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Catchment-scale urbanization diminishes effects of habitat complexity on instream
macroinvertebrate assemblages

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Abstract

While provision of in-stream habitat complexity remains common practice in efforts to restore streams, the evidence of positive effects on in-stream communities is inconsistent. In streams of urban catchments, where both reach-scale habitat manipulation and catchment-scale actions to ameliorate the disturbance regime of urban stormwater runoff are common management responses, clearer understanding of the effects of habitat complexity under different degrees of urban impact are needed. We experimentally assessed the effect of increased surface complexity in wood, the dominant hard substrate in our 18 study reaches on 14 small streams, on in-stream macroinvertebrate assemblages across a range of urban impact. Increased surface complexity increased abundance of most taxa, but this effect was less pronounced in urban streams, partly because of the reduced species pool tolerant of urban stormwater impacts, and partly because of a lesser response of some species to increased complexity in more urban streams. Collectively these taxon-specific effects resulted in small, uncertain increases in taxon richness with increased complexity in rural streams, and no change in richness of the less diverse assemblages of urban streams. Increased abundances suggest increased availability of refugia or resources with increased surface complexity, while the reduced effect of complexity in urban streams suggests that any refuge or resource provided by greater surface complexity is less effective in more disturbed environments receiving urban stormwater runoff. The reduced abundance of sensitive taxa in more urban streams, and the resultant reduced richness, confirms that urban stormwater runoff acts as a strong environmental filter, limiting the species pool available for community assembly. Restoration of habitat complexity in streams without catchment-scale drivers of degradation is likely to have positive benefits to in-stream biotic assemblages, but the efficacy of such approaches in catchments subject to urban stormwater runoff will be greatly diminished. In such cases, restoration activities should first be aimed at controlling the larger-scale problem.

Keywords: Habitat surface complexity, urban stormwater runoff, hierarchical multi-taxon model, stream macroinvertebrate assemblage

Introduction

Structurally complex habitats have been widely observed to support more individuals and more species than simple habitats in terrestrial (e.g. Lassau et al. 2005), marine (e.g. Dean and Connell 1987b), and freshwater (e.g. Taniguchi et al. 2003) environments. Habitat complexity may

influence community assembly and species persistence through mechanisms such as an increased provision of resources or niches, permitting greater niche partitioning (e.g. Willis et al. 2005), or provision of refugia from predation or from physical stressors (Dean and Connell 1987a).

However, exceptions have been reported, with increased habitat complexity being associated with lower diversity, for instance in ant communities (Lassau and Hochuli 2004), or gastropod diversity peaking at an optimal level of corraline-algal complexity (Kelaher 2003). A clearer understanding of the circumstances under which increased habitat complexity increases biological diversity would help direct context-specific decisions on restoration and conservation actions.

Despite the exceptions, the widely observed relationship between habitat complexity and biotic richness and abundance has driven the practice of manipulating physical complexity as a major component of efforts to restore ecosystems that have been simplified by human impacts (Hobbs and Cramer 2008). Provision of structurally complex physical habitat is particularly common in efforts to restore riverine ecosystems (Hilderbrand et al. 2005). Despite large expenditure on the restoration of river and stream ecosystems (Palmer et al. 2005), measurable restoration of stream ecological structure or function is rare (Bernhardt and Palmer 2011). Palmer et al. (2010) found that most studies of biotic response to restoration of in-stream habitat heterogeneity failed to detect significant increases in taxon richness with increased habitat complexity (structural complexity of a single habitat element) or heterogeneity (complexity afforded by qualitatively different habitat elements). A commonly cited cause of such failures is a mismatch between the scale of restoration activity (usually habitat provision at the reach scale) to the scale of the dominant degrading process (often catchment-scale alterations to hydrology and water quality) (Bernhardt and Palmer 2011).

Catchment-scale urbanization is a severely degrading process for stream ecosystems. Loss of sensitive species and shifts in ecological function are observed in urban streams globally (Walsh et al. 2005), resulting from the interactive effects of altered flow regimes, channel form (Vietz et al. 2014, Hawley and Vietz 2016), and water quality (Hatt et al. 2004, McGrane 2016). In most modern cities, the dominant cause of such degradation is urban stormwater runoff draining directly to streams through networks of stormwater drainage systems (Walsh et al. 2016b). Urban stormwater runoff increases the frequency and magnitude of in-stream disturbance, both hydraulic disturbance arising from larger, more frequent high-flow events, and water quality disturbance associated with polluted and thermally altered runoff (Walsh et al. 2005, Somers et al. 2013). It

also reduces in-stream habitat complexity, through increased capacity of streams to transport sediments (Russell et al. 2020), causing simplification of in-stream habitat, such as the loss of bars, benches and woody debris (Vietz et al. 2014).

Two distinct common management responses have sought to address these impacts. Stormwater management practices aiming to mitigate the substantial catchment-scale drivers of increased disturbance and resulting degradation are becoming more common, but have rarely been applied at sufficient intensity or extent to achieve measurable improvement in ecological structure or function (May and Horner 2002, Walsh et al. 2016a). At the same time, reach-scale physical habitat restoration projects, seeking to mitigate habitat simplification, have remained common in streams of urban catchments (Bernhardt and Palmer 2007), despite the catchment-scale disturbances being a primary driver of that simplification. Thus, restoration of physical habitat complexity and heterogeneity (the two are usually interwoven in stream ecosystems: Downes et al. 1998) is a management tool that has been applied across a wide range of disturbance regimes. Yet few studies have assessed if community response to increased habitat complexity varies along a disturbance gradient. Habitat complexity is reported to have a greater positive effect on community cover and species richness of the less diverse invertebrate communities in rocky-shore environments of higher latitudes than in less dynamic rocky shores of lower latitudes (e.g. Bracewell et al. 2018). However, such a latitudinal trend was not observed in mangrove forests, that have less dynamic environments than rocky-shores, with habitat complexity afforded by oyster beds increasing invertebrate abundance and species richness similarly across the same latitudinal gradient (McAfee et al. 2016). Such examples show the complexity of interactions between the effects of disturbance regimes and biogeographic context, but do not provide clear guidance on contexts like streams in urban catchments, where change in the disturbance regime is human-induced, and could potentially be a target of management action instead of or as well as increasing habitat complexity.

