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Invertebrate richness and diversity in parks situated along a gradient of urbanisation

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Abstract

Urbanisation entails significant habitat loss leading to degradation of biodiversity and ecosystem services, and fragmented landscapes. Urban parks, which can take the form of large forest remnants, lawns, or a combination of the two, provide habitat for some species. The type of park and its location relative to other land uses affect the communities of species it supports. This study examined the composition of invertebrate communities, with emphasis on species richness and diversity of Coleoptera in parks along a gradient from low to high levels of urbanisation intensity, measured as the proportion of impervious surface within a surrounding buffer. The diversity of invertebrates differed only between parks at each end of the urbanisation gradient and a consistent, although non-significant, trend of increasing diversity from high to low intensity surrounding urbanisation. Parks situated closest to a large green space (>30 ha in area; typically semi-natural, such as a reserve), had highest invertebrate richness, abundance and diversity. Increasing proportion of impervious surface had only a minor impact on invertebrate communities, likely due to the pre-selection of species tolerant to fragmentation and non-native vegetation. However, increasing urban densification will likely harm invertebrate diversity. Coleoptera communities were similar across all parks, although parks with patches of high-quality vegetation presented slightly different assemblages, potentially supporting less urban-tolerant species. While lawns are not completely sterile environments for invertebrates, enhancing vegetation heterogeneity in urban green spaces and creating green corridors for dispersal will improve invertebrate richness and diversity in urban parks, while retaining their amenity value.

Keywords Coleoptera · Invertebrate diversity · Urbanisation gradient · Green spaces · Urban parks

Introduction

Urbanisation transforms natural and semi-natural landscapes into heavily modified built environments with fragmented patchworks of green spaces, ranging in size, quality and ecosystem function (Faeth et al. 2011; Lepczyk et al. 2017; Li et al. 2019). While expansion of cities has created a net loss of biodiversity (Andersson et al. 2014; Zhang 2016), generalist and highly adaptable species can often successfully exist within the modified urban matrix (Luck and Smallbone 2010; Werner 2011). Some urban-sensitive species can even be found in large, connected green spaces with structurally complex vegetation that provides necessary habitats and resources (Beninde et al. 2015; Threlfall et al. 2017).

Arthropods constitute a very diverse group of organisms that occupy a wide array of niches and microhabitats, and support many ecosystem services such as pollination, biological pest control, nutrient cycling and decomposition (Losey and Vaughan 2006). Insects are currently facing significant global declines in their populations in terrestrial ecosystems (Hallmann et al. 2017; Sánchez-Bayo and Wyckhuys 2019), including cities (Jones and Leather 2012; Martinson and Raupp 2013). Urbanisation and its resultant habitat loss has been identified as one of the main drivers of insect species declines, with generalist species replacing habitat specialists (Sánchez-Bayo and Wyckhuys 2019). In their meta-analysis of studies on urban arthropods, Finoglio

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et al. (2020) concluded that urbanisation reduces the diversity and abundance of terrestrial arthropods, although the extent of impact differs between taxonomic groups, with Coleoptera and Lepidoptera being most affected, consistent with patterns observed across multiple landscape types (Sánchez-Bayo and Wyckhuys 2019).

The prevalent approach of investigating arthropod communities along a gradient, often in a range of habitats, has revealed different patterns of species richness and abundance along the gradient (McDonnell and Hahs 2008). Many studies have observed that species richness and abundance tend to decline with increasing levels of urbanisation, with the lowest richness values found in the urban core (Niemelä and Kötze 2009; Martinson and Raupp 2013; McKinney 2008; Blair and Launer 1997). However, arthropod abundance can also sometimes increase with increased urbanisation (Gagne and Fahrig 2011; Turrini and Knop 2015), usually due to the presence of invasive or dominant species. Other studies have found no patterns in abundance and/or species richness of invertebrates along a gradient (Alaruikka et al. 2002; Martinson and Raupp 2013), with increases in some specialists corresponding with decreases in others, obscuring any patterns (Hornung et al. 2007). For example, patterns of activity-density (which represents population density and surface activity of Carabidae across soil surfaces) and species richness of carabids along a gradient can differ depending on whether they are specialists or generalists (Magura et al. 2008; Tóthmérész et al. 2011; Kaspari and Beurs 2019). Predatory species such as carabid beetles with strict forest habitat requirements, poor dispersal ability and large body sizes tend to be most vulnerable to urbanisation (Martinson and Raupp 2013).

Green spaces such as urban parks, forest fragments, roadside verges and gardens frequently play an important role in supporting some arthropod species assemblages (Watts and Larivière 2004; Hornung et al. 2007; Barratt et al. 2015; Carpaneto et al. 2010; Fenoglio et al. 2020). However, vegetation structure and composition vary significantly between different types of green spaces (Threlfall et al. 2016), as does the level of management intensity, with parks located closer to the city center usually managed more intensively than those at the edges (Aronson et al. 2017). Local characteristics of green spaces such as vegetation diversity, fragment size, intensity of management and structural and micro-climate heterogeneity are known to influence the survival of species and diversity of some invertebrate assemblages (Gibb and Hochuli 2002; Sattler et al. 2010; Vergnes et al. 2013; Bates et al. 2014; Braschler et al. 2020).

Urban invertebrate biodiversity is also affected by interacting mechanisms operating at both local and landscape scales (Vergnes et al. 2013; Adams et al. 2020). Surrounding features such as roads and the extent of impervious cover (paved surfaces and built structures) can strongly negatively affect arthropod diversity and abundance by comprising inhospitable land for invertebrates to cross (Jones and Leather 2013; Lagucki et al. 2017). In order to investigate the impact of surrounding landscapes on carabid activity-density while controlling for the characteristics of the green space, Fattorini et al. (2020) sampled within a single green space along an urban-rural gradient in Rome and found peak activity-density in the suburban portion of the gradient.

In this study we sampled invertebrate taxa in parks located along a gradient of surrounding urbanisation density to evaluate the extent to which the proportion of impervious area in buffers surrounding parks influenced invertebrate richness, abundance and diversity in the parks. Parks are usually designed for recreational purposes and consist mostly of lawn with some maintained vegetation around the perimeter (Neilson et al. 2014). Given that increasing urbanisation is associated with lower volumes of vegetation, which is usually less diverse, we predicted a decline in invertebrate richness, relative abundance and diversity in parks surrounded by higher levels of urbanisation. We tested the influence of dominant vegetation type (lawn or shrubs) on invertebrate relative abundance, diversity and richness, predicting higher diversity and richness in parks dominated by shrubs. Connectivity between green spaces links otherwise isolated communities, avoiding local extinctions by supporting movement of wildlife between habitats (Rudd et al. 2002; LaPoint et al. 2015). Since higher connectivity between green habitats should promote dispersal for at least some invertebrate species, we also tested the influence of proximity to a large natural green space and predicted that invertebrate communities in parks closer to large fragments should have higher invertebrate richness, relative abundance, and diversity.

Methods

Study sites

We sampled invertebrates in 20 parks situated across four levels of urbanisation intensity (UI) in Dunedin, New Zealand (population ~ 100,000; (June 2020, Stats NZ). Urbanisation intensity was characterised as the proportion of impervious surfaces (Penone et al. 2013), with areas with a higher proportion of impervious surfaces indicating higher UI. Parks were selected based on the proportion of surrounding impervious surface within two concentric circular buffer zones (e.g. Hou et al. 2020), the inner one with a diameter of 100 m around the park encompassing the immediate surroundings, and the outer with a diameter of 200 m (Suppl. Material Fig. S1.) encompassing a larger area. For UI values of proportion of impervious surfaces in the inner and outer zones: Level 1: none; Level 2: <50% inner and outer zones; Level 3: <50% inner and > 50% outer zones; Level 4: >50% inner and outer zones.

