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The overlooked margins: how cities impact diversity of plants and terrestrial invertebrates along urban streams

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Abstract

The effect of different urbanization levels on terrestrial biodiversity associated with riparian zones remains poorly studied, despite the important ecosystem services it provides in cities. Studies focused on aquatic ecosystems in urban streams reported decreases in ecological quality and species richness, and lack of sensitive taxa. Thus, we investigated the impact of urbanization on riparian zone flora and terrestrial invertebrates using as case studies nine urban streams spanning an urbanization gradient in the Portuguese city of Coimbra. An unexpectedly high number of taxa were identified (163 plants, 80 terrestrial invertebrates), 80% new registrations for the region and one endemic-rare plant. Yet, diversity varied across streams, β-diversity reaching 39% Bray-Curtis similarity and averaging 25%, due to many underrepresented terrestrial taxa ($N=62$ observed only in one site). Variation across the urbanization gradient reached 59% in plants and 82% in terrestrial invertebrates. High numbers of non-native taxa (13%; $N=32$), mostly plants, suggested urbanization factors, e.g. human interference and discharge variation, may have favored invasions. Indeed, constructed natural spaces along streams, like parks, supported less biodiversity. Moreover, plant richness, especially of riparian plants, was correlated negatively with percentages of surrounding impervious areas and positively with water quality. This shows urbanization has negative effects on riparian vegetation, and water quality impacts both aquatic and terrestrial communities. Our results stress urban streams as novel ecosystems constituted by high numbers of non-native taxa, and the significance of riparian zones for biodiversity preservation. Less intense intervention on riparian vegetation is recommended to increase biodiversity.

Keywords Flora · Freshwater · Insects · Invasive species · Riparian corridors · Urbanization

Introduction

The migration of people from rural to urban areas coincides with the increase in human population on Earth. The number of people living in cities was expected to reach 6.3 billion by 2050, while it had surpassed 6.68 billion by 2019 (United Nations 2012; United Nations 2019). A direct consequence of this is an increase in the level of urbanization that causes a loss of natural ecosystems, an increase of impervious surfaces, and water, soil and air pollution (Camacho et al. 2021; Franklin et al. 2002). These processes lead to habitat loss and fragmentation (Liu et al. 2016), which may leave certain ecosystems untouched or with very little alteration yet exposed to the surrounding urban environment and cut off from other natural regions. This limits the ability of individuals to move between natural areas and to reproduce, which lowers the diversity of species and favours most tolerant taxa that can survive in small areas (Wilson et al. 2016). Therefore, creating biological corridors that support the survival of numerous species is crucial, as is maintaining and improving natural regions within urban areas (Rudd et al. 2002; Kong et al. 2010). In addition, natural urban spaces with their animals and plants benefit city inhabitants'

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physical and mental well-being (Carrus et al. 2015; Kondo et al. 2018; Feio et al. 2022).

On the other hand, the human activities that take place in cities create, directly or indirectly, ecological niches that do not exist in other environments and that alter ecosystem functioning, which may suppress or promote certain plant and animal species (Salinitro et al. 2018; Kolenda et al. 2021). For example, the materials used in buildings and pavements, or the height of the buildings, determine the *heat-island* effect, i.e. a zone of the city where temperatures are higher than in its surroundings (Yang et al. 2016). Also, the interactions between human populations and urban biodiversity can change the behaviour of animals regarding their feeding habits and reproduction, which in turn impacts species they interact with (Luniak 2004; Torun 2016; de Oliveira 2020). Urban species richness is also a result of humans that deliberately or accidentally influence biodiversity. Indeed, considerable parts of urban biodiversity are defined by the city inhabitants that bring in non-native species, either accidentally or as ornamental species or pets (Elmqvist et al. 2013; Zari 2018). There are actually many studies on urban biodiversity but much remains unknown (Elmqvist et al. 2013), particularly on urban aquatic ecosystems (but see Booth et al. 2016; Serra et al. 2019a; Ranta et al. 2021).

Plants are particularly relevant in stream ecosystems due to their functions (Wolters et al. 2018; Larson et al. 2019). In small streams of temperate climate zones most of the energy provided to the system comes from the riparian vegetation (Finlay 2001). Fallen leaves and small branches provide ecological niches and are the major food source of invertebrate shredders which are then predated by other invertebrates, fish, amphibians, or birds (Graça et al. 2001; Feio et al. 2002; Serra et al. 2019b). Plant height and canopy density also determine the level of shade over the water, thus controlling temperature and primary production; plants prevent erosion and deposition of sediments and create a buffer zone between the aquatic component and the urban environments around them (Ferreira et al. 2021). In addition, riparian zones provide ecosystem services essential to urban areas such as regulating the air temperatures, providing more humidity to the air, mitigating the climatic extremes, or filtering air, soil and water pollutants (Ranta et al. 2021). It is therefore key to understand the state of the riparian urban zone and its biodiversity.

Although studies have explored the effects of varying levels of urbanization on different taxonomic groups in streams and riparian vegetation (Urban et al. 2006; King et al. 2011, 2016; Paredes del Puerto et al. 2021), few studies have focused on terrestrial invertebrates in the banks and margins, but see for example Smith et al. (2009) on the terrestrial phase of aquatic stream insects. Terrestrial invertebrates found along the banks of rivers and streams are made up of adults of the aquatic insects orders Diptera, Ephemeroptera, Trichoptera, Plecoptera and Odonata, but also of fully terrestrial taxa of the orders Coleoptera, Lepidoptera and Hymenoptera. Despite their small size, these animals provide important ecosystem services such as pollination or soil aeration and decomposition of organic matter (Aizen and Feinsinger 2003; Ranta et al. 2021; Steward et al. 2022).

The main goal of this study was to investigate if urbanization: (i) affects plants and terrestrial invertebrates associated to streams, (ii) constrains the local species pools (α diversity) and leads to the differentiation between streams within the city (β-diversity), and (iii) relates with the presence of non-native species and their effect on biodiversity over a gradient of urbanization. Understanding these effects will improve the management of lotic ecosystems within cities and how to promote their rehabilitation.

Methods

To assess the impact of urbanization on diversity of plants and terrestrial invertebrates of riparian zones of urban stream ecosystems we used as a case study the city of Coimbra, central Portugal, and nine stream sections covering an urbanization gradient. Recent ecological and hydrological studies in the streams of this city provided background information for this study (Marques et al. 2007; Serra et al. 2019a; Arco et al. 2012; Zerega 2020; Ranta et al. 2021).

Study area

The city of Coimbra, central Portugal is medium-sized (EU 2005) and built along River Mondego, and its hills and valleys. It has an area of 319.40km^2 and 143.396 inhabitants (*ine.pt*), and a population density of 448.9 inhabitants/km^2 in 2019 (*pordata.pt*). Coimbra's hydrology was changed during the city's history by the increasing urbanization along the river. In the 20th century, much of the soil became artificial and impervious surfaces with new drainage pathways, contributing to a higher flood risk (Tavares et al. 2012; Kalantari et al. 2017).

The study area is located in the Temperate Broadleaf and Mixed Forests biome (Ding et al. 2016) and in the Csb climate, i.e. temperate with dry and moderate summers (*ipma.pt*). The average temperature varies between 6ºC in December-January and 20ºC in July-August, and precipitation varies between 200 mm in December-January and almost zero in July-August (*portaldoclima.pt*). The year 2020 was particularly hot and dry, with an average temperature of 16 ºC and the precipitation was 85% of the yearly average (IPMA 2021a).

Study sites

Nine stream sections within the city of Coimbra (Fig. 1) were selected for this study, covering different urbanization levels (see Table 1), from densely urbanized sites, to areas with a lower urbanization and closer to a natural state in the outskirts of the city. The segments of the studied streams ('sites') were defined with a length of ca. 100 m to guarantee a uniform sampling. The sites were numbered according to sampling order.

Elevation, straight-line distance to the source and to the main river were measured using Google Earth (satellite images, Table 1). Furthermore, a 1 km x1 km buffer zone was defined around each stream segment and the percentage of impervious area (IS) for the total land use in the buffer zone, a surrogate for the degree of urbanization, was calculated by using Google Earth functions (Table 1).

In addition, water samples were collected in each stream and later analyzed for their concentration (mg/l) in ammonia, nitrite, nitrate, phosphate and total dissolved solids (TDS), dissolved oxygen (DO; %) and electric conductivity (µS/cm).

Sampling and identification of biodiversity

Plants and terrestrial invertebrates were surveyed from November of 2019 to January of 2021. Surveys were

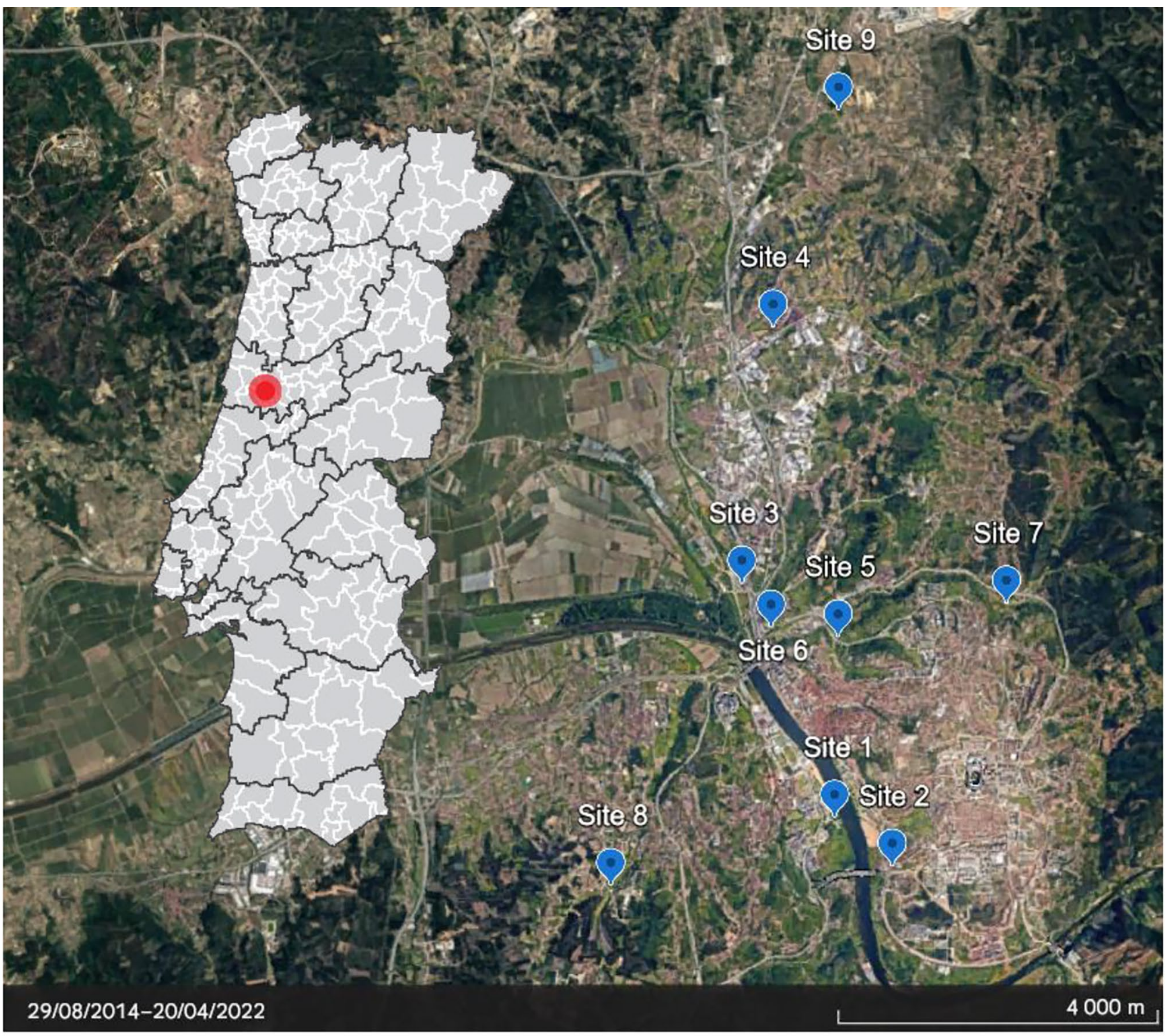

Fig. 1 Location of Coimbra in a map of Portugal (obtained from *comarcas.tribunais.org.pt*) and the location of the nine study stream sections marked in Google Earth

Table 1 Geographical and hydrological characteristics of each of the stream sections (Elev, elevation; IS, Impervious Surface)

Site #	Site name	Geographic coordinates	Elev (m)	Catchment	IS (%)	Relevant land uses	Dist. to source (m)	Dist. to main river (m)
1	Exploratório	40.19852 N, 8.4278010 W	21	N/A	57	Roads, parks	880	70
2	Vale das Flores	40.19313 N, 8.41946 W	20	Vale das Flores	74	Roads, buildings	1880	280
3	Coimbra-B	40.22451 N, 8.441234 W	35	Gorgulhão	41	Roads, train tracks, parking	2640	530
4	Eiras	40.25291 N, 8.436664 W	14	Eiras	40	Roads, buildings, gardens	5640	3820
5	Hospital	40.21857 N, 8.427322 W	31	Coselhas	33	Roads, buildings	5320	980
6	Casa do Sal	40.21962 N, 8.43703 W	21	Coselhas	43	Roads, parks	5760	430
7	S. Romão	40.2223 N, 8.402945 W	60	Coselhas	13	Roads, agriculture	2600	2850
8	Covões	40.19112 N, 8.460405 W	87	Covões	3	Roads, agriculture	1760	3000
9	Fornos	40.27697 N, 8.427147 W	23	Eiras	20	Roads, agriculture	7160	6540

conducted up to a width of ca. 10 m in both margins, or less when constructed areas were closer to the stream channel. A uniform sampling effort was guaranteed among sites by visiting each stream the same number of times ($N=6$) and standardizing the period of the day. Presence-absence data were obtained, along with a field observation and estimation of the dominant taxa at each site, i.e. those that occupied a larger area.

Plant taxa were identified either from photographs or sampled and preserved in a herbarium (Pinho et al. 2016). The selected specimens were those with visible species-specific traits within that 10-m corridor along the established length (100 m) of each of the stream margins. Identifications were supported by the online databases *flora-on.pt* and *invasoras.pt*, and the identification keys in *Flora Iberica* (Castroviejo 1986–2021) and *Nova Flora de Portugal* (Franco 1971, 1984; Franco and Afonso 1994, 1998a, b).

Invertebrates were identified through active observations – as the vegetation did not allow for methods like sweep netting - and photographs within that same corridor, using field guides (Bellman 2011; Chinery 2012) as well as online databases and identification keys (*molluscs.at*; *atlashymenoptera.net*; *naturdata.com*; *leafmines.co.uk*). When observed on plants, the type of relationship between the invertebrate and the plant (pollination, herbivory) were registered whenever possible.

The presence of native, non-native, endemic and invasive species was also ascertained, with the support of online databases (*flora-on.pt*, *viva.fct.unl.pt*, *almargem.org, araneae.nmbe.ch*, *invasions.si.edu*, *invasoras.pt*, *plantsoftheworldonline.org*, *bugguide.net*). The European and Mediterranean Plant Protection Organization (EPPO) worldwide database, *gd.eppo.int* provided information on which terrestrial invertebrates are recognized as pests and which plant species serve as hosts. Classification of plants into riparian and non-riparian was done through the lists of taxa included in official protocols for monitoring stream biodiversity (INAG 2008). Information regarding Raunkiær plant life forms was gathered for the plants that were identified to species level through *flora-on.pt*, using the subcategorization system of the database.

Biodiversity metrics and data analysis

Two biodiversity metrics were considered in this study: (1) the α-diversity to measure the amount of diversity at each site; and (2) the β-diversity, which determines whether there are differences between various streams inside the city; these differences would primarily result from urbanization because the study area is small and the potential causes are unlikely to be other large-scale environmental factors, such as climate or geology, which typically limit the diversity of streams and rivers. To measure α-diversity we used total richness (for all taxa); β-diversity was calculated separately and together for the two biological groups studied through the application of the Bray-Curtis similarity coefficient to the biological data matrices (plants and invertebrates) (Bray and Curtis 1957). The Bray-Curtis matrices were then used to perform Non-metric Multidimensional analyses (NMDS) and cluster analyses to allow a visual inspection of the similarity of sites and a hierarchical cluster analysis (unweighted pair group method using arithmetic averages, UPGMA) to establish groups of sites (Primer7; Clarke and Gorley 2015).

To investigate the relationship between urbanization and biodiversity, Pearson correlations were calculated between the diversity metrics of each site and two urbanization measures, i.e. percentage of impervious area and a global water quality index. These measures of urbanization were selected for their potential to affect the stream ecosystems. A catchment area with a high percentage of land covered by impervious materials will be affected by changes in groundwater and channel recharge, flash floods, and runoffs carrying pollutants to the streams, such as heavy metals or nutrients that ultimately may affect riparian areas and stream water (Tasdighi et al. 2017; Chishugi et al. 2021). In addition, the substitution of natural materials by artificial ones in the stream banks also alters hydrogeomorphology. On the other hand, unefficient sewage systems in urban aglomerations may cause an excess of nutrients and organic contamination of urban stream waters. All these factors stress and disturb the urban flora and fauna (Miserendino et al. 2011; Zerega et al. 2021).

The global water quality index was obtained from an ordination (Principal Component Analysis) of the water quality parameters data for all sites (ammonia, nitrate, nitrite, phosphate, dissolved ogygen, conductivity and TDS), which were transformed using the log $(x+1)$ function and normalized. The resulting scores from PC1 and PC2 were used as a water quality index. Finally, the BIO-ENV test (a test that uses rank correlations to define the best sets of environmental variables to explain similarities in biological data) was used to determine which urbanization variables were best correlated with the β-diversity found at the urban stream sites (Primer7; Clarke and Gorley 2015).

Results

A total of 243 taxa (163 plant and 80 terrestrial invertebrate taxa) were found in the study area, of which 207 were identified to the species or genus level (Tables S1 and S2). Two plant species were endemic to the Iberian Peninsula: *Antirrhinum linkianum* and *Scrophularia grandiflora*. Thirty-two taxa are non-native species for this region, corresponding to 13% of the taxa observed. Most of the non-native taxa were plants (29 taxa) associated to the riparian corridors. Out of the 32 non-native species, nine were classified as invasive species, which accounts for 4% of the total of all species registered, and 28% of the non-native species registered. The total species richness (Table 2) varied between $N=78$ at site 8 (Covões) and $N=32$ at site 6 (Casa do Sal).

Diversity of plants and terrestrial invertebrates in the urban streams

Within plants, a total of 164 taxa were identified, belonging to 35 orders and 64 families, of which 62 to 92% at each site were herbaceous, followed by shrubs (Supplementary Information Table S1). The most common families were Asteraceae, Poaceae and Fabaceae. A total of 93 plant taxa were considered underrepresented (occuring in only one out of nine sites). Most of them are also herbaceous, but the underrepresented taxa also included trees such as *Cupressus lusitanica*, *Sambucus nigra*, *Quercus* spp., *Populus alba*, *Acer negundo* and *Eriobotrya japonica*, species that were most likely planted.

One site (site 8, Covões) stood out with a considerably higher species richness (68 taxa), followed by a site with 41 taxa (site 9, Fornos), while the lowest richness was 28 taxa (at sites 1, Exploratório and 6, Casa do Sal). The dominant species at the site with the highest richness were *Alnus glutinosa* and *Quercus* cf. *robur* for riparian trees, *Trifolium repens* and *Foeniculum vulgare* for shrubs and herbs, and *Rorippa nasturtium-aquaticum* among the aquatic plants (macrophytes). At the sites with the lowest richness, the dominant species were *Parietaria judaica* and *Hordeum murinum* (herbaceous plants).

Out of all plant taxa identified, 29% (47 taxa) are included in INAG (2008) as species associated with Portuguese stream margins, or typically riparian species (Supplementary Information Table S3). The number of riparian species in each site was between 7 and 19 but varied considerably in how it related to the overall site plant diversity (Table 3). These species were at their lowest diversity in site 4 (Eiras), where they also represented the lowest percentage of total plant diversity. By contrast, the highest number of riparian plant species was observed in site 8 (Covões) but they represented only 28% of the total identified plant diversity. In site 6 (Casa do Sal), over half the plant diversity (54%) corresponded to riparian plants.

In terms of Raunkiær life-form categories (Braun-Blanquet 1979) (Supplementary Information Table S4),

Table 2 Total number of taxa (identified to the lowest possible level), plant taxa, invertebrate taxa, endemic taxa, non-native taxa and invasive taxa observed within the predefined sampling areas of each of the nine sites (10-m wide corridors along each margin of a 100-m section of the stream)

Site	Total taxa	Plants	Invertebrates	Endemic taxa	Non-native taxa	Invasive taxa
1. Exploratório	45	28	17	0	6	2
2. Vale das Flores	37	30	7	0	8	4
3. Coimbra-B	59	40	19	1	7	4
4. Eiras	44	32	12	0	6	3
5. Hospital	50	40	10	0	9	4
6. Casa do Sal	32	28	4	0	10	3
7. S. Romão	52	37	15	0	10	2
8. Covões	78	68	10	1	7	3
9. Fornos	59	41	18	0	6	1

Table 3 Number of plant taxa included in reference lists of riparian plant species (INAG 2008) observed within the predefined sampling areas of each site (10-m wide corridors along each margin of a 100-m section of the stream), and the corresponding percentage of the total number of plant taxa, with the lowest and highest values in bold

	Sites								
	1	2	3	4	5	6	7	8	9
Number of riparian plant taxa	12	8	10	**7**	16	15	14	**19**	16
Plant taxa (%)	42.9	26.7	25.0	**21.9**	40.0	**53.6**	37.8	27.9	39.0

Table 4 Bray-Curtis similarities between study sites, namely the average, minimum and maximum values obtained, considering plants and terrestrial invertebrates together and separately, as well as the site combinations that the minimum and average values correspond to

Sites	Average similarity (%)	Minimum similarity		Maximum similarity	
		(%)	Sites	(%)	Sites
All groups	25	5%	4 and 6	39	3 and 5
Plants	29	7%	4 and 6	44	3 and 8
Terrestrial invertebrates	12	0%	6 and all others, 7 and 2	25	7 and 9

hemicryptophytes, typically herbaceous perennials such as grasses, were the most common plants in the stream sites. Phanerophytes, woody perennials like trees and shrubs, were the most represented group in site 1 (Exploratório), due to its location in a public park with planted trees. Therophytes, annual plants that survive to winter in the form of seeds and complete their lives rapidly in favorable conditions, were the most common in site 9 (Fornos), and the most represented along with proto-hemicryptophytes in sites 2 and 4 (Vale das Flores and Eiras, respectively).

Within terrestrial invertebrates, a total of 80 taxa were observed (Supplementary Information Table S2). The most diverse terrestrial orders in the riparian corridors were the Diptera represented by a total of 16 taxa, the Hymenoptera by eleven taxa and the Araneae by ten taxa. The most common terrestrial invertebrate was an unidentified Acari species present at six sites, as well as the snail *Cepaea nemoralis* and the butterfly *Pararge aegeria* (five sites) and the hemipteran *Cicadella viridis* (four sites). Site 3 (Coimbra-B) revealed the highest diversity with 19 taxa, followed by sites 1 and 9 (Exploratório and Fornos, respectively) with 17 taxa. In contrast, only four taxa were observed in site 6 (Casa do Sal), one of them a parasite in the orange trees planted in the park close to the stream (*Trioza erytreae*). The dominant taxon across the study area in addition to *C. viridis*, observed in large numbers wherever present, was an unidentified species of ants. *Calopteryx haemorrhoidalis* and *Calopteryx virgo*, two dragonflies, notable species as they have aquatic and terrestrial phases, were observed in three sites (Hospital, Casa do Sal and Fornos). We found one invasive terrestrial invertebrate, *Vespa velutina*, present at one site (site 1, Exploratório).

Variations in the diversity of plant and terrestrial invertebrate communities within Coimbra city

Analyses of β-diversity (Table 4; Fig. 2) revealed that the similarity among sites, considering together the two biological groups studied, varied between 5% (sites 4 and 6) and 39% (sites 3 and 5) (Bray-Curtis coefficient), with an average of 25% of similarity among all sites. Richness (Table 2) varied 52% between the most and least urbanized sites (sites 2 and 8, respectively). Plants values mirrored this global pattern, while terrestrial invertebrates similarities are much lower, including values of 0%. The global pattern of variation between sites is also different, as can be seen in NMDS results (Fig. 2a-c).

The ordination of sites through Non-Metric Multidimensional Scaling (NMDS) and Cluster analyses (Fig. 2) based on plants and invertebrates showed that sites 1 and 4 are the most distinct, but no clear groups were formed (Fig. 2a). The same analyses using plants (Fig. 2b) did not reveal clear groups either. For terrestrial invertebrates (Fig. 2c), results showed that sites 1 and 6 (Exploratório and Casa do Sal, respectively) were isolated, and the remaining streams formed two distinct groups based on their biological communities: group A constituted by sites 2, 3, 4 and 5, with an average of 47% of impervious area; and group B by sites 7, 8 and 9, with an average of 12% of impervious area.

SIMPER analyses using the grouping obtained for terrestrial invertebrates showed that the two groups were represented by 3–5 taxa, which were responsible for the similarity among sites within each group (Table 5). Within group A, there was an average similarity of 22%, which was entirely accounted for by an unidentified Acari species, the butterfly *Pararge aegeria* and the snail *Cepaea nemoralis*. Group B presented an average similarity of 24%, and 91% of it was accounted for by three insect species, the Acari species and *C. nemoralis*.

