



City as a filter: urban density affects taxonomic and functional diversity of foliage dwelling spiders

Anna Piquet · Elena Piano · Marco Tolve ·
Marco Isaia

Received: 6 August 2024 / Accepted: 24 November 2024
© The Author(s) 2024

Abstract

Context Urbanization affects landscape structure, functions and local environmental conditions, with major impacts on biodiversity. An evaluation of its effects on biodiversity, including both taxonomic and functional diversity, is thus compelling, with a specific focus on taxonomic groups providing fundamental ecosystem services. Spiders are ideal biological models for urban ecology studies because they are renowned bioindicators and can be found abundantly along urbanization gradients.

Objectives In this work, we aim at evaluating the filtering role exerted by urbanization at landscape

scale on foliage-dwelling spider communities both at functional and taxonomic level.

Methods We assessed the response of foliage-dwelling spiders to urbanization in Torino (NW-Italy), by sampling their communities in urban parks along an urbanization gradient and in a control area located in a nearby natural park. We tested their response in terms of taxonomic and functional diversity to urban density and six landscape metrics. Results of statistical models (GLMMs) were used to predict values of the current biodiversity in the city and its values under different future scenarios of urbanization (i.e. 2040, 2050).

Results Spider abundance and species richness decreased in the city compared to the control area and along the urbanization gradient. Variation in the community composition was mostly due to species replacement (67%) within the control area, and to species loss in the urban area (62%). This pattern was mostly due to the loss of specialized foraging guilds, such as pollinator-feeding spiders. Functional dissimilarity among samples within the urban area was mostly explained by functional loss (69%), suggesting an environmental filter favoring species preadapted to urban conditions. By projecting biodiversity measures in two “greener city” scenarios, we identified 8 priority areas in the city where management actions should be implemented.

Conclusions Our findings underscore the role of urbanization in shaping spider communities, favoring generalist species and specific functional traits.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10980-024-02019-3>.

A. Piquet · E. Piano (✉) · M. Tolve · M. Isaia
Department of Life Sciences and Systems Biology,
University of Torino, via Accademia Albertina 13,
10123 Turin, Italy
e-mail: elena.piano@unito.it

A. Piquet
e-mail: anna.piquet@unito.it

M. Tolve
e-mail: marco.tolve@unito.it

M. Isaia
e-mail: marco.isaia@unito.it

A. Piquet · E. Piano · M. Isaia
National Biodiversity Future Center, Piazza Marina 61,
90133 Palermo, Italy

The prediction on future scenarios proved to be useful to identify areas where increasing the surface of urban parks may contribute most effectively to spider biodiversity.

Keywords Urban ecology · Spiders biodiversity · Biotic homogenization · Arthropods · Land use · Urban planning

Introduction

The process of urbanization has major environmental effects on biodiversity and related ecosystem services, acting simultaneously on the landscape and the local scale. At the landscape scale, the extensive cover of impervious surfaces is responsible for loss and fragmentation of natural and semi-natural habitats, which translates in the creation isolated small patches of residual habitat (Fenoglio et al. 2021; Chatelain et al. 2023).

At the same time, at the local scale residual patches may undergo extreme physical and chemical changes, e.g. temperature increase, alteration of soil nutrient cycling and gas exchange, soil trampling creating a cascade of ecological perturbations such as the facilitation of the invasion of alien species, changes in species abundance or resources availability. In addition, stochastic events, such as habitat destruction by human activity, anthropogenic transportation or the introduction of exotic species, seem more important in urban areas than in other habitat types (Parris 2016). Species communities in urban areas are thus far from equilibrium and undergo constant change in adapting to the disturbances and changes that characterize their urban environments (Sattler et al. 2010b).

From an ecological perspective, environmental changes and habitat fragmentation simultaneously act as strong environmental filters on biotic communities by ultimately determining the species composition within urban residual patches (Concepción et al. 2015; Brice et al. 2016; Piano et al. 2020b). On the one hand, species composition in urban residual patches is ruled by the mechanisms explained by the theory of island biogeography (MacArthur and Wilson 1967). More in detail, patches of isolated habitat located far from the source patch, show lower species richness. These patches are more likely to be colonized by good dispersers (see Piano et al.