The parks were selected, and the UI measured using satellite images from Google Earth Pro and a combination of Ilastik (https://www.ilastik.org) a semi-automated pixel and object classification and segmentation software, and Fiji (https://fiji.sc), an imaging tool that measures the areas of classified objects. We imported a satellite image of Dunedin city into Fiji and spatially calibrated it with reference to the scale bar in Google Earth pro. The calibrated satellite image was then imported into Ilastik. Four categories were defined as ‘training labels’; trees, lawns, buildings and roads. We classified ‘known areas’ of each of these four categories to train Ilastik. Amenity parks were classified as ‘lawn’. Following training, Ilastik is able to predict and classify the remaining areas. The newly classified map was exported as a LUT (Lookup Table) file and imported into Fiji. Using the measurement tool in Fiji, we measured the proportion of the buffers comprised of built and paved structures (roads and buildings). By spatially calibrating the original image using Ilastik we ensured that the unit of measurement in Fiji corresponded with Google Earth measurements. Locations of the parks sampled at each urbanisation level are shown in Suppl. Material Fig. S2.

Parks were categorised by their dominant vegetation type: shrub-dominated, including reserves and urban forest fragments, or lawn-dominated, such as rugby grounds and playgrounds. We also measured the straight-line distance from the outer edge of each park and the nearest semi-natural green space larger than 30 ha using a Google satellite image and the built-in measuring tool. We chose a relatively large area because larger patches have been shown to contain significantly more biodiversity: on average, patches with an area less than 27 ha experience a rapid decline in species richness of multiple taxonomic groups (Beninde et al. 2015).

Collection and identification of invertebrates

Invertebrate samples were collected in April (autumn) 2022 under consent from the Dunedin City Council Parks and Reserves. Collections were made in good weather conditions between 1000 h and 1500 h to standardise for invertebrate activity (Popic et al. 2013).

Each park was sampled on one occasion using five pitfall traps, five shrub beating sites and six blower-vac sites. Parks differed in their configuration; some were primarily lawn with shrubs around the perimeter, while others were primarily shrub/forest with smaller sections of lawn, often in the centre. Shrubs were selected only along park site edges, or off pathways in nature reserves. We used a decision tree to select five shrubs at each park site at which to place pitfall traps and collect samples using shrub beating (Suppl. Material Fig. S3). If a shrub was (1) native, (2) between 30 cm and 300 cm in height, and (3) spatially arranged in a cluster larger than 2 m^2, it was selected as a point for sampling. Native shrubs < 3 m in height and arranged in clusters larger than 2 m wide were prioritised for sampling to standardise the selection of shrubs.

Shrub-beating samples were collected from the selected five shrubs: in a downward motion, ten forceful strokes were applied to branches around the shrub using a cushioned stick. A neutral-coloured up-turned umbrella was placed underneath the targeted area of the shrub to catch all fallen debris including invertebrates. All invertebrates collected in the umbrella were transferred into a labelled container filled with 70% ethanol. Flying and fast-moving invertebrates were removed first using an ‘aspirator’ designed for capturing insects. Other invertebrates were removed using either soft-touch forceps or a fine-bristled paintbrush. Large invertebrates that were easy to identify, such as stick insects and cicadas, were recorded, and released at the site.

Pitfall traps (8.38 cm base diameter, 1.75 cm funnel opening) were set under the same five shrubs after shrub beating samples were collected and placed within 1 m of the shrub’s base with a metal cage on top to deter larger non-target species such as pets and vertebrates. We installed five pitfalls at each site under five separate shrubs. Some traps were removed by the public (5%), and these were recorded as missing samples. Traps were filled with 100mL of monopropylene glycol, an odourless preservative, and left for three nights before collection.

Grass-dwelling invertebrates were collected from lawns using a STIHL SH 86 C-E blower vac set on suction. The blower vac was adapted such that a metal sheath and attached mesh netting was inserted at the mouth of the intake tube to trap and capture invertebrates. A 50 cm-by-50 cm quadrat was randomly placed on the lawn, ensuring it was at least 1.5 m away from the lawn edge, including paths, and from previous samples. Regularly mowed lawn was targeted, i.e., we did not sample rank grass. The quadrat area was vacuumed systematically, beginning at the top corner, and ending at the diagonally opposite corner using slow downward strokes from top to bottom. This was repeated at each corner, resulting in the quadrat being fully ‘vacuumed’ four times to ensure invertebrate collection was thorough (Tozer et al. 2016). Once the whole quadrat was vacuumed, the collection bag was removed, and the contents were emptied into a fine mesh bag and placed in a cool insulated container. Chilling the invertebrates slows down the movement of invertebrates without killing them (Deiner and Altermatt 2014).

In the laboratory, each lawn sample was processed using Tullgren funnels (heat extractors) located at Invermay Research Centre (Crook et al. 2004). Samples were emptied out on to a mesh tray at the top of the funnels. An empty container was used to collect litter that initially fell through the mesh, and this was then carefully placed back on the tray. A container part-filled with monopropylene glycol as a preservative was then placed underneath the funnels and the top of the Tullgren funnel was closed. A 100 W light bulb was turned on to provide a heat gradient, causing invertebrates to escape through the mesh and down the funnel to be collected in the preservative. The samples were left in the heat extractors for 24 h and the collection containers were removed for invertebrate identification.

Each sample was examined under a low power binocular microscope and all the invertebrates were identified to lowest feasible taxonomic rank, given resources and time available for identification. All invertebrates were identified to their order which is referred to henceforth as taxonomic group. Coleoptera collected in pitfall traps were identified to species or morphospecies and Coleoptera collected from shrub-beating and from lawns were identified to family. A collection of Coleoptera from an earlier study of Coleoptera from Dunedin gardens was used as a reference collection (Barratt et al. 2015). Because invertebrates except for Coleoptera were identified only to order or at a higher taxonomic resolution, it was not always possible to differentiate between native and exotic species.

Statistical analyses

Data were organised and analysed using Microsoft excel, R studio (version 2024.07.1; Posit Team 2024) and Primer (version 7.0; Clarke and Gorley 2015). Averages were calculated for each park from the replicates of each collection method (e.g., the average of the five pitfall traps). Averages from each sampling method were entered separately into the analyses. The following dependent variables were used in the analyses: (1) taxonomic group richness (count of unique taxa); (2) relative abundance (abundance of specific order/total abundance all invertebrates); and (3) diversity represented by the Hill-Shannon (Hill q1) (Roswell et al. 2021) and calculated using the vegan package [hill_q1 <- exp(shannon_diversity)]. The three independent variables were (1) urbanisation intensity level (1–4); (2) dominant vegetation type of either shrub species or grass; and (3) straight-line distance to the nearest established green space larger than 30 ha, entered as a continuous variable.

Generalised Linear Models (GLMs) were used for all analyses with the 'vegan' package (version 2.6–10; R Core Team 2024; Oksanen et al. 2025). The distribution family was Gaussian for normally distributed data, and Negative Binomial GLMs were used to account for overdispersion, while Gamma GLMs were used for skewed data. The log link function was applied to both Negative Binomial and Gamma models to handle the skewness and to maintain consistency across models. Linear models (LM) were not used for these analyses to ensure uniformity in model structure. Assumptions of normality, independence, constant variance, and linearity were checked for all GLMs using histograms, following the approach outlined by Abdulkabir et al. (2015)

Data from pitfall traps and shrub-beating samples were analysed in the same model, with the collection method included as a fixed effect to account for methodological bias and variation without reducing degrees of freedom. McFadden pseudo R^2 values (Jackman 2020) were calculated. Lawn samples were analysed separately using, Welch's Two-Sample t-test to compare means between the two vegetation types in parks; lawn-dominated, or shrub-dominated (R Core Team 2024).