Streams of urban catchments thus permit us to ask questions that will help guide management investment by stream managers, such as: given a gradient of urban stormwater impacts, at what point is provision of more complex habitat in a simplified stream likely to increase biodiversity? How large is that increase compared to the increase expected from catchment-scale actions to ameliorate the disturbance regime of urban stormwater runoff (Walsh et al. 2016a)? We thus use stream ecosystems across a range of urban impacts to assess if responses to small-scale habitat

complexity vary with catchment-scale impacts associated with urbanization. For a complexity treatment, we use wood blocks of different surface complexity to mimic woody debris, the dominant hard substrate in our study streams. We added complexity to the wood blocks by cutting grooves that mimicked those found on partially decayed wood in streams. O'Connor (1991) demonstrated such complexity increased macroinvertebrate species richness in rural lowland streams. Our experiment does not aim to replicate the effects of full-scale reach restoration, but to test if the effect of a central element of restoration theory and practice, increased habitat complexity, varies across an important anthropogenic disturbance gradient. We use a hierarchical multi-taxon model to assess differences in abundance of taxa between two types of wood surface in streams with catchments ranging from forested to fully urban, with particular interest in the potential interaction between surface complexity and urban impact. To frame the problem in a context of relevance to management, we use the model to predict and compare assemblage responses to habitat complexity in two scenarios that a manager might typically need to prioritize restoration actions: a rural stream and a moderately urban stream.

We found that increased surface complexity increased abundance of most taxa, but this effect was less common in urban streams, partly because of the reduced species pool tolerant of urban stormwater impacts, but for some species, because of a lesser response to increased complexity in more urban streams. Collectively these taxon-specific effects resulted in a tendency for small, uncertain increases in taxon richness with increased complexity in rural streams, and no change in richness in less diverse assemblages of urban streams. These findings point to a need to prioritize mitigation of catchment-scale impacts of urban stormwater over small-scale habitat manipulation.

Methods

Study area

Eighteen stream reaches of similar morphology and physiography were selected on streams draining the hills on the eastern edge of the Melbourne metropolitan area, Victoria, Australia (Fig. 1), a temperate region with ~800-1200 mm/y rainfall with winter rainfall only marginally higher than that of summer (e.g. Commonwealth of Australia 2019). The sites had catchments of 4–37 km², with catchments with a mix of urban, forested and agricultural land. Streams were of a similar width (~1.5–2.5 m): urban streams had mostly bare clay lined stream beds, most likely because of increased transport capacity of the urban flow regimes eroding the channels to their in-

situ clay (Russell *et al.* 2020), while the selected reaches of most non-urban sites were dominated by sand or silty sediments. Woody debris was the dominant hard substrate in the streams. Sites lined with mature riparian vegetation were selected, but vegetated widths varied from cleared private properties with 2–3 m of vegetation present on either side of the stream, to intact reserves with extensive riparian forest on either side of the stream. Dominant vegetation in the area included evergreen native trees such as *Eucalyptus viminalis*, *E. obliqua*, *Acacia melanoxylon*, *A. dealbata*, and exotic shrubs such as the semi-deciduous *Rubus fruticosus* spp. agg. (VicFlora 2016).

We estimated the effect of urban stormwater runoff by effective imperviousness (EI), the proportion of catchment covered by impervious surfaces with direct sealed drainage connection to the stream. Our primary data source was a semi-automated classification of impervious areas across the region in 2009 commissioned by Melbourne Water (Fig. 1: Kunapo 2017). For all except the two most urban catchments, we verified and corrected mapped impervious polygons, and determined their connection to stormwater drainage through a combination of field-measurements and visual estimates of surfaces from multiple images available on near-map.com overlain with maps of council drainage networks, and Google street-view. We assumed that 90% of impervious surfaces in the two most urban catchments, which are entirely serviced by stormwater drainage system, were connected to the drainage system.

Experimental design

The experimental wood substrates were rectangular 120-mm wide, 25-mm deep blocks of *A. melanoxylon*, of two types; smooth blocks with low complexity and grooved blocks with higher complexity, afforded by 4 2-mm deep, 4-mm wide grooves cut into each of their upper and lower surfaces (Fig. 1). The grooves mimicked those found on decaying natural wood in streams, after O'Connor (1991). Blocks were cut to size so that regardless of complexity, surface areas of all wood substrates were held constant (0.93 m²) to reduce sampling effects: smooth blocks were 300 mm long, while grooved blocks were 270 mm long.

At each of the 18 sites, four wood blocks of each treatment, attached to metal stakes and randomly distributed throughout a 30-m reach. The stakes were hammered into the streambed to a depth that allowed the attached blocks to sit in the water column with their major sides horizontal and grooves oriented along the flow, approximately 10 cm below the water surface. The blocks were deployed into sites in the austral fall, April 4–8, 2011, and were sampled four weeks later (May 2–9, 2011). Studies that have employed the use of artificial substrates found macroinvertebrate

density and species composition typically remains relatively static after 4 weeks of colonization (Lamberti and Resh 1985, O'Connor 1991, De Pauw et al. 1994).

Each block was sampled using a “snag bag” (Gowns et al. 1999), a large 250- μ m-mesh bag. At the time of sampling any fine sediment settled on a woodblock was noted, as was any algal growth or debris that was unavoidably included in the sampler. Collected macroinvertebrates were preserved in 70% ethanol and identified in the laboratory to the lowest taxonomic level possible with available resources. Orthocladiinae, Chironominae, Ephemeroptera, Plecoptera, and Trichoptera, were identified to genus, as were families represented by a single genus in the study (Lumbriculidae, Physidae, Tateidae, Hydridae). Tanypodinae, Ancylinae and Naididae were identified to sub-family. Other taxa were identified to family, except Nemertinea, Tricladida, Temnocephala, Hirudinea, and Hydracarina, which were identified no further.

Over the study period, many stakes holding woodblocks were dislodged during high-flow events. As a result, some woodblocks were lost before they could be sampled, and others were compromised because the dislodged woodblock was partially or completely buried in the sediments. Dislodged woodblocks were more common in sites with greater EI (Fig. 2), indicating a problem of physical stability of hard substrates in sites subject to urban stormwater runoff. We excluded samples from the model if they were lost, buried or if >20% of the surface was sitting above the water level at time of sampling. We included data from dislodged woodblocks that were unburied and able to be sampled without disturbing the surrounding sediment.