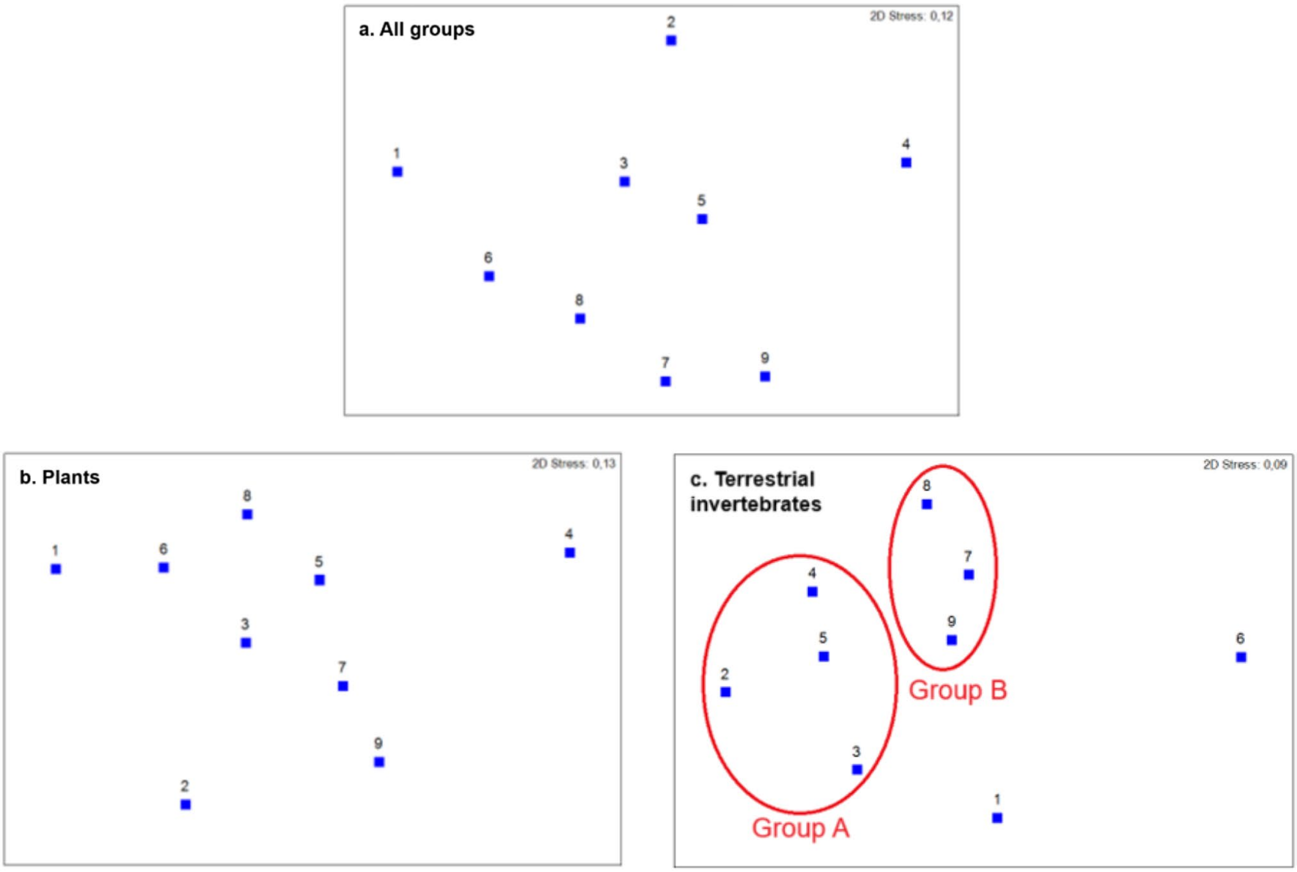

Fig. 2 Non-metric Multidimensional Scaling analysis (NMDS, using Bray-Curtis coefficient matrices) for the lists of observed taxa of both studied groups together and separately, with site groupings obtained from Cluster analyses (unweighted pair group method using arithmetic averages, UPGMA) marked in red. **(a)** All groups, **(b)** Plants, **(c)** Terrestrial invertebrates

Table 5 SIMPER results (taxa contribution being 100% for Group A and 91% for group B) for the similarities between sites within the groups obtained in analyses of terrestrial invertebrate assemblages, discounting the outliers (sites 1 and 6)

Group A		Group B	
Taxa	Contrib%	Taxa	Contrib%
Acari	41.2	*Chrysomela populi*	30.4
Pararge aegeria	41.2	*Cicadella viridis*	30.4
Cepaea nemoralis	17.7	*Apis mellifera*	11.2
		Acari	10.4
		Cepaea nemoralis	8.8

Correlation with urbanization

In general, taxa richness varies with urbanization (Fig. 3), and there is an overall tendency for a decrease with the increase in impervious area in the surroundings. For example, site 2 (Vale das Flores), had the second lowest richness (37 taxa) and the largest impervious area (74%), and site 8 (Covões) had the smallest impervious area (3%), and the highest richness (78 taxa). An overall trend of inverse proportionality with impervious surface is supported by plant richness (Fig. 3b), whereas terrestrial invertebrate richness does not follow this pattern (Fig. 3c). Significant negative Pearson correlations ($p \leq 0.05$) between the percentage of impervious surfaces and taxa richness confirmed this trend for both groups together (Pearson r = -0.47), plants (r = -0.42) and specifically riparian plants (r = -0.73). The richness of terrestrial invertebrates was not correlated with urbanization.

In the Principal Components Analysis based on water chemical and physical parameters of the study sites, the two first axes accounted for 82% of variation among sites (PC1 = 49%, PC2 = 33%). The resulting loading plot (Fig. 4) and scores (Supplementary Information Table S5) showed that sites 2 and 3 are segregated from the remaining

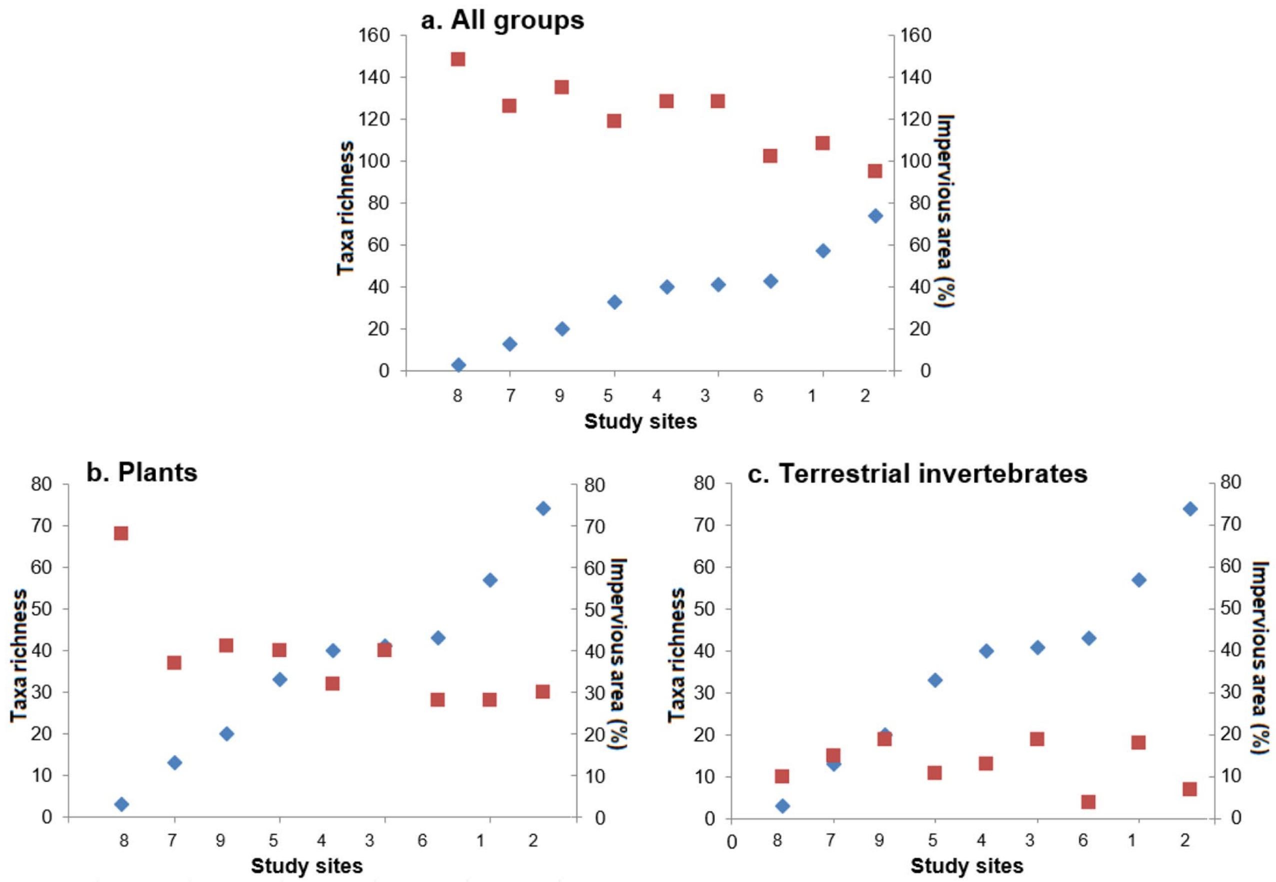

Fig. 3 Variation of taxa richness (red squares) values along an urbanization gradient (percentage of impervious area: blue diamonds) obtained by ordering sites by ascending percentage of impervious surface. **(a)** All groups, **(b)** Plants, **(c)** Terrestrial invertebrates

over PC1 due to higher concentrations of nutrients. PC2 segregated sites 1 and 6 due to a higher conductivity and total dissolved solids concentration.

There were significant correlations between PC2 scores and total richness ($r = 0.69$) and plant richness ($r = 0.70$), and with the richness of underrepresented plants ($r = 0.70$), and between PC1 scores and the percentage of riparian plants (r = -0.68). No significant correlation was obtained with terrestrial invertebrates.

According to the BIO-ENV analysis (correlation coefficient < 0.45, Table 6), the urbanization variables that had a stronger correlation with β-diversity were concentration of nitrate and nitrite, conductivity, total dissolved solids and percentage of impervious surface.

Discussion

Our study showed that urban streams and their riparian areas can hold a rich biodiversity, including endemic plant species, but also many non-native species, in this case representing 13% of the total richness. We also observed a clear negative association between the richness and distribution of plants and the degree of urbanization, given by the percentage of impervious surfaces and the water physico-chemical quality. This agrees with other studies on the effect of urbanization on biodiversity (White and Greer 2006; Zúñiga-Sarango et al. 2020), showing that lower levels of urbanization and better water quality result in higher richness.

The β-diversity of the study area also revealed great variation among urban streams. One hundred and fifty-five taxa, corresponding to 64% of all taxa found in the study, were observed only in one site and are thus considered underrepresented in the universe of streams studied. From these 88% native, 12% non-native, and 2% invasive taxa. Although these results suffer from a small sample size, they raise two important concerns: (1) urbanization could ultimately lead to the extinction of many taxa in a region; and (2) non-native taxa appearing in just one site could be used as an early warning for the beginning of an invasion process. In both cases, measures should be taken to prevent the disappearance of a species in a region and the spreading of non-native species to adjacent streams. For example, two endemic plant species present in the study area (*A. linkianum* and *S.*

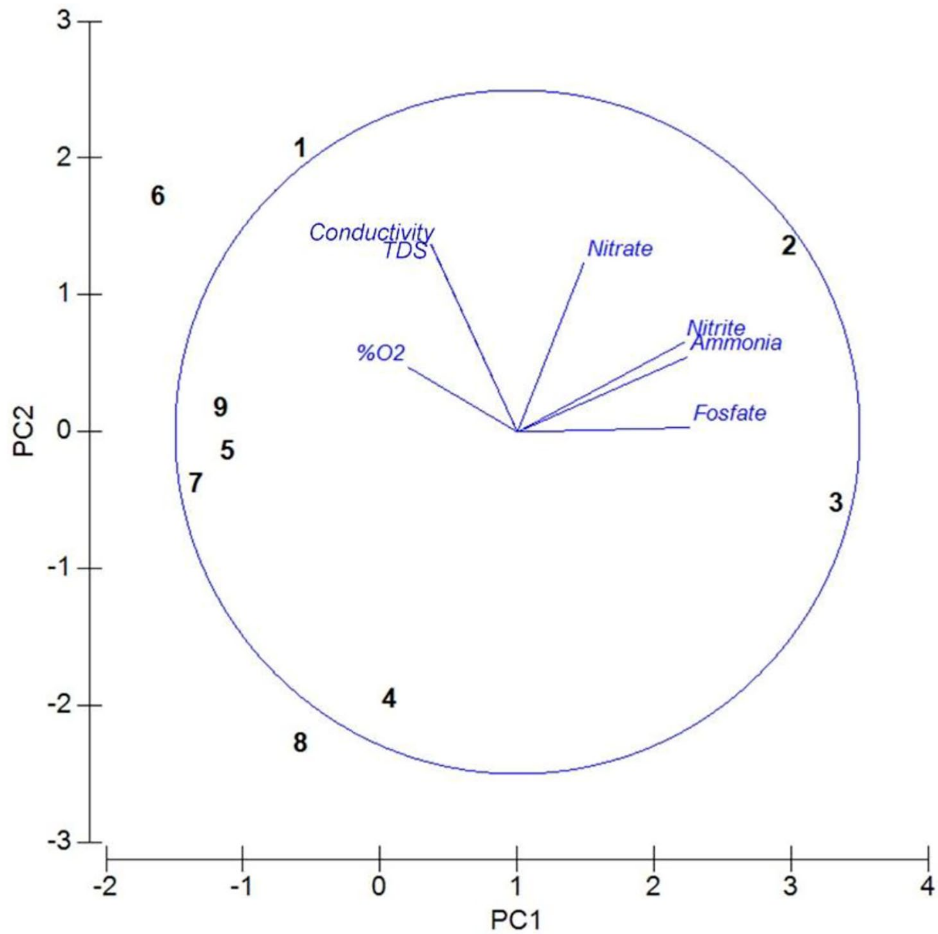

Fig. 4 Principal Component Analysis (PCA) plot obtained for physical and chemical variables of water (transformed by log (x + 1) and normalised) of all study sites

Table 6 Results of the BEST analysis (Bio-Env) correlating β-diversity with the measures of urbanization used: concentration of nitrate and nitrite (mg/L), conductivity (μS/cm), total dissolved solids (TDS; mg/L) and impervious surface areas (IS; %)

Number of variables	Correlation coefficient	Variables
3	0.500	Conductivity, TDS, IS
2	0.499	Conductivity, IS
2	0.499	TDS, IS
4	0.471	Nitrate, conductivity, TDS, IS
4	0.460	Nitrite, conductivity, TDS, IS

grandiflora) were only found in one site each and are considered "uncommon" and "rare", respectively, by the Red List of Vascular Plants of Continental Portugal (*flora-on.pt*). Furthermore, we found 32 taxa exclusively at one site (Covões). This calls for the special protection of these urban ecosystems that host rare species (Dana et al. 2002; Nilon 2011; Sander and McCurdy 2021). The establishment of urban reserves, which forbid further occupation in particular areas and provide guidelines for their conservation, is one potential means of protection. This type of protected areas already exists in some countries and cities, such as Plovdiv in Bulgaria or in Hong Kong (Mollov 2005; Ng et al. 2018), however, they frequently only focus on terrestrial systems, particularly plants. Lotic ecosystems present additional challenges, as anthropogenic activities upstream can have considerable impacts on biodiversity (but see Caro-Borrero et al. 2021).

In our study, one site (site 8, Covões) stood out with the highest global richness (78 different taxa). This was probably because of the rich riparian vegetation, which included tall alders, oaks and willows, despite the surrounding areas being affected by eucalyptus plantations and urbanization (Ferreira et al. 2015). Other studies have also shown that the plant richness can be at its highest in places with an intermediate level of urbanization for several possible reasons: species can be introduced to new environments through cities; moderate human disturbance can provide new conditions that facilitate the proliferation of a wider variety of plants;

and numerous plants are able to survive in small areas allowing them to benefit from the heterogeneous patchwork of habitats that urbanization-related land uses provide (McKinney 2008; Shwartz et al. 2014). On the other hand, site 1 (Exploratório) showed the lowest plant richness (only 28 taxa) but also a distinct community of spiders, with three abundant species. This stream is the smallest under study, and even though it appears more natural at first glance as it is within an urban park, it is also highly modified. Most of the stream's length is taken up by city infrastructure, and the park which was constructed about ten years ago, added new species in the margins and extensive lawns to the surrounding area. Similarly, the poorest site in terms of total richness (site 6, Casa do Sal, $N=31$) and one of the sites with the highest number of non-native taxa ($N=10$) is located inside a small urban park and surrounded by lawns. In both cases these sites have intermediate levels of impervious surfaces (43–57%) and nutrients. This shows that created green and blue areas within cities do not necessarily contribute to the preservation of biodiversity, as shown by other authors (Robinson and Lundholm 2012; Smith et al. 2015; Ge et al. 2019). The reason is these "created ecosystems" did not take into consideration the natural structure of the ecosystems nor the conditions to host all biological elements, as well as the maintenance of ecosystem processes (Smith et al. 2006).

Plants in the urban streams

Regarding the woody plants, species observed in the study area match other Portuguese riparian ecosystems (Aguiar and Ferreira 2005) and some of the species registered in other Mediterranean streams (Stella et al. 2013). However, there is only about 16–29% overlap between the reference lists of Central Portugal for riparian species (Aguiar et al. 2019; Ranta et al. 2021) and the full list of plant taxa identified in this study. This indicates that most taxa listed were not observed, and most taxa observed here were not listed. This is relevant considering that a large inventory of freshwater plants was made for the assessment of the ecological condition of rivers in the region. This disparity is also partially explained by the high number of non-native plant species found in our streams (29 taxa).

In addition, the presence of nine invasive species as significant elements of the urban flora associated to these streams is also relevant, as these species can have considerable impact on the ecosystems (Rahel 2002; Havel et al. 2015; Alonso et al. 2019). The ability of rivers and streams to function as corridors for circulation and dispersion of plants aids in invasive species' spread across these ecosystems. The fact that the water flows through cities exposes it to species introduced by humans, and fluctuations in water level create new spaces for colonization (Richardson et al. 2007). This aligns with what was observed in the sites closest to residential areas, where some plant species introduced by humans became part of the riparian vegetation, such as *Eriobotrya japonica*, *Ipomoea indica*, *Rosa* spp. and *Solanum* spp. An invasive *Oxalis pes-caprae* was observed at most sites except three, contributing to homogeneization of the flora across the study area. The species, originating in South Africa and currently present across Portugal, spreads easily due to the vast swaths it creates eventually becoming one of the dominant species (*invasoras.pt*). On the other hand, fruit-eating birds aid in the spread of *Phytolacca americana*, suggesting that, as other authors have pointed out, the bird fauna may be contributing to this species' invasion of urban streams (Stella et al. 2013). *Acacia dealbata* was also registered in the riparian corridors and is particularly relevant due to how successfuly it has spread. Introduced in Portugal as an ornamental plant (Lorenzo et al. 2010), it is notably problematic as an invasive species, partly due to how efficiently it attracts pollinators (Correia et al. 2014). The proliferation of this species, that is functionally different from native ones, affects the chemical cycles of an ecosystem and ultimately changes trophic chains (Ferreira et al. 2021). Finally, the reed *Arundo donax* was also registered in most sites and is known to spread partly through fragments that float down streams, making this another invasion closely associated with lotic ecosystems and dependent on the streams to persist (Lambert et al. 2010). The poor management of streams in urban areas, with frequent cuts that leave fragments of the reeds inside water, facilitates this process.

Indeed, a factor that can influence the diversity of riparian plant species and the number of non-native and invasive species is the management of the urban streams (Jones and Leather 2013; Jakobsson et al. 2018; Perry et al. 2020). In site 1 (Exploratório), the cutting of tree branches populated by a damaging pest eliminated a species but contributed to the health of these trees, while in site 5 (Hospital), the drastic pruning observed rendered the plants unable to support invertebrates or nesting birds (Jones and Leather 2013). Because less intense human intervention on riparian vegetation has been shown to result in increased biodiversity, this human intervention on riparian vegetation must be carefully considered (Robinson and Lundholm 2012; Watson et al. 2020).

In terms of life forms in the study area, most of the sites were dominated by herbaceous species (hemicryptophytes) along with annual plants that die after they reproduce, surviving unfavourable conditions like winter or drought in the form of seeds (therophytes). This can be explained by the type of climate of the region - Mediterranean, with dry and hot summers (Sotomayor 1988). Therophytes have also been associated with highly disturbed and urbanized sites

(Muzafar et al. 2019), which is the case of sites 2 and 1 (Vale das Flores and Exploratório, respectively). Nevertheless, they were the most represented group in site 9 (Fornos), one of the least urbanized. Our results warrant deeper studies that consider in depth the abundance of each species and life form and can potentially bring a valuable perspective to further analyses of the effects of urbanization (Bloch-Petersen et al. 2006).

Finally, the water physio-chemical quality of the streams was correlated to the total richness and plant taxa richness. This confirms that water characteristics in streams can impact both aquatic and terrestrial biodiversity (Schindler et al. 2016; Serra et al. 2019a). According to research, urbanization-related changes in soil chemistry can have an impact on weed density and taxonomic in riparian zones, as well as the ability of the riparian fauna to provide ecosystem services (Hogan and Walbridge 2007; Grella et al. 2018). The distribution of riparian plant species can be affected by a multitude of factors from the nutrients in the water and the speed of currents to the type of soil and how it retains humidity (Aguiar et al. 2019). Indirect effects of changes in water chemistry on terrestrial taxa can also include, for example, alterations to the aquatic invertebrates-based diets of land animals (Kelly et al. 2019). Additionally, urbanization leads to changes in water and soil chemistry over time, making riparian biodiversity a product of both past and present-day conditions (Harding et al. 1998; Preston et al. 2003). As such, the taxa observed may be influenced by the history of changes within the land use and water chemistry parameters that were not analyzed.

Terrestrial invertebrates in the urban streams

Within terrestrial invertebrates the most common, besides the unidentified Acari species, were the leafhopper *Cicadella viridis* and the snail *Cepea nemoralis*, that are known as ubiquitous and abundant taxa in urban, peri-urban and pristine habitats (Ożgo 2011; Wang et al. 2019). The butterfly *Pararge aegeria*, known to easily adapt to urbanization (Kaiser et al. 2016) was observed in all sites except the least urbanized ones, which could indicate a preference for more disturbed sites or a reason for lower abundance in more pristine ones (Máthé and Batáry 2015). On the other hand, some taxa like the beetle *Chrysomela populi* were observed in our study only at the least urbanized sites thus being a potential indicator of ecological integrity of ecosystems (Gerlach et al. 2013). This beetle and the honeybee (*Apis mellifera*) were the main species responsible for similarities in terrestrial invertebrate assemblages of the least urbanized sites, also suggesting a vulnerability of *A. mellifera*, an extremely important generalist pollinator, to the effects of urbanization (Hung et al. 2018; Burdine and McCluney 2019).

Among arthropods, the diversity of spiders found in our sites ($N=10$) was lower than the number of spider species previously suggested in the city of Coimbra (Branco et al. 2019 registering 317 in the province as a whole), which may be explained by different sampling methods. *Linyphia hortensis* and *Araneus diadematus*, found in sites 1 and 2, respectively, are common in urban areas, albeit with altered habits within cities (Nagy et al. 2018; Dahirel et al. 2019). *Pisaura mirabilis*, one of the species observed in site 1 (Exploratório), is a generalist species, non-sensitive to moderately sensitive to disturbances (Tajthi et al. 2017; Nagy et al. 2018). *Zygiella x-notata* on the other hand, seen in site 2 (Vale das Flores), the most urbanized site, is very tolerant to disturbances (Kralj-Fišer et al. 2017), which is in agreement with the local conditions. Indeed, the conditions within cities can bring a multitude of factors that can affect species distribution such as prey availability, city infrastructure increasing or decreasing spaces for spinning webs or building burrows, and the presence of artificial light (Dahirel et al. 2019; Kolenda et al. 2021). In the specific case of streams, flow regulation and water pollution can lead to a decrease in substrate availability for web-spinning spiders and severe changes to their feeding habits, as the aquatic insects that are more tolerant to pollution constitute low quality food for these spiders (Sanchez-Ruiz et al. 2017). Observations in this study point to the presence of complex spider assemblages in the study area that are affected by urbanization in both direct and undirect ways that suggest paths for further investigation.

Overall, we found many terrestrial invertebrate species ($N=62$) considered underrepresented. This would require further indepth studies for this group, including more standardized and quantitative sampling efforts. However, it again indicates that there are very different terrestrial conditions associated to the margins of streams within a city. This is not unexpected, considering the wide variety of conditions and uses of the margins of streams that we observed as consequence of the urbanization process: from roads, sidewalks, cycle paths and buildings immediately constructed in the margins of some streams, to agricultural fields, urban orchards or grass lawns, banks occupied by invasive reeds such as the *Arundo donax* (and other herbaceous plants), or even strips of integrous and complex riparian vegetation. This variety of conditions leads to a wide diversity of habitats and different soil compositions, thus constraining the terrestrial invertebrates and other fauna.

Regarding the invasive terrestrial invertebrate species, only one was detected, i.e. *Vespa velutina*. This species is native to China and its presence is considered a danger to humans (Choi 2021). It was first detected in mainland Portugal in 2011 and has since expanded rapidly with no signs of halting, posing a threat to native bees. River valleys may function as corridors for this expansion (Carvalho et al. 2020; Laurino et al. 2020; Paixão et al. 2021).

Other invertebrate species registered in three sites have the potential to act as pests: *Lauritrioza alacris* infesting *Laurus nobilis* trees in sites 1 and 7 (Exploratório and S. Romão, respectively), and *Trioza erytreae* infesting a *Citrus* x *sinensis* tree in site 6 (Casa do Sal), both known hosts for these species (*gd.eppo.int*). While *L. alacris* is native to the Mediterranean region (Mifsud 2020), *T. erytreae* originates from northeast Africa and has been present in Portugal since at least 2015, posing a threat to citrus due to its ability to be a vector for the bacteria *Liberibacter* spp., which causes a serious disease in these plants (Cocuzza et al. 2017). Another notable case of parasitic associations between species was the occurrence of *Cynips tozae* galls in a *Quercus robur* tree in site 8 (Covões). The hemipteran *Eurydema ornata* (Linnaeus, 1758) was observed in site 3 (Coimbra-B) and it is known to associate with plants of the Brassicaceae family (*gd.eppo.int*), which are present in this site, but this association was not observed.

Instances of pollination by insects were recorded as well, albeit decreasing along the urbanization gradient. Matching the literature, the generalist pollinator *Apis mellifera* (Hung et al. 2018) was observed on the widest variety of plant taxa, and the plant of known generalist character *Torilis arvensis* (Gibson et al. 2006) presented the widest variety of pollinators. Generalist plants are important for ecosystem-wide plant-pollinator interactions as they lure in a variety of pollinator insects that counter the effects of urbanization and habitat fragmentation (Ashworth et al. 2004; Biella et al. 2019; Wenzel et al. 2020). The observations made in the study area suggest potential for further studies in this field.

Our study reveals the impacts of urbanization on the terrestrial realm of lotic ecosystems that has been vastly overlooked despite their importance for biodiversity conservation and as providers of numerous ecosystem services to the population of cities. From the management perspective, our study highlights the need to rethink city planning to consider all the requirements of stream ecosystems, including the different biological terrestrial elements and the links among them, as changes to one part ultimately impact the whole, as shown by others (Faeth et al. 2011; Feio et al. 2017; Rivaes et al. 2021). Monitoring and control measures should be undertaken to preserve the native biodiversity of urban streams and assure that they are not a vehicle for the dissemination of invasive species. The management of riparian corridors should be the least interventive possible to preserve the integrity of the ecosystems and thus the habitats for different biological groups of species. Measures towards the transference of relevant and practical information on the adequate management of these streams to the city decision makers are thus essential. It is also important to raise awareness of populations to prevent the emergence of new invasions.

Our study also indicates that beside impervious surfaces, urban parks, although usually considered natural areas within cities, may not preserve the regional pool of biodiversity due to a high degree of human intervention, for example, grass lawns, sidewalks, paved accesses, children's playgrounds, or sports infrastructures and extensive pruning of vegetation. On the other hand, well-preserved urban nature should also promote the interconnectivity between fragmented natural areas, increasing global biodiversity and consequently the performance of ecosystem services (Shwartz et al. 2014).

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Data availability Data used in this study is available on demand through a written request directly to the authors.

Declarations

Ethics approval Not applicable. Plants and invertebrates are not subject of ethical approval.

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