An NMDS (non-metric multidimensional scaling) model was produced in Primer for the Coleoptera species collected in pitfall traps to identify differences in community composition. We used a Bray-Curtis resemblance matrix to show the dissimilarities of Coleoptera community composition collected in pitfall traps from parks across the four urbanisation levels.

Results

A total of 43,998 invertebrates were collected from 20 parks around Dunedin City, belonging to 21 taxonomic groups (Table 1). Acari and Collembola were the most abundant orders, representing 31% of all invertebrates collected from parks.

The relative abundance of invertebrates did not vary significantly with urbanisation intensity and the R^2 value was low (GLM: df = 18.52, $p > 0.05$; $R^2 = 0.05$; Fig. 1a). Parks in level 3 has the highest mean of 15.55 ± 4.10, one site showed an unusually high total abundance compared to other parks, which influenced the overall mean (outlier). Otherwise, means ranged between 7.52 ± 3.03 and 8.38 ± 3. 03.

There was a significant difference in the Hill-Shannon number (Hill q = 1) between level 1 UI, where the highest diversity was observed (mean = 3.85 ± 0.24; Fig. 1b) and level 4 UI, where the lower diversity was observed (mean = 2.59 ± 0.26) (GLM: t = 3.19, df = 19.17, $p < 0.001$, $R^2 = 0.29$, Tukey post-hoc: $p = 0.005$). The difference between level 1 and level 3 parks (mean = 3.16 ± 0.26) showed a trend toward significance ($p = 0.059$), suggesting slightly lower diversity at level 3. No significant differences were found between level 1 and level 2 (mean = 3.11 ± 0.26; $p = 0.22$)

Table 1 The total number of invertebrates collected from 20 parks across Dunedin using three collection methods: blower vac, shrub-beating and pitfall traps

Taxonomic groups	Blowervac (lawns)	Shrub-beating	Pitfall traps	Total
Acari	21,840	152	140	22,132
Collembola	10,502	41	549	11,092
Hemiptera	4,051	521	86	4,658
Araneae	745	451	53	1,246
Diptera	2,043	72	69	2,184
Coleoptera	408	56	53	517
Hymenoptera	324	75	57	456
Psocoptera	0	390	16	406
Crustacea	227	3	133	363
Thysanoptera	266	3	6	275
Annelida	225	0	14	269
Lepidoptera	195	29	10	234
Mollusca	13	34	6	53
Myriapoda	12	0	19	31
Orthoptera	1	0	27	28
Opiliones	0	3	21	24
Neuroptera	14	1	0	15
Dermaptera	0	4	1	5
Pseudoscorpionida	0	2	2	4
Blattodea	0	2	0	2
Platyhelminthes	1	0	0	1
Total	**40,897**	**1,839**	**1,262**	**43,998**

or among the intermediate categories (levels 2, 3, and 4; $p>0.05$).

The taxonomic richness of invertebrates did not show an increase as the surrounding UI decreased, the difference was not significant and the R^2 value (0.16) was low (Fig. 1c). The effect of urbanisation level was not significant on taxa richness (GLM: df = 16.76, $p > 0.05$ for all levels). However, there was a marginally non-significant result, suggesting that level 3 UI had higher taxa richness compared to level 1 UI (GLM: t = 1.7, df = 37, $p = 0.083$). The range between means did differ greatly, although was likely influenced by outliers present in level 3 and 4 (mean 4 UI = 3.21 ± 0.30 and mean 3 UI = 4.08 ± 0.41; Fig.1a). Parks situated in level 1 UI, which had the lowest mean value (3.17 ± 0.55) and level 2 UI (2.58 ± 0.55), although no outliers were present.

Coleoptera identified to family

In total, 517 Coleoptera individuals and 24 species/morpho species (identified from pitfall traps) were collected from 14 different families (Table 2) across 20 urban parks in Dunedin. Curculionidae and Staphylinidae were the most abundant families; the majority (almost 80%) were collected in blower vac samples from lawns.

Urbanisation intensity significantly influenced abundance when comparing parks from low UI in level 1 with parks in high UI in level 3 (GLM: t=2.37, df=34, $p=0.02$; R^2 0.11=0.13, Fig. 2a), and level 4 (GLM: t=2.58, df=0.24, $p=0.01$). Post-hoc analysis supported this trend, where parks in level 1 (mean=0.93±0.15) had significantly higher abundance than parks in level 3 (mean=0.37±0.18; $p=0.05$) and level 4 (mean=0.30±0.19; $p=0.02$). No difference was observed when comparing parks in level 1 with lower UI in level 2 (mean=0.62±0.18).

A trend was also observed where urbanisation significantly influenced the Hill-Shannon number (Hill q1) between parks UI in level 1 (mean=1.09±0.02) and 3 (mean=1.02±0.03) (GLM: t=2.12, df=34, $p=0.04$; R^2 = 0.19, Fig. 2b). This was again supported by a post-hoc test ($p=0.05$). No significance was detected when comparing parks in low UI in level 1 and intermediate UI in level 2 (mean=1.11±0.03, df=34, $p=0.6$) and 4 (mean=1.04±0.03, df=34, $p=0.1$), although, their means suggest a negative trend of increased UI on diversity.

A significance difference for Coleoptera family richness was also detected when comparing parks between level 1 and 4 (GLM: t=1.15, df=34, $p=0.004$; R^2 = 0.27, Fig. 2c). and level 1 and 3 (GLM: t=2.69, df=34, $p=0.04$). However, the post-hoc Tukey test did not indicate a significant difference ($p>0.05$), indicating a small, but significant trend. This trend was also observed, with a decrease in the mean for parks at level 3 (mean=0.30±0.11); however, the effect was not statistically significant (GLM: t=2.69, df=34, $p=0.33$).

Coleoptera identified to species

Thirty-five species of Coleoptera were identified from pitfall traps (n = 56 individuals collected) (Suppl. Material Fig. S4), 27 of which were native. *Ctenognathus otagoensis* (Bates) (Carabidae) was the species most commonly collected (Table 2). Bray-Curtis NMDS analysis (Fig. 3) with a stress factor of 0.01 showed that Coleoptera communities in parks situated in level 1 UI were very similar, as were communities in parks situated in level 2 UI. Coleoptera communities in parks situated within level 3 UI were mostly similar to those of levels 1 and 2, except in one outlier, Woodhaugh Garden. Coleoptera communities in parks situated within level 4 UI were relatively dissimilar, except for one park.

Richness, relative abundance and diversity in relation to dominant vegetation type

Trends showed that invertebrate relative abundance, diversity and taxonomic richness were all higher in parks that were dominated by shrub vegetation: Relative abundance (t(18.35): mean shrubs=412.12±138, mean

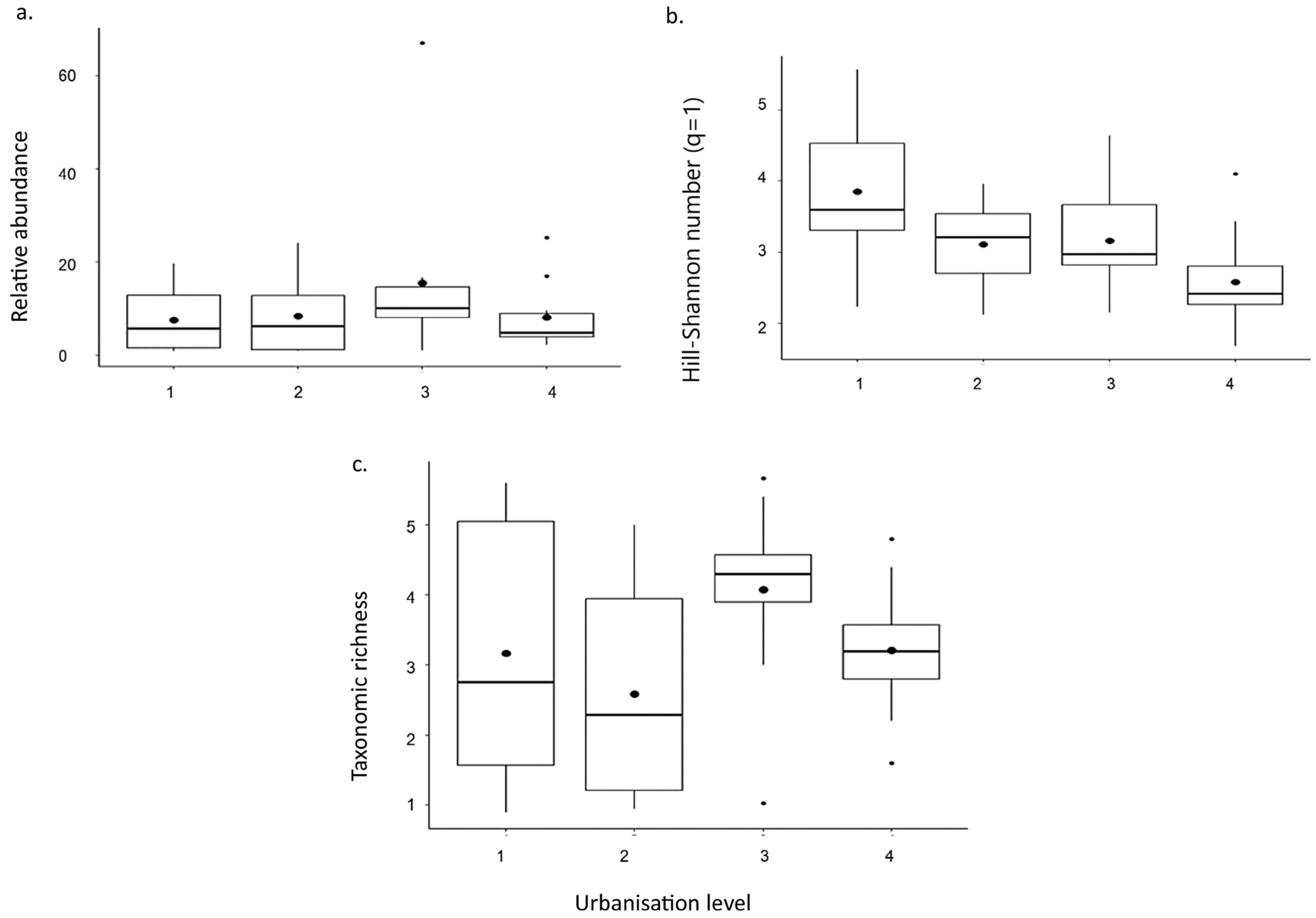

Fig. 1 (**a**) Relative abundance (**b**) Hill-Shannon number (Hill q = 1) (**c**) Taxonomic group richness of invertebrates collected from shrub beating samples and pitfall traps across 20 parks in Dunedin, New Zealand, situation in four levels of urbanisation intensity (UI), with level 1 representing lowest UI and level 4 highest UI

Table 2 The total number of Coleoptera collected from 20 parks across Dunedin using three collection methods: blower vac (408), shrub-beating (53), and pitfall traps (56)

Coleoptera family	Blower-vac (lawns)	Shrub-beating	Pitfall traps	Total
Curculionidae	169	7	14	190
Staphylinidae	137	5	7	149
Ptiliidae	34	0	0	34
Latridiidae	6	22	2	30
Tenebrionidae	27	0	2	29
Carabidae	9	0	13	22
Chrysomelidae	12	4	2	18
Leiodidae	4	11	2	17
Scarabaeidae	4	0	3	7
Cerambycidae	0	4	2	6
Zopheridae	4	0	2	6
Damaged (no ID)	0	0	5	5
Coccinellidae	2	0	0	2
Anthicidae	0	0	1	1
Byrrhidae	0	0	1	1
Total	**408**	**53**	**56**	**517**

lawns = 232.38 ± 138, $p = 0.14$, Fig. 4a), Hill-Shannon diversity (Hill q1) (t(18.61): mean shrubs = 1.16, ± 0.04 mean lawns = 1.22 ± 0.04, $p = 0.62$, Fig. 4b), and taxonomic richness (t(18.61): shrub mean = 9.42 ± 1.2, lawn mean = 7.23 ± 1.2, $p = 0.002$, Fig. 4c). A significant difference was found only for taxonomic richness, which was higher in parks dominated by shrubs.

Similarly, Coleoptera families showed trends where means were highest in shrub dominated data for abundance (t(15.53): mean shrubs = 4.21 ± 0.21, mean lawns = 2.35 ± 0.21, Fig 5a), Hill-Shannon number (Hill q1) (t(18.65): mean shrubs = 0.38, ± 0.04 mean lawns = 0.26 ± 0.04), and taxonomic richness (t(18.07): shrub mean = 1.58 ± 0.98, lawn mean = 1.13 ± 0.98). Although, no significance was detected for any groups ($p > 0.05$).

Richness, abundance and diversity of invertebrates in relation to proximity to a large green space

The relative abundance of invertebrates did not vary significantly with distance to the nearest large green space

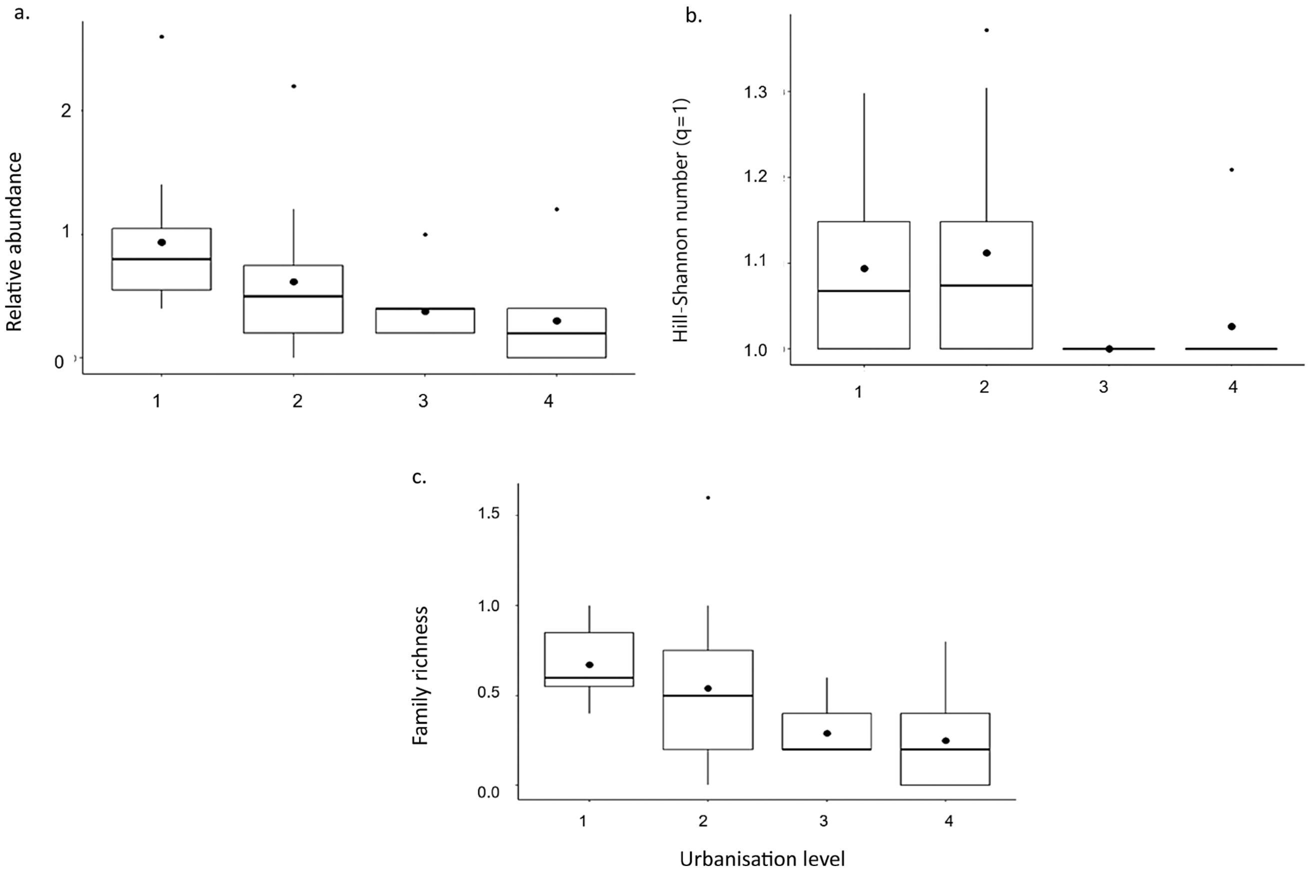

Fig. 2 Relative abundance (**a**), Hill-Shannon number (**b**), and family richness (**c**) of Coleoptera families collected across 20 parks in Dunedin, New Zealand, along a gradient of urbanisation intensity (UI): level 1 UI represents the lowest level of urbanisation intensity, and level 4 the highest

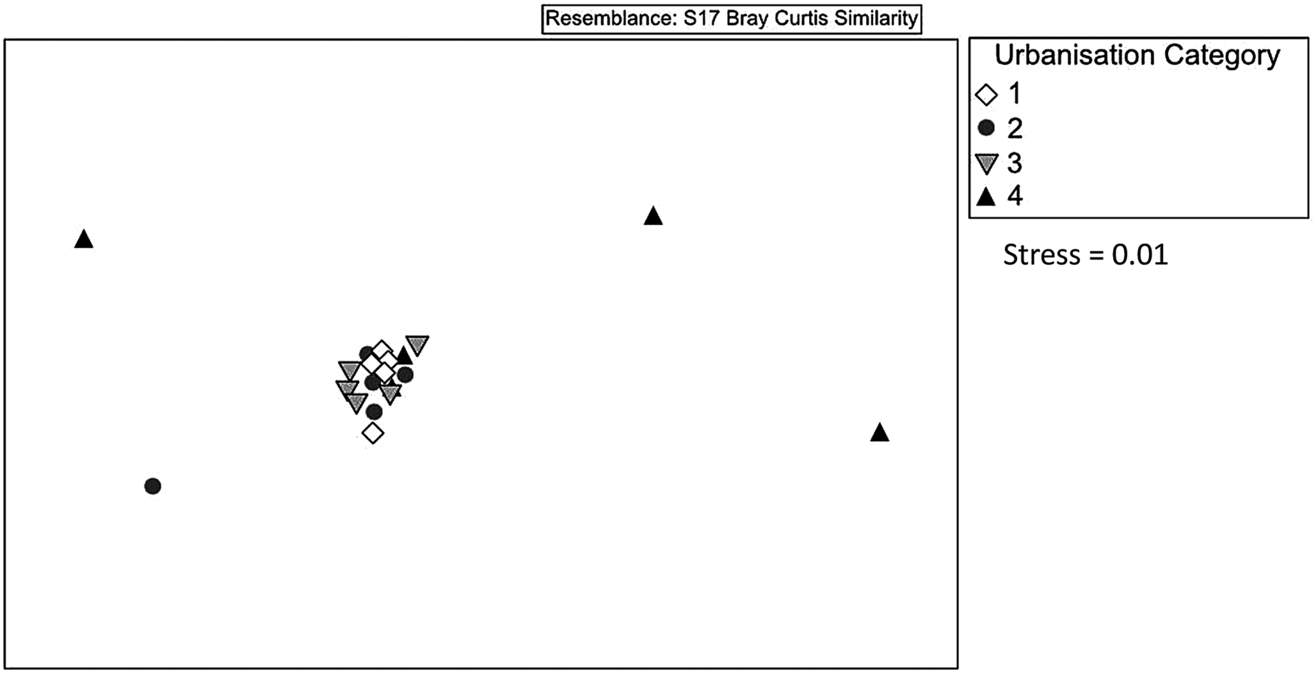

Fig. 3 NMDS (non-metric multidimensional scaling) using a Bray-Curtis dissimilarities of Coleoptera community composition from samples collected in pitfall traps across 20 parks in Dunedin, New Zealand, situated along a gradient of urbanisation intensity (UI): level 1 was lowest UI and level 4 highest

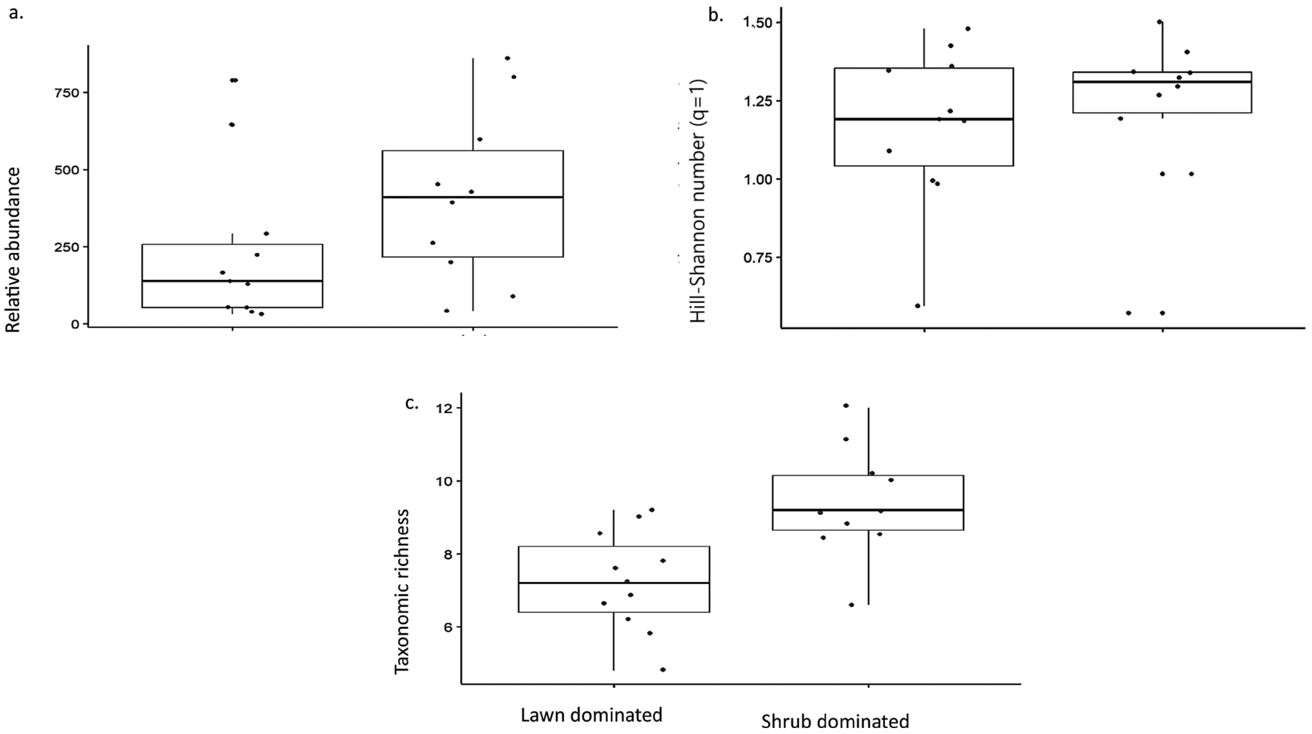

Fig. 4 (**a**) Relative abundance, (**b**) Hill-Shannon numbers, (**c**) Taxonomic group richness of invertebrates collected across 20 parks in Dunedin, New Zealand, in relation to dominant vegetation type (lawn or shrubs)

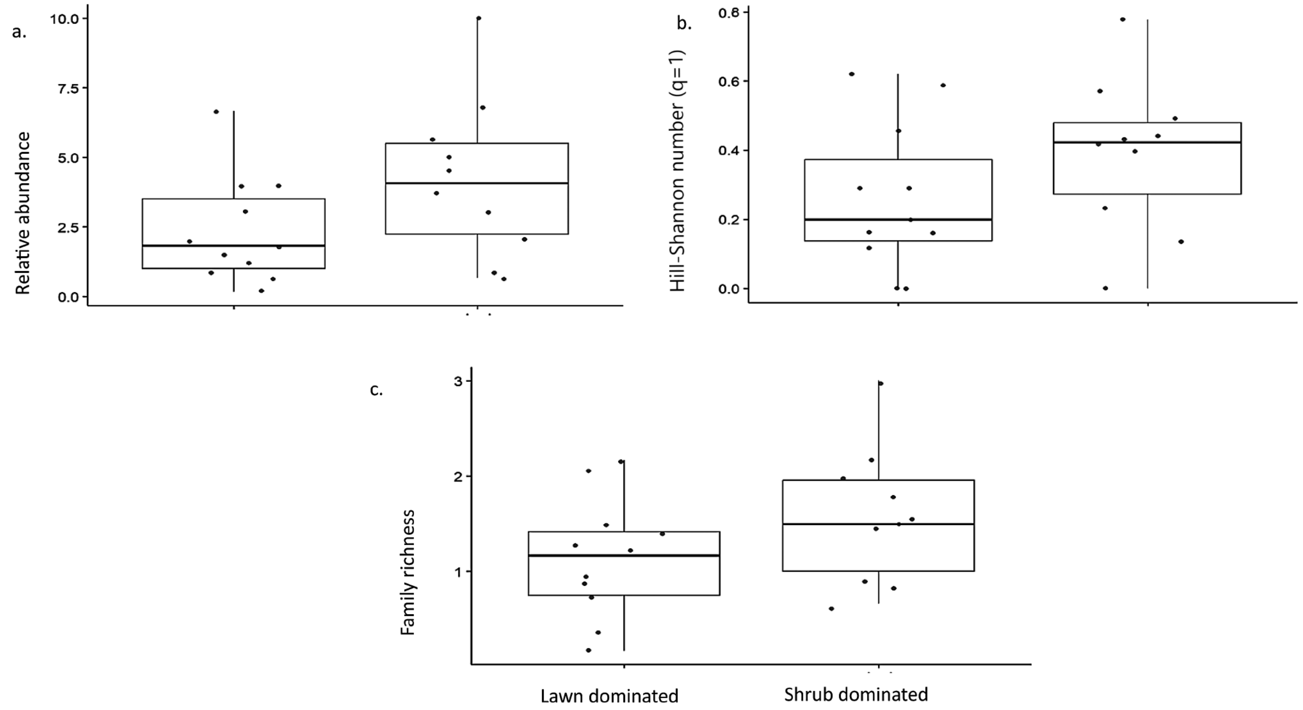

Fig. 5 (**a**) Relative abundance (**b**) Hill- Shannon numbers (**c**) Family richness of Coleoptera collected across 20 parks in Dunedin, New Zealand, in relation to dominant vegetation type (lawn or shrubs)

intensity and the R² value was low (Negative Binomial GLM: z=0.49, df=39, p=0.16; R² = 0.03; Fig. 6a). There was, however, a signficant decline in Hill-Shannon numbers (Hill q1) as the distance from a green space increased (Gamma GLM: t=3.64, df=39, p=0.0007; R² = 0.30; Fig. 6b). Taxonomic group richness did not vary significantly with distance (Negative Binomial GLM: z=0,49, df=39, p=0.6; R² = 0.06; Fig. 6c).

Results did not vary significantly when looking at Coleoptera family relative abundance (Negative Binomial GLM: z = 1.24, df = 36, p = 0.21; R² = 0.03; Fig 7a), Hill-Shannon numbers (Hill q1) (Gamma GLM: t = 1.54, df = 36, p = 0.28; R² = 0.04; Fig 7b), and Coleoptera family richness (Negative Binomial GLM: z = 1.05, df = 36, p = 0.12; R² = 0.06; Fig 7c) in relation to park distance from the nearest green space. However, there was a general negative trend observed with distance from a large green space and Coleoptera relative abundance, richness and diversity.

Discussion

We found consistent but non-significant trends of increasing richness, relative abundance and diversity of invertebrate taxonomic group and Coleoptera families in parks situated along a gradient of surrounding decreasing intensity of urbanisation (proportion of impervious surfaces). Significant differences were found only between invertebrate diversity, and Coleoptera family abundance, richness and diversity in parks at each end of the urbanisation gradient, suggesting a certain threshold or critical point was reached at which impacts were manifested. This negative trend supported our hypothesis.

These data provide some support for the "increasing disturbance" hypothesis (Gray 1989), which describes species richness and abundance as declining with increasing levels of urbanisation, with lowest richness found in the urban core (Niemelä and Kötze 2009; Martinson and Raupp 2013; McKinney 2008; Blair and Launer 1997). We found no significant differences between parks situated within levels 2 and only some for level 3 urbanisation intensity, where impervious surfaces made up less than half of both