2017 for an example in ground beetles and Merckx and Van Dyck 2019 for lepidopterans), likely resulting in a combination of a specific subset of highly dispersive species. Abiotic constraints due to isolation also prevent the installation of sensitive species, filtering those who are able to cope with the local environmental conditions, in accordance with the habitat templet theory (Southwood 1977, 1988). Considering this, urban patches are expected to have, on average, less diverse communities than (semi-)natural ones due to the depletion of species displaying maladaptive traits, e.g. low dispersive, specialist species (e.g. Merckx et al. 2018; Piano et al. 2020a; Ancillotto and Labadessa 2023). At the same time, urbanization may cause species turnover with respect to natural areas due to substitution of sensitive taxa by species displaying higher urban affinity, e.g. highly dispersive, generalist species (e.g. Melliger et al. 2017; Argañaraz et al. 2018; Callaghan et al. 2021, 2023).

Although urbanization is expected to negatively affect biotic communities, studies investigating the effect of urbanization on the abundance and/or species diversity report controversial results, displaying either positive or negative relationships depending on the considered taxa (e.g. Faeth et al. 2011; Jones and Leather 2012; Fattorini 2014; Turrini and Knop 2015; Saari et al. 2016; Lagucki et al. 2017; Fenoglio et al. 2020; Piano et al. 2020b, c; Svenningsen et al. 2022). These outcomes underlie the need of integrating species richness and abundance patterns with information on functional traits. In particular, embracing a functional approach represents an effective way to move forward research on ecological communities (Chase et al. 2018; McGill et al. 2006). Traits are morphological or physiological attributes or aspects of the realized niche measured at the species level, considering “functional” any trait which impacts fitness indirectly via its effects on growth, reproduction and survival (Violle et al. 2007; Webb et al. 2010), depicting a species adaptation to the environment (Menezes et al. 2010)—e.g. dispersal capacity, body length, feeding strategy, thermal tolerance, voltinism, etc. Simultaneously exploring changes in species diversity and shifts in their functional profile could therefore shed light on the main selective forces acting on urban communities, also providing highlights on possible repercussions on ecosystem functionality (Hooper et al. 2005; Cardinale et al. 2012).

The functional approach has already been successfully applied to several iconic taxa in urban ecology, e.g. birds, butterflies, and plants (e.g. McIntyre, 2000; Beninde et al. 2015; Concepción et al. 2015; Collins et al. 2021; Zeng et al. 2024). Literature evidence from these groups provides much more consistent results, demonstrating that generalist and flexible ecological traits, combined with good dispersal capacity, are better suited to survive in urban areas, whereas low-dispersive, highly specialist species are disadvantaged (e.g. Callaghan et al. 2021, 2023). On the other hand, studies describing trait selections for other groups of high potential interest in ecological studies are more scattered, hampering a proper evaluation of the role of the environmental filter exerted by urbanization. For instance, despite representing key organisms in trophic food webs, being responsible for both top-down and bottom-up regulation (Bruggisser et al. 2012), spider communities are poorly represented in urban ecology studies. The few works on the topic confirm the great potential of applying a functional approach to ground-dwelling spiders (Piano et al. 2020a, c; Bazzato et al. 2022; Cabon et al. 2024; Arganaraz et al. 2023; Dampney et al. 2023), while studies on the foliage-dwelling counterpart remain scant (but see Dahirel et al. 2017; Argañaraz et al. 2018).

To fill this knowledge gap, we here examined the taxonomic and functional response of foliage-dwelling spider communities to urbanization. Foliage-dwelling spiders display different dispersal capacity, i.e. they can disperse better than their ground counterpart, and they occupy a different ecological niche, i.e. they are strongly influenced by the vegetation structure (de Souza and Martins 2005). Being able to reach the most suitable habitats via highly efficient dispersion methods, i.e. ballooning (Bell et al. 2005; Blandenier, 2009), they are expected to be exposed to different selective pressures compared to ground-dwelling spiