**0.89 [0.65, 1.13]**	**0.89 [0.61, 1.17]**
Structure	-0.11 [-0.45, 0.24]	-0.08 [-0.37, 0.21]	-0.12 [-0.44, 0.20]
Structure ~			
Urbanisation	**0.72 [0.54, 0.90]**	**0.68 [0.49, 0.87]**	**0.68 [0.49, 0.87]**
χ^2 (df)	83.122 (32)	60.669 (24)	26.317 (17)
P	0.000	0.000	0.069
n	44	44	44
RMSEA [90 % CI]	0.191 [0.141, 0.241]	0.186 [0.129, 0.245]	0.112 [0.000, 0.191]
SRMR	0.144	0.105	0.038
CFI	0.847	0.884	0.967
TLI	0.785	0.826	0.946
NFI	0.781	0.828	0.915
AIC	976.655	853.987	732.402
ECVI	3.389	2.742	1.825

D	Model 1	Model 2	Model 3
Index	full	excl. SingScore	excl. SingScore, mass loss
	β [95 % CI]	β [95 % CI]	β [95 % CI]
Function ~			
Urbanisation	**0.91 [0.64, 1.19]**	**0.89 [0.65, 1.14]**	**0.87 [0.61, 1.13]**
Structure	-0.14 [-0.47, 0.20]	-0.11 [-0.41, 0.19]	-0.12 [-0.42, 0.18]
Structure ~			
Urbanisation	**0.70 [0.50, 0.89]**	**0.66 [0.44, 0.88]**	**0.67 [0.45, 0.88]**
χ^2 (df)	77.070 (32)	58.794 (24)	26.133 (17)
P	0.000	0.000	0.072
n	39	39	39
RMSEA [90 % CI]	0.190 [0.136, 0.245]	0.193 [0.131, 0.256]	0.117 [0.000, 0.202]
SRMR	0.161	0.124	0.047
CFI	0.839	0.870	0.961
TLI	0.773	0.805	0.937
NFI	0.762	0.807	0.901
AIC	880.967	772.544	666.010
ECVI	3.156	2.584	1.644

RMSEA = Root Mean Square Error of Approximation; SRMR = Standardised Root Mean Square Residual; CFI = Comparative Fit Index; TLI = Tucker-Lewis Index; NFI = Normed Fit Index; AIC = Akaike Information Criterion; ECVI = Expected Cross-Validation Index.

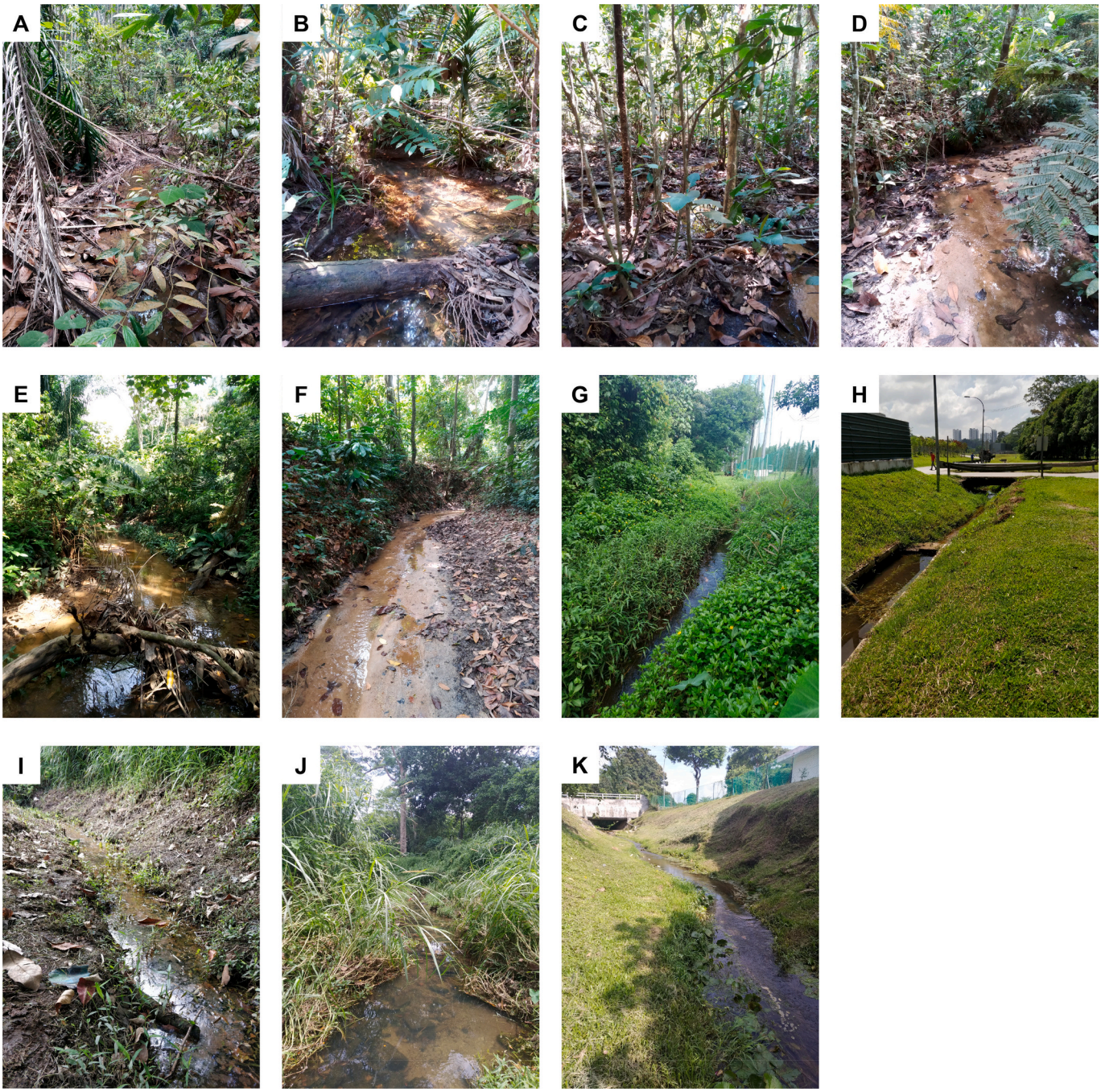

Fig. A.1. Photos of selected streams within (A-D) forest reserves, (E-G) buffer zones between forest and open-country areas, and (H-K) open-country urban areas.