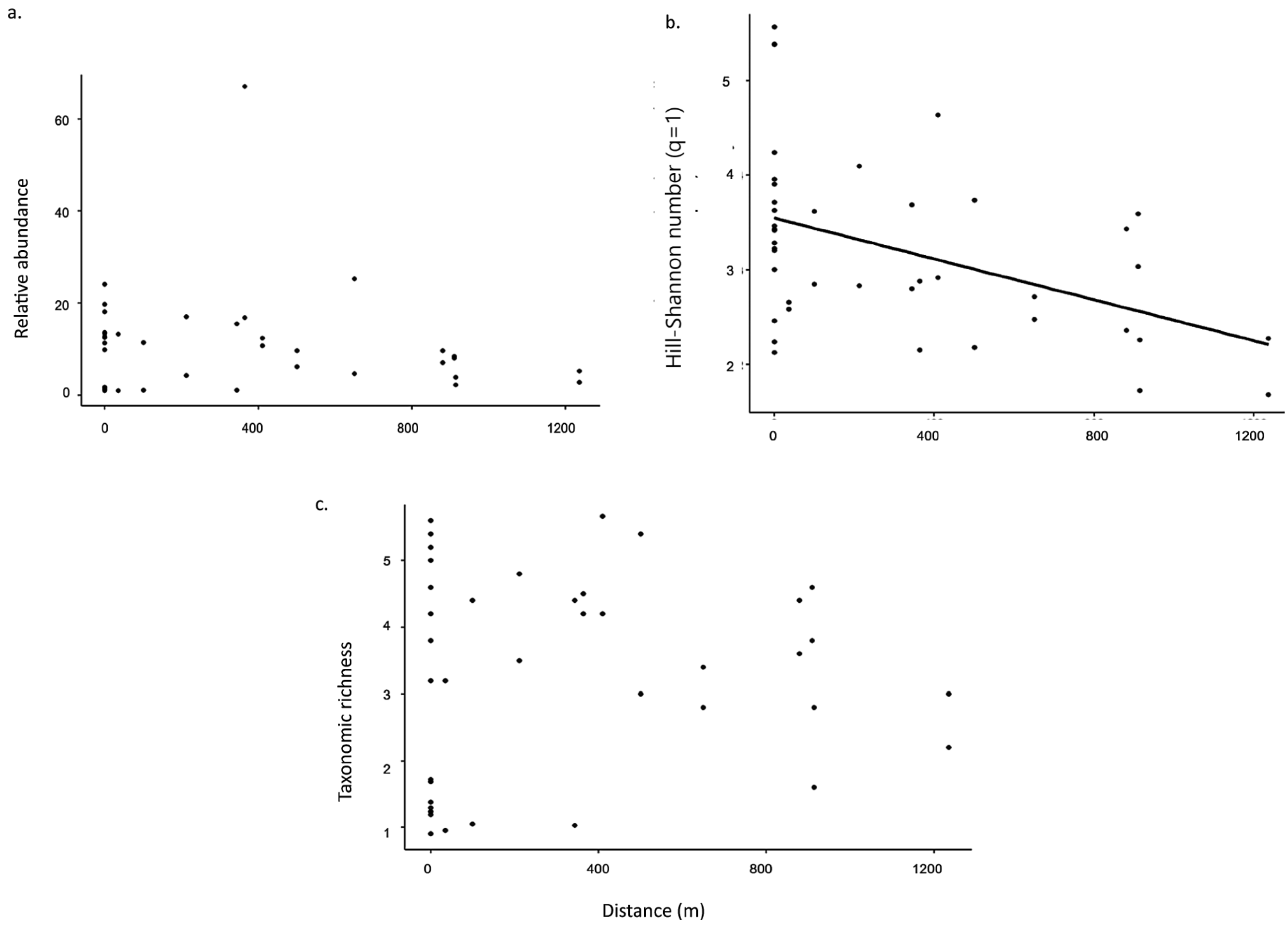

Fig. 6 (**a**) Relative abundance of invertebrates, (**b**) Hill-Shannon numbers, (**c**) Taxonomic group richness of invertebrates collected across 20 parks in Dunedin, New Zealand, in relation to distance from a green space >30 ha

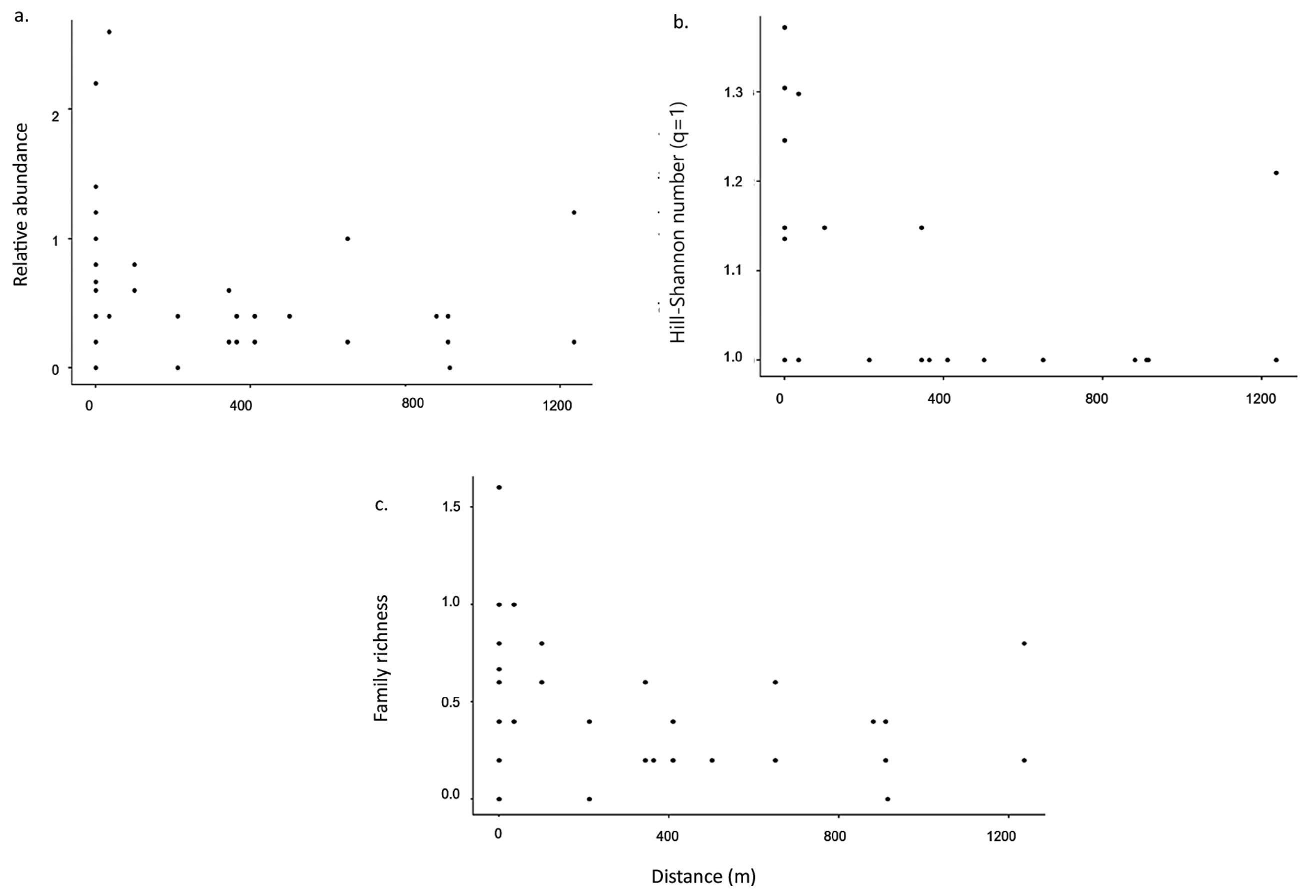

Fig. 7 (**a**) Relative abundance of Coleoptera, (**b**) Hill-Shannon numbers, (**c**) Family richness of invertebrates collected across 20 parks in Dunedin, New Zealand in relation to distance from an established green space > 30 ha

surrounding buffers (level 2), and more than half of the outer buffer area (level 3). However, when impervious surfaces comprised more than half of both surrounding buffers (level 4), invertebrate diversity decreased significantly. It is important to note that our study measured urbanisation intensity using a 100 m buffer zone from the sampling site (suppl. Material Fig. S1 and S2): this meant that a larger proportion of park habitat was included in the buffer area when larger parks were sampled. Larger parks with lower edge density, generally located on the outskirts of urban areas, tend to support greater arthropod diversity (Liu et al. 2020) due to reduced edge effects and greater habitat heterogeneity. In contrast, smaller parks with higher edge density, typically in urban cores, tend to have lower arthropod diversity, likely due to increased edge effects, limited habitat complexity, and barriers that restricted movement between highly urbanised areas. Given that level 1 parks in our study tended to be larger than level 3 and 4 parks, they include more park area within the buffers which would have boosted diversity.

Koji et al. (2024) also explored the impact of the proportion of impervious surface cover in larger buffer areas around small neighborhood parks in Japan, and reported strong effects on carabid species diversity and spider traits. A higher proportion of impervious surface tends to be associated with simplified habitats and reduced vegetation diversity and volume, which will limit the variety of niches that can be occupied and dispersal between green spaces, and ultimately resilience of insect communities occupying parks embedded in a highly modified matrix (Colding 2007).

Studies on effects of urbanisation on species richness and diversity of various taxa (invertebrates, plants, mammals, birds, reptiles and amphibians) have revealed consistent trends, in that species richness and diversity often decline in areas of highest urbanisation (McKinney 2008; Gagne and Farhrig 2011; Penone et al. 2012; Persson et al. 2020), as was also found in this study. However, the reported impacts of moderate levels of urbanisation on diversity vary between studies. Higher diversity at moderate levels could occur if competitive species, such as invasive and successional species, inhabit these areas as well as native species (McIntyre 2000; McKinney 2008). It is possible that the lack of significance we found between parks situated in levels 2 and 3 urbanisation intensity was due to non-native successional species replacing specialist native species in level 2 parks (McKinney 2006).

The abundance of certain invertebrate species such as habitat generalists and non-native species is often greater in more urbanised areas (McKinney 2008; Gagne and Fahrig 2011; Fenogilo et al. 2020, Piano et al. 2020), including small neighbourhood parks (Koji et al. 2024), or alternatively, shows no pattern along a gradient (Alaruikka et al. 2002; Martinson and Raupp 2013) if decreases in abundance of some species (e.g., specialists) are compensated for by increases in others (Hornung et al. 2007). We found no evidence for an increase in relative abundance of invertebrate orders in parks surrounded by the highest proportion of impervious surfaces in our study. Except for a subset of samples (Coleoptera collected in pitfall traps), we were able to identify invertebrates only to order or a higher taxonomic group and consequently it was not possible to differentiate between native and exotic species, generalists and specialists, and invasive and successional species in order to understand better which species were being lost in parks located within areas with higher proportion of built structures. However, most (69%) Coleoptera identified to species were native.

Coleoptera is a highly diverse insect order, in terms of taxonomic and ecological diversity (Farrell 1998), and in urban areas is a well-studied group that displays a range of tolerances which are related to factors such as dispersal ability, habitat affinity and trophic position (Martinson and Raupp 2013). Coleoptera communities tend to decline in diversity as urbanisation intensifies along a gradient and specialist and large often predatory species are lost (Niemelä and Kotze 2009; Sadler et al. 2006; Tóthmérész et al. 2011; Martinson and Raupp 2013; Vergnes et al. 2014). Kuschel (1990) found fragment size and local forest cover were important indicators for Coleoptera; large, diverse patches supported higher levels of Coleoptera diversity.

However, many beetle species are relatively insensitive to urbanisation gradients, or vary in their responses between studies (Martinson and Raupp 2013). Sometimes a lack of decline in species diversity is the result of shifts in community composition; for example, a loss of forest specialist species compensated for by an influx of non-forest species (Magura et al. 2010). The many open habitats typically found in urban areas such as lawns, moss and gravel support increases in open habitat specialist, generalist, and opportunist species (Gagné and Fahrig 2011; Jones and Leather 2012; Madre et al. 2013; Tóthmérész et al. 2011; Vergnes et al. 2014). Structural heterogeneity of vegetation (Brose 2003), and vegetation composition are important determinants of Coleoptera diversity and abundance in urban areas (Jaganmohan et al. 2013; Magura 2008Niemelä and Spence 1994; Small 2003; Small and Lu 2006; Smith et al. 2006a, 2006b; van Heezik et al. 2016) as is the presence of native vegetation (Kuschel 1990).

In this study, mean richness and diversity of invertebrate orders were higher in parks where shrubs were the dominant vegetation type when compared to parks with less complex vegetation in the form of lawns (playing fields), as predicted by our hypotheses. The recreational and aesthetic values of lawns are barriers to their replacement with more diverse and complex vegetation (Kushel 1990; Yang et al. 2019). However, as indicated by this study, lawns are not completely sterile environments. One park (Woodhaugh Garden), which is valued highly as a multi-functional space (Freeman et al. 2022) and was categorised as having 'lawn-dominated' vegetation, consistently displayed high levels of invertebrate richness, relative abundance and diversity. Woodhaugh Garden also has a significant area of native vegetation with an intact forest remnant, which likely supported richer invertebrate communities, as has been shown elsewhere in New Zealand (Kuschel 1990). Increasing the presence of shrubs does not necessarily entail reducing the recreational value of green spaces but can improve the habitat complexity and plant species richness and therefore improves the diversity and richness of invertebrate communities.

The NMDS model identified that the species assemblage in Woodhaugh Garden differed from those in other parks. As an example of a forest fragment within an urban gradient, it is possible that some forest-sensitive species may have been able to inhabit this park, that were absent from other parks. A study conducted in the North Island of New Zealand by Watts and Larivière (2004) on Coleoptera in urban reserves found 23 different families of Coleoptera, however, there was a notable difference in species richness and abundance in reserves compared to larger forested areas. Forest-sensitive species are unlikely to inhabit urban parks, resulting in a similar assemblage of urban-tolerant species found across urban green spaces (Kotze et al. 2022) Incorporating forest patches into parks could provide more habitat for forest-sensitive species.

The NMDS analysis identified that Coleoptera communities from parks were similar, except for parks situated in higher levels of urbanisation intensity (level 4). Most parks in level 4, and one park from level 2 were situated further from the general cluster in the model, indicating a dissimilarity in communities present based on the Bray-Curtis index. The change in community structure observed in parks from higher levels of UI may reflect a decline in urban-tolerant species that are present throughout the gradient and a threshold reached as a result of environmental stress from habitat loss, homogenisation and fragmentation (Koji et al. 2024). Disturbance in ecosystems can cause sudden shifts from the original ecological condition to alternate compositions and assemblages of organisms (Hobbs and Norton 2004; McDonnell and Pickett 1990). Community structure will then depend on local-scale colonisation by new opportunistic Coleoptera assemblages in response to local environmental conditions (Sol et al. 2013).

Parks with higher surrounding urbanisation were generally smaller, dominated by lawns, and located farther from large green spaces. We found consistent but non-significant trends of increasing richness, relative abundance and diversity of invertebrate taxonomic groups in parks close to a large green space, supporting our final hypothesis. These parks had higher relative abundance, richness and diversity of invertebrate groups, emphasising the importance of connectivity between small and large green spaces in an urban environment. Large green spaces likely serve as ecological refuges and act as sources of colonisation for nearby parks.

Metapopulation theory is often used to explain the impacts of the patchy arrangement of green spaces typically found in urban areas (Niemelä 1999; Vergnes et al. 2012). Populations of animals in green spaces are separated in space by a matrix of built-up areas, the extent to which they can interact with each other varies depending on characteristics of the species and of the urban matrix habitat (Vergnes et al. 2012; Lepczyk et al. 2017). Smaller, less diverse habitats are still able to provide refuges for some small-sized species when connectivity to larger patches exists (Angold et al. 2006; Hunter and Hunter 2008; Fattorini et al. 2011a and b; Jones and Leather 2012).

Connectivity between habitats plays an important role in influencing invertebrate richness and abundance (Fattorini et al. 2019). The quality of these habitats will also determine the diversity of invertebrates present (Angold et al. 2006), as we found in Woodhaugh Garden. Urban habitat quality is generally low because of the modified landscape. The shrubby park perimeter habitat was not diverse enough to support higher invertebrate diversity. Nevertheless, the urban matrix habitat was sufficiently permeable to enable dispersal of invertebrates from larger, more diverse green spaces within the landscape. These are likely to be generalist species, which are able to use a wide range of habitats, facilitating dispersal between patches of good habitat (Magura et al. 2013; Sadler et al. 2006).

Trends of increased invertebrate richness and diversity in parks closer to larger green fragments provide evidence that invertebrates can disperse using the urban matrix. Enhanced matrix habitat quality could improve dispersal between urban green spaces and support specialist invertebrates that are less tolerant towards the pressures of urbanisation. This can be achieved by increasing plant diversity and vegetation structural complexity around the perimeters of parks, or including a patch of high-quality vegetation, as was the case in Woodhaugh Garden.

While the gradient of proportion of impervious surfaces did not have a large impact on invertebrate communities in our study, this may be because urban invertebrates are preselected for tolerance to fragmentation and dominance of non-native vegetation. However, with increasing densification of buildings due to growing human populations, species are likely to reach limits to their tolerance. To mitigate further detrimental impacts, vegetative heterogeneity of existing urban green spaces, such as amenity parks, should be enhanced. This may include replacing some areas of lawn with small areas of diverse native shrub and tree species growing to various heights to create vertical structural complexity. Focussing on enhancing structural and compositional diversity in parks between larger green spaces will provide additional habitat and facilitate invertebrate dispersal between larger green fragment through providing stepping stones and corridors for dispersal.

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Declarations

Competing interests The authors declare no competing interests.

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