These sample exclusions did not strongly unbalance the study design. The sample with the highest effective imperviousness (Fig. 1) retained only a single woodblock, and was removed from the model, because it lacked a grooved treatment. Similar numbers of grooved and smooth treatments were excluded from other sites: 54 grooved and 51 smooth treatments remained in the model (Appendix S1: Fig. S1a). Sedimentation on experimental blocks and debris in samples affected grooved and smooth blocks evenly among sites (Appendix S1: Fig. S1b,c).

Model structure

We assessed the influences of small-scale wood surface complexity and catchment-scale urban stormwater runoff on the composition of in-stream macroinvertebrate assemblages with a hierarchical multi-taxon model (Gelman and Hill 2007). Such models assume taxon-specific parameters are random draws from common assemblage hyper-distributions, where the mean of

the hyperdistribution represents the ‘average’ taxon parameter and the standard deviation measures the variation in that parameter among the assemblage. Hierarchical multi-taxon models improve the certainty of taxon-specific parameter estimates compared to single-taxon models, particularly for taxa with sparse data (Ovaskainen and Soininen 2011).

The response variable was abundance of each taxon per wood block (equivalent to density of 0.093 m⁻²). In each of the 17 sites, there were 1–4 replicate wood blocks of each of two levels of surface complexity (*C*, categorical, smooth or grooved: Appendix S1: Fig. S1a). Each site had a single level of EI that quantified urban stormwater impact. EI was scaled and transformed, as described below, to form the continuous predictor variable *I*. Ninety-three taxa were collected from the wood blocks after 4 weeks of deployment. Thirty-six of those taxa occurred in at least 7 of the 17 sites, while 23 occurred at only 1 site, 18 of which occurred in only a single sample (Appendix S2: Table S1). All taxa were included in the model.

We assumed the abundance of each taxon on each block ($y_{i,j}$) was drawn from a Poisson distribution:

$$y_{i,j} \sim \text{Poisson}(\lambda_{i,j}) \quad (1)$$

where $\lambda_{i,j}$ is the mean abundance of taxon *i* at site *j*. The experimental design was spatially nested. Each site had multiple wood-blocks, and some sites were located on the same stream (four streams with two sites, Fig. 1). To account for this non-independence in abundance among sites, we included a random site effect, $\epsilon_{i,j(k)}$ for taxon *i* in site *j* in stream *k*, and a random stream effect, $\eta_{i,k}$, for streams with more than one site. $\eta_{i,k}$ was multiplied by D_k , equal to 0 for streams with a single site, and 1 for streams with two sites. Thus,

$$\ln(\lambda_{i,j(k)}) = \mu_{i,j(k)} + \epsilon_{i,j(k)} + D_k \eta_{i,k} \quad (2)$$

where $\mu_{i,j(k)}$ is a fixed effect modelling the expected count per block of taxon *i* at site *j* in stream *k*. The random effects were drawn from a normal distribution with estimated mean and standard deviation for each taxon.

We modelled $\mu_{i,j(k)}$ as a linear function of the two experimental effects and their interaction: surface complexity (C , with one of two categories, c , within site j), and urban stormwater runoff (I , one value, I_j , for site j). We used smooth block surface as the reference category of C , such that the effect of C represents the difference between grooved and smooth surfaces. I was log-transformed and scaled EI thus: $I = \ln(EI) - \ln(\min(EI))$. The reference condition (the intercept) of I therefore represents the site with the minimum EI in the study area (0.006%). Thus:

$$\mu_{i,j(k)} = \beta_{1,i} + \beta_{2,i}I_{j(k)} + \beta_{3,i}C_{c(j(k))} + \beta_{4,i}I_jC_{c(j(k))} \quad (3)$$

where $\beta_{1,i}$ is the intercept of the model, representing the abundance of taxon i on a smooth wood block in a site with near-zero urban stormwater impact; $\beta_{2,i}$ represents the effect of overall I on abundance of taxon i ; and $\beta_{3,i}$ represents the effect of a grooved surface compared to a smooth surface on abundance of taxon i . The interaction effect $\beta_{4,i}$ assesses if the difference in taxon abundance between grooved and smooth surfaces varies with degree of urban stormwater impact. All β parameters were drawn from assemblage-level hyper-distributions, specified as normal distributions with estimated means and standard deviations. We derived the model using the Markov chain Monte Carlo sampler of Stan (Carpenter et al. 2017).

The model satisfied tests for convergence, effective sample size, and Bayesian Fraction of Missing Information (Stan Development Team 2018: see Appendix S1 for more details).

We quantified model accuracy by correlation coefficients (R) and by mean errors between predicted and observed abundances (log-mean abundances of each taxon in each combination of site and surface complexity). To assess potential bias in model predictions, we calculated the slope of a regression of predicted abundance as a function of observed abundance. We also applied the same tests to the model's estimates of combined abundance and richness of all taxa and of EPT taxa.

The model predicted abundances of all taxa at each site well (mean R for all taxa 0.87, range 0.55–1.00), without bias for the 51 taxa occurring in >5 samples (mean slope 0.98, range 0.5–1.8). Abundances of the rare 42 taxa (occurring in ≤ 5 samples) tended to be underestimated (mean slope 0.52). However, this underestimation for rare taxa did not contribute strongly to model predictions of assemblage-level metrics (e.g. for total abundance R 0.96, slope 0.92, whether rare taxa were included or not). In summary, the multi-taxon model concords well with the data,

affording confidence in the model's assessment of our experimental effects on the macroinvertebrate assemblage. See Appendix S2 for more detail.

Model prediction for management guidance

Stream managers seeking to prioritize stream reaches for restoration of habitat complexity need to know if the response of biotic assemblages will vary with the degree of catchment-scale impacts.

We thus used the model to predict assemblage responses to habitat complexity in streams with contrasting degrees of urban stormwater impact. We used the model to predict abundances of all taxa (with average site and stream random effects) on smooth wood blocks and on grooved woodblocks in a rural reach (EI 0.03%) and in a moderately urban reach (EI 15%), and assessed differences among the four scenarios (rural smooth, rural grooved, urban smooth, urban grooved).

In addition to abundance of each taxon, we also assessed the effects of surface complexity in the two contrasting reaches on summary metrics like those used to assess stream health in the region of our study (taxon richness, richness of Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa: Government of Victoria 2004), as well as combined measures of abundance (of all taxa and EPT taxa). Taxon richness (T) for a particular subset of taxa was calculated as:

$$T = \sum_i \Psi_i \quad (4)$$

where Ψ_i is the occurrence probability of taxon i in the subset of taxa, calculated as the Poisson probability of abundance >0 : $\Psi_i = 1 - e^{-\lambda_i}$.

Results

Overview

Responses to urban stormwater impacts (I) in the assemblage varied from negative (sensitive) to positive (tolerant). In Fig. 3, taxa are ordered by their response to I , and each taxon is allocated a color (used in Fig. 4) to indicate its position in the range between sensitivity (blue hues) and tolerance (red hues) to urban impacts.

Taxa tended to be more abundant on grooved blocks than on smooth blocks overall (Fig. 3, positive surface complexity (C) effect, 19 taxa with a positive median coefficient and 95% credible intervals not overlapping 0), but the effect of surface complexity differed with urban impact in two primary ways. Firstly, for some sensitive taxa for which no interaction between I

and C was indicated, the effect of surface complexity was small compared to the large effect of urbanization, resulting in near-zero abundances on either block type in urban sites. Secondly, taxa with a positive C effect and a negative $I:C$ interaction were more abundant on grooved blocks than smooth in the absence of urban impacts, but not in urban streams.

Some taxa were less abundant on grooved blocks than smooth, and this trend was more common in streams with urban impacts.

These taxon-specific trends resulted in small, uncertain predictions of greater total abundance and greater taxon richness on grooved than on smooth surfaces in the absence of urban impacts, but smaller differences in the less taxon-rich assemblages of streams with urban impacts.

Taxon-specific effects

Twelve taxa were more abundant on grooved blocks than on smooth blocks regardless of urban impact (Fig. 4a, b; positive C effect, no interaction, Fig. 3). The two most abundant of these taxa (Naididae oligochaetes and the chironomid *Paratanytarsus/Rheotanytarsus*) and three other taxa (Ceratopogonidae, Tricladida, and the leptocerid caddisfly, *Triplectides*) were equally abundant, and responded consistently to surface complexity, in rural and urban streams (Fig. 4a, b). The other 7 taxa that were consistently more abundant on grooved blocks were all more sensitive to urbanization (blue shades in Fig. 4). For these taxa, the effect of C was small compared to the strong negative effect of I : their abundances at 15% EI were typically an order of magnitude less than at 0.03% EI (Fig. 4a, b).

Six taxa (top 6 taxa in Fig. 4c) were more abundant on grooved than on smooth blocks in non-urban streams, but not in streams with 15% EI (Fig. 4c, d, those taxa with a positive C effect and a negative interaction effect, Fig. 3).

Another twelve taxa responded negatively to C under at least one treatment. Two sensitive taxa (*Illiesoperla* and *Austrocerca*) were less abundant on grooved blocks than on smooth blocks regardless of urban impact, but were an order of magnitude less abundant at 15% EI than at 0.03% EI (Fig. 4c, d). *Asmicridea* was also less abundant on grooved blocks than on smooth blocks, and this tendency was stronger in more urban streams than less urban (Fig. 4c, d). Abundances of *Botryocladus*, Pisidiidae and Tubificinae did not differ between grooved and smooth blocks at 0.03% EI, but were lower on grooved than smooth blocks at 15% EI (Fig. 4c, d).

Assemblage-level effects

Differences in assemblage level metrics between surface complexities and urban levels predicted by the models generally had high levels of uncertainty (Fig. 5). The largest differences in

abundance and richness were between rural (0.03% EI) and urban (15% EI) sites. Mean EPT abundance and richness were lower at 15% EI than at 0.03% EI, although the 95% confidence intervals overlapped in some cases (Fig. 5b–d).

Small, uncertain increases in total and EPT abundance and richness were predicted on grooved blocks compared to smooth blocks at 0.03% EI (Fig. 5). No increases in abundance, and smaller increases in richness were predicted at 15% EI. The predicted increases in EPT richness associated with surface complexity are not biologically meaningful. For instance, the model predicts 2–4 EPT taxa on blocks of either surface complexity type at 0.03% EI, and 1–2 EPT taxa on blocks of either complexity at 15% EI (Fig. 5d).

Discussion

Our study has demonstrated that habitat complexity contributed to increased abundance of many macroinvertebrate taxa, which results in a likely increase in taxon richness, in streams with little human impact. In contrast, the effect of habitat complexity on taxon richness was less pronounced in streams impacted by urban stormwater runoff, despite increases in abundance of some taxa with increased complexity. The reduced abundance of sensitive taxa in more urban streams, and the resultant reduced richness, confirms that urban stormwater runoff acts as a strong environmental filter, limiting the species pool available for community assembly (e.g. Walsh 2004, King et al. 2011). Most taxa that colonized blocks in streams with high EI (taxa which can therefore tolerate stormwater impacts) were more abundant on grooved than on smooth blocks. However, for some such taxa, increased abundance on grooved blocks was only observed in the absence of urban stormwater impacts, suggesting that any refuge or resource provided by grooves is less effective in more disturbed environments receiving urban stormwater runoff. The likely increase in taxon richness with increased habitat complexity in streams receiving little human impact was small (~10%). The smallness of this increase, and the lack of an increase in streams impacted by stormwater runoff, were a product of contrasting responses of taxa to habitat complexity, which dampened assemblage-level responses in abundance and richness. The hierarchical multi-taxon model we used permitted this insight, and helps to identify potential mechanisms of taxon-specific responses to increased habitat complexity under different disturbance regimes.

The most widely proposed mechanism for increased species richness with increased habitat complexity is the greater diversity of niches available with greater complexity, allowing species to

partition resources and co-occur (e.g. Willis et al. 2005). Our results, and those of similar studies (e.g. O'Connor 1991, Douglas and Lake 1994, Downes et al. 1998) are consistent with this hypothesis, but as Downes et al. (2000) noted, it is difficult to refute because of the unknown multidimensionality of niches. Our study has not formally identified resources that might be afforded by the grooves in our experimental blocks. However, the grooves reduced the area of each of the upper and lower flat surfaces by 22% compared to smooth blocks, and created new horizontal and vertical surfaces with different aspects and hydraulic environments not present on smooth blocks. This increased diversity of surfaces on grooved blocks could potentially increase algal growth to favour grazers, increase sediment and detritus deposition to favour detritivores, provide refugia from large predators (O'Connor 1991, Douglas and Lake 1994), or provide a larger range of hydraulic conditions favouring a greater diversity of filter feeders (Downes and Jordan 1993). The greater hydraulic diversity could also provide refuge from hydraulic stress during high-flow events. We are not able to definitively identify which of these effects, if any, drove responses of taxa. However, our analysis of assemblage-wide, taxon-specific responses showed counter-acting responses of different taxa that provide some evidence of interspecific interactions. It is the balance of the increased abundance of some species and reduced abundance of others that must drive the commonly observed disproportionate increase in species richness in response to habitat complexity compared to increases in total abundance (Downes et al. 1998).

The functionally diverse group of taxa, *Polypedilum*, Empididae, *Potamopyrgus*, *Tanytarsus*, Tanypodinae, were more abundant on grooved blocks in rural streams but not in urban streams (Fig. 4c, d). Their persistence in urban streams suggest some tolerance to the impacts of urban stormwater runoff, but the lack of response to increased complexity in urban streams suggests the resources afforded by grooves in rural streams are less available in urban streams. One possible explanation is that the grooves could provide refuge from physical disturbance in rural streams, but are insufficient for effective refuge from the increased chemical and physical stressors of urban stormwater flows.

Negative responses to increased complexity suggest either a direct response to the 22% reduction in outer horizontal surface area (which would require an unlikely strong habitat preference for that habitat) or increased competition with taxa that are favoured by the greater diversity of habitat afforded by the grooves. Hydropsychid caddisflies, which build silk nets to filter food from the water column, are known to be territorial (Hemphill 1988). The contrasting responses of two such

taxa, *Asmicridea* (less common on grooved blocks) and *Cheumatopsyche* (more common), could be explained by the hydraulic diversity afforded by grooves providing superior flow microenvironments for *Cheumatopsyche*, thus creating a competitive advantage over *Asmicridea* that was lacking on smooth blocks. Interference competition is also a possible driver of contrasting trends in the scraper/shredder grypopterygid stoneflies, *Illiesoperla* (less common on grooved blocks) and *Dinotoperla* (more common, Fig. 4c, d). The strongly negative response to increased complexity of Tubificinae in urban, but not rural, streams (Fig. 4c, d) is difficult to explain. However, the contrasting positive response to increased complexity in urban streams of the invasive *Lumbriculus* (Fig. 3, probability of positive interaction between *C* and *I* almost 95%) is also suggestive of a negative interaction between these two oligochaete taxa.

The nets of hydropsychids can also modify habitat to increase colonization of other species (Tumolo et al. 2019). Thus greater overall hydropsychid abundance on grooved blocks than smooth could contribute to the positive effect of grooved blocks in other taxa, and this effect would be greater in rural streams than in urban streams where abundances of hydropsychids are lower. Such complex interactions could explain the contrasting responses of taxa such as Tubificidae, *Botryocladus* and Pisiidae to complexity (little or no response in rural, negative in urban, Fig. 4c, d). These observations of contrasting responses among taxa to habitat complexity in different disturbance regimes provide an explanation of the commonly observed disproportionate increase in species richness with habitat complexity compared to increases in total abundance (Downes et al. 1998). However, our suggested mechanisms of interspecific interactions remain speculative, particularly given the mostly supra-specific taxonomic resolution of our data. We note, for instance, that Downes and Jordan (1993) found differing responses to surface complexity in two species of *Asmicridea*. Further investigation is clearly needed to understand the nature of resources provided by habitat complexity such as that provided by our grooved blocks, and the nature of interspecific interactions that may cause contrasting responses to complexity.

The rarity of sensitive taxa in urban streams is likely a result of intolerance to the physical or chemical disturbances associated with increased frequency, magnitude, and pollutant concentrations of high flows associated with urban stormwater runoff (Walsh et al. 2005). The effect of habitat complexity is a moot point for such species in urban streams, where they are unlikely to colonize or persist because of larger-scale constraints. It is unlikely that the lack of

colonization by sensitive taxa to the wood blocks in more urban streams was a result of our 4-week deployment period being too short. The assemblage composition recorded on blocks in the most urban sites was similar to that found in samples of existing habitat in these sites (e.g. Walsh 2004). All of our sampling sites had high-quality forest within 5 km, a distance beyond which dispersal of colonizers is considered unlikely (Sundermann et al. 2011). At the most urban site, which was also the most removed from high-quality forest (~4 km for Brushy Creek), one or a few individuals of several sensitive species (the stonefly *Dinotoperla*, the caddisfly *Taschorema*, and an immature leptophlebiid mayfly) were collected from woodblocks. Thus rather the rarity of sensitive taxa in streams with higher levels of urban stormwater impact is less likely to be a result of a lack of colonizers than of a lack of persistence under the heightened disturbance regime.

Management implications

Reach-scale restoration projects aiming to increase biodiversity often consist of in-stream works, such as the addition of large woody debris (Larson et al. 2001, Scealy et al. 2007), or restoration of channel morphology such as riffle-pool sequences in channelized reaches (Violin et al. 2011) or braided channels (Jähnig et al. 2008). More commonly, reach-scale projects can be longer-term projects aiming to achieve similar in-stream objectives through the restoration of riparian vegetation (Bernhardt et al. 2005), which ultimately can alter instream habitat in many ways, including shading, provision of organic matter, as well as increased habitat heterogeneity with addition of woody debris (Pusey and Arthington 2003). A primary mechanism for recovery of in-stream biota in all of these sorts of projects is the restoration of in-stream habitat heterogeneity (providing a diversity of qualitatively different habitat structures) and complexity (habitat structures with surface complexity to diversify microenvironments). These two aspects of habitat restoration are usually interwoven in stream ecosystems (Downes et al. 1998). The small-scale manipulation of surface complexity in our experiment did not aim to replicate the scale or heterogeneity of these typical approaches to reach-scale restoration. We have, however, demonstrated that the aspects of these projects that increase habitat complexity are likely to contribute to a small increase in biodiversity in streams that lack larger catchment-scale constraints. More importantly, such an outcome is unlikely in streams that are subject to catchment-scale urban stormwater impacts.

Our study sheds light on the apparent conflict between the understanding of ecological mechanisms by which increased habitat complexity promotes biodiversity, and the lack of

consistent demonstration of increases in species richness with increased in-stream habitat complexity (Palmer et al. 2010). Increases in species richness tend to be small. For instance, the increase in species richness on grooved, horizontal blocks compared to smooth horizontal blocks in O'Connor's (1991) study in a rural lowland river was ~10%, which is similar to the increase observed in taxon richness in our study (Fig. 5c). Such small responses in part result from the contrasting trends of some taxa to habitat complexity observed in our study, which dampen assemblage-level responses in abundance and richness. Thus, an assessment of the frequency of statistically significant results without consideration of effect sizes (e.g. Palmer et al. 2010) is likely to confound low statistical power with responses that are small compared to other sources of variability.

Nevertheless, given that increased habitat complexity is usually an intrinsic element of increased habitat heterogeneity, the conclusion of Palmer et al. (2010) that 'physical heterogeneity should not be the driving force in selecting restoration approaches for most degraded waterways' is supported by the likely small effect on richness in streams without catchment-scale constraints (if such summary measures of assemblage composition are the measure of success). The small effect of increased habitat complexity on species richness is even smaller in streams with urban stormwater impacts than those without.

The argument against the use of increased habitat complexity as a restoration approach in urban streams is stronger again when the physical stability of placed habitat is considered. The increased rate of dislodgement of our experimental structures with EI as a result of high-flow events (Fig. 2) is indicative of the physical harshness of streams subject to urban stormwater runoff. Loss of emplaced large-woody debris through sediment burial or high-flow transport was also reported in urban streams of Seattle (Larson et al. 2001). Russell et al. (2020) determined that urban stormwater runoff causes "excess bedload transport capacity, which mobilises and removes bed sediment, produces channel incision and enlargement, and reduces channel complexity". They concluded that reintroducing roughness or sediment to urban channels (i.e. actions typically undertaken in reach-scale restoration projects) should only be considered after mitigation of urban stormwater flows has sufficiently reduced transport capacity. Sufficient mitigation requires stormwater control measures between hillslope sources of runoff and the stream that mimic the pre-development flow regime in quality and quantity, typically requiring significant runoff volume being prevented from running to the stream (Walsh et al. 2016a).

In summary, our results suggest that restoration of habitat complexity in streams without catchment-scale drivers of degradation is likely to have small, positive benefits to in-stream biotic assemblages, but the efficacy of such approaches in catchments subject to urban stormwater runoff will be greatly diminished. For streams of urban catchments, restoration activities should first be aimed at controlling the larger-scale problem, which is typically the altered water quality, reduced base flows, and increased intensity and frequency of storm-flows caused by urban stormwater runoff.

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Data Availability

Data are available from the Open Science Framework: <https://doi.org/10.17605/OSF.IO/GMJC5>.

Figure captions

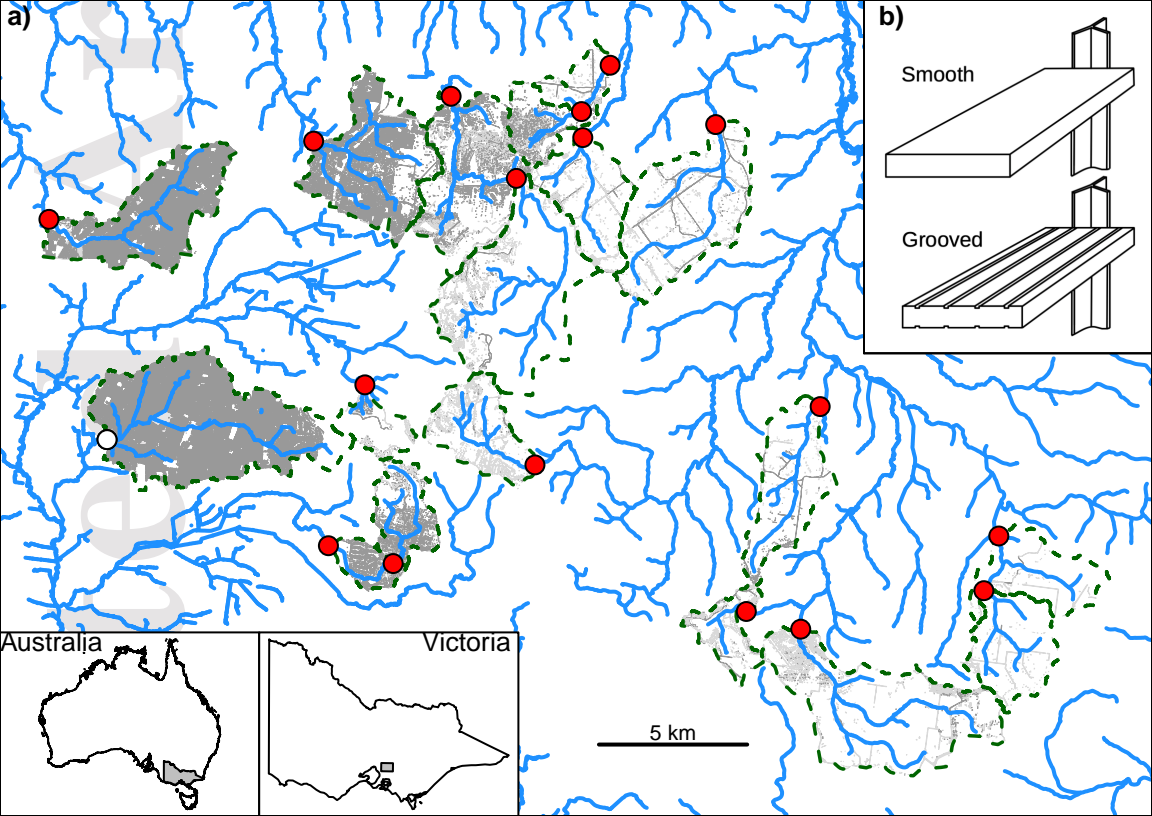
Fig. 1. a) The 18 study sites and their catchments. Impervious areas in each catchment are shaded by their connection to the stormwater drainage system (dark-grey connected, light-grey draining informally to land or to a stormwater control measure). Impervious areas outside catchments are not shown. The site marked by a white circle is Blind Creek: all but one woodblock in this site was lost, and resultantly data from this site were not included in the multi-taxon model. Inset maps show the location of the main map (grey rectangle) in Victoria, Australia. b) The two surface complexity treatments, smooth and grooved wood blocks, mounted on metal pickets.

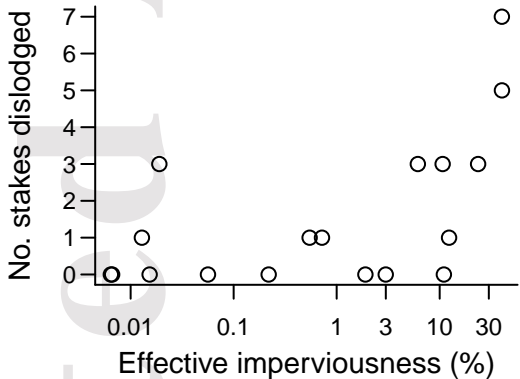
Fig. 2. Number of wood blocks dislodged from each site during the experiment, plotted against effective imperviousness (on a log-scale).

Fig. 3. Median and 95% credible intervals for the coefficients of the effects of I (effective imperviousness, log-transformed and scaled), C (surface complexity), and their interaction on the 93 taxa in the multi-taxon model. Taxa are arranged in order of their response to I , and the color bar to the left, indicating relative sensitivity (Sens.) and tolerance (Tol.) to I , serves as a key to taxon identity in Fig. 4. Appendix S2: Table S1 lists taxonomic affinities of all taxa.

Fig. 4. The direction and magnitude of the surface complexity effect (C) at each level of urbanization on predicted median abundance of the 24 taxa for which an effect of surface complexity or interaction between surface complexity and effective imperviousness (EI, dashed lines) was indicated with 95% probability. a) and b) show taxa with a positive C effect, b) and c) show taxa with a negative C effect, or a $C:I$ interaction (where I is EI, log-transformed and scaled). In each panel, abundance of each taxon (color-coded by urban sensitivity as in Fig. 2) on each block type (S, smooth; G, grooved) at two levels of I : a), c) rural conditions with little urban stormwater impacts (rural, EI = 0.03%) and b), d) moderately urban conditions (urban, EI = 15%).

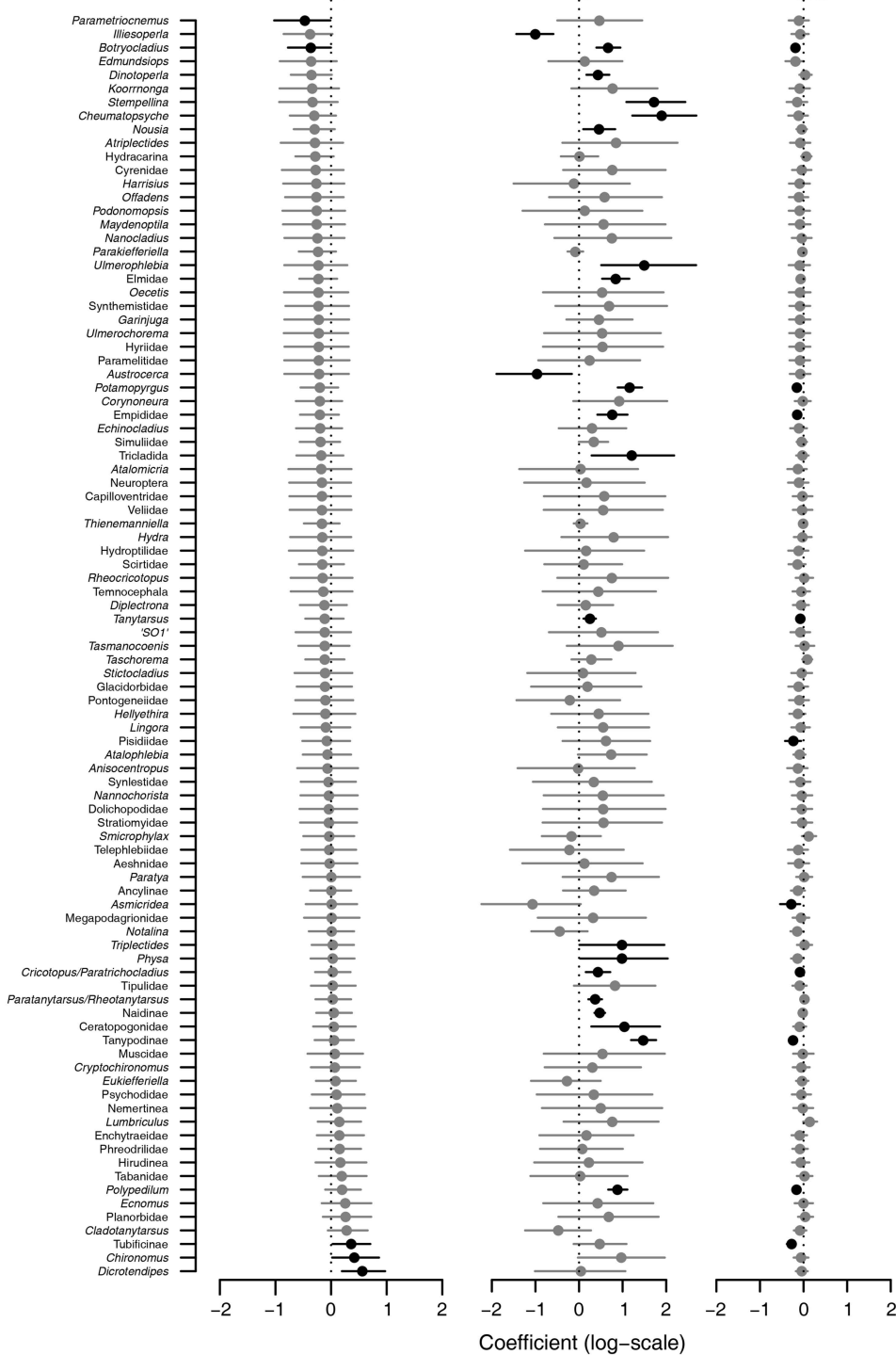
Fig. 5. Responses of summary metrics derived from model predictions at two levels of I : rural conditions with little urban stormwater impacts (EI = 0.03%) and moderately urban conditions (EI = 15%) for smooth (S) and grooved (G) woodblocks. Median and 95% credible intervals of a) abundance of all invertebrates; b) abundance of Ephemeroptera, Plecoptera and Trichoptera (EPT) taxa; c) total taxon richness; and d) EPT richness, per woodblock.