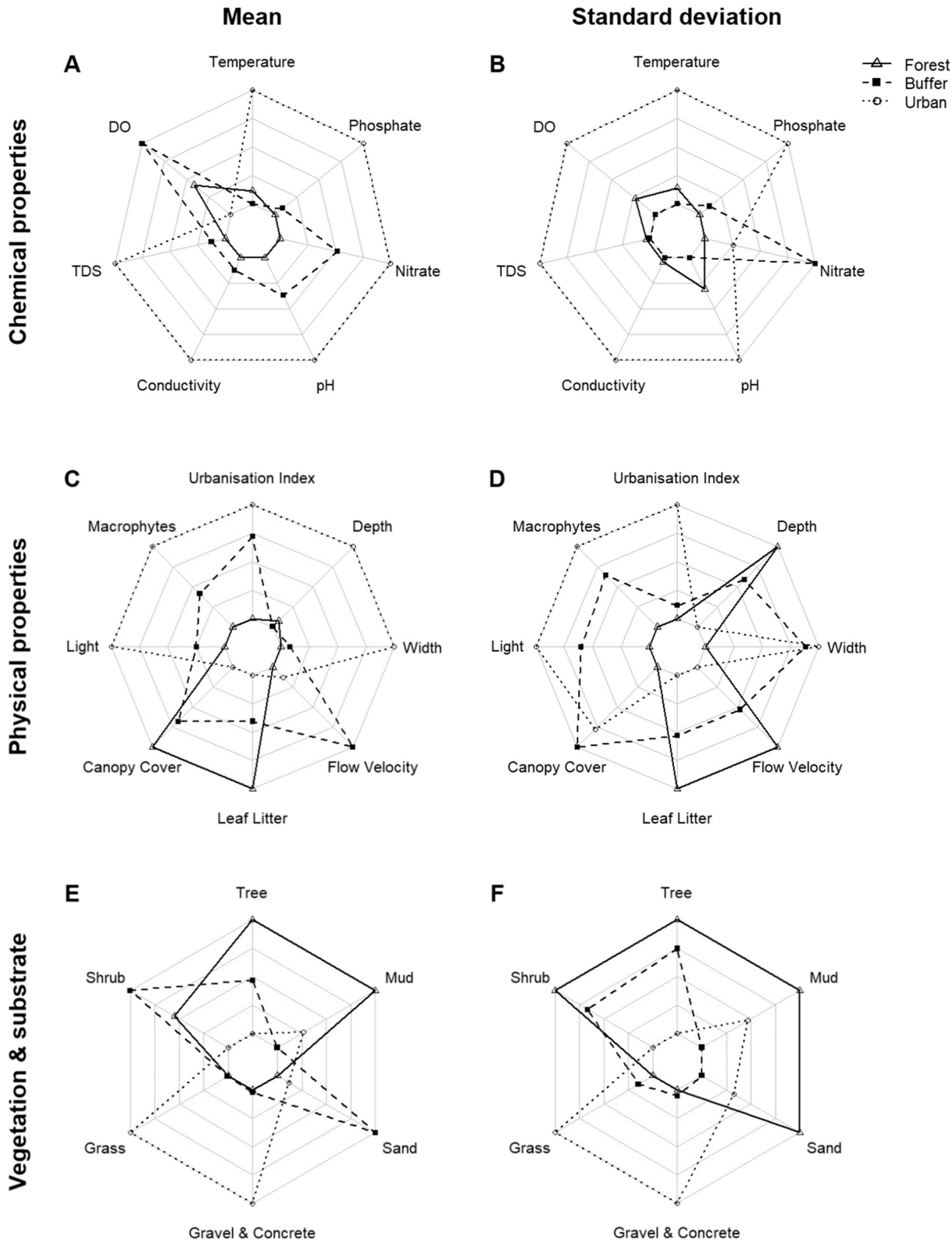

Fig. A.2. Stream characteristics of the studied forest, buffer and urban sites in Singapore. Sites were defined by (A,B) chemical (DO = dissolved oxygen, TDS = total dissolved solids), (C,D) physical and biotic properties, as well as (E,F) composition of vegetation and substrate. Arithmetic means of the recorded properties are presented in the left-hand panels (A,C,E; Table A.3) and their standard deviations in the right-hand panels (B,D,F).

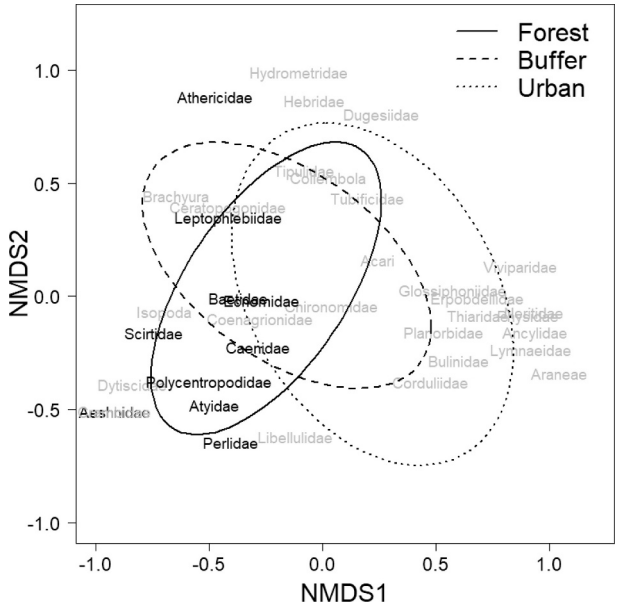

Fig. A.3. Non-metric multidimensional scaling (NMDS) of macroinvertebrate-community variation at the studied sites (ellipsoid hull around habitat type). Pollution-sensitive taxa (tolerance score: ≥ 6) are highlighted in black. For higher taxonomic classifications see Table A.5.

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