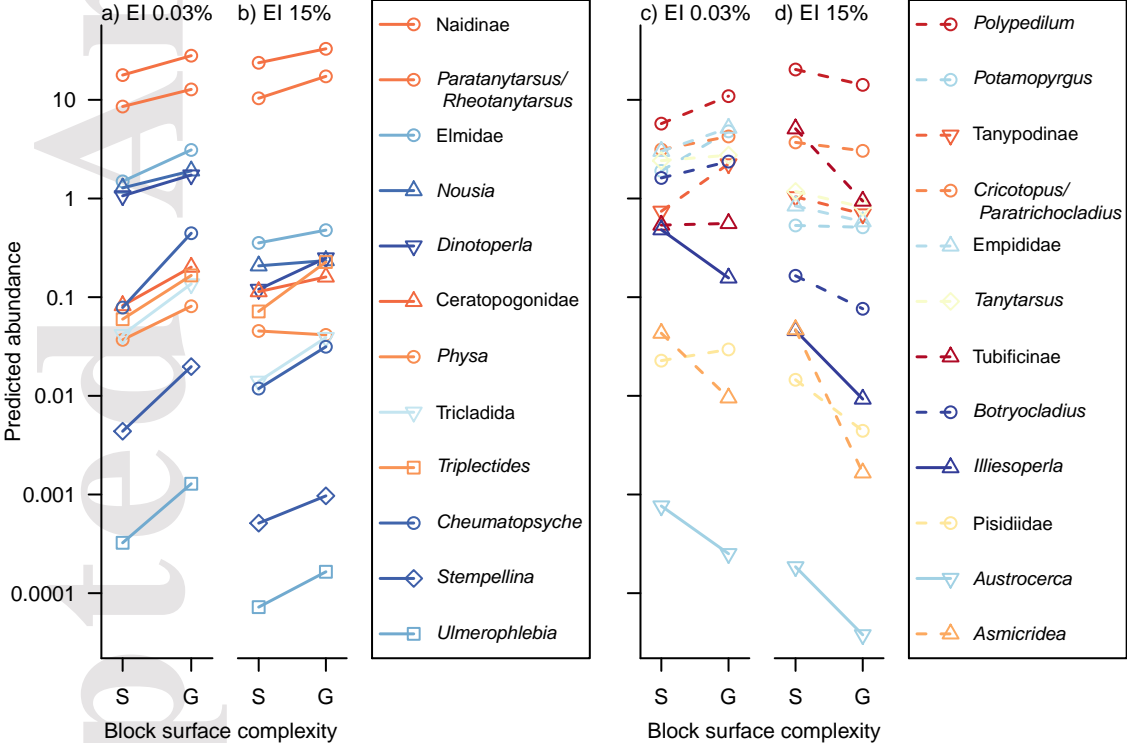


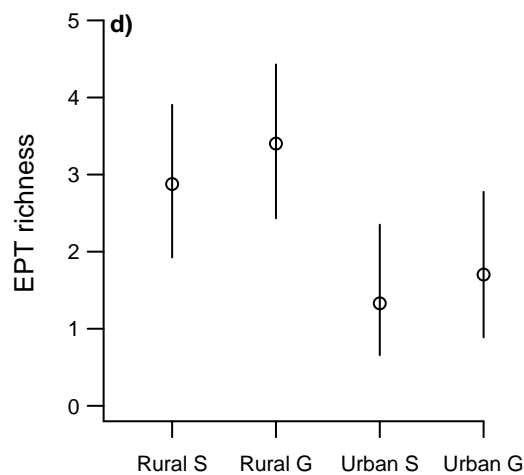
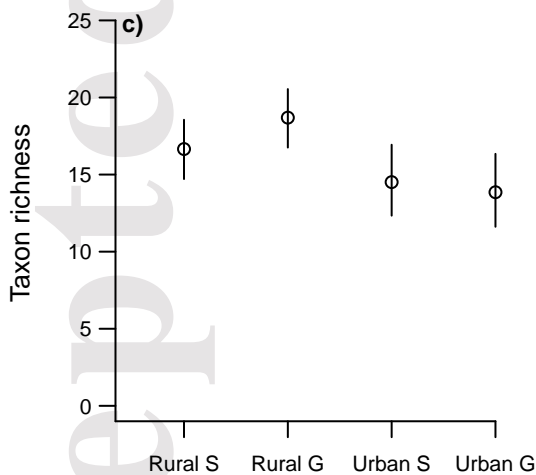
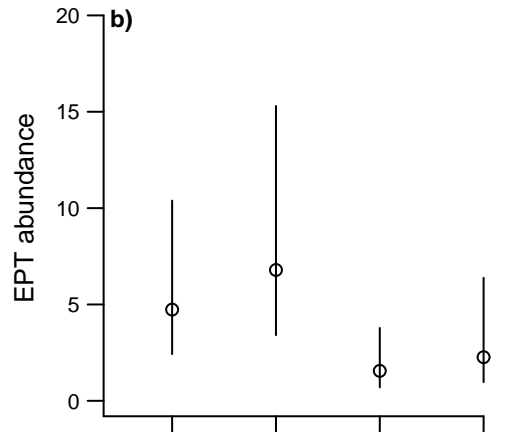
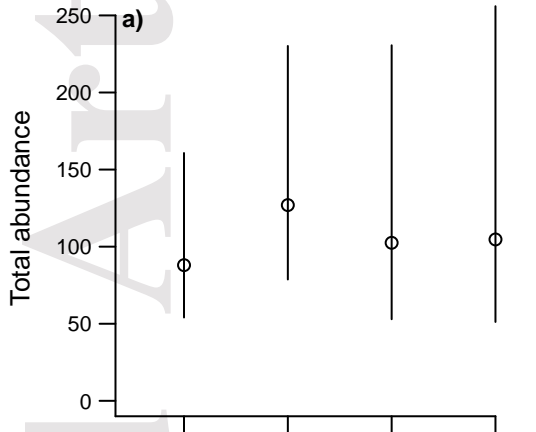


Sens.

Tol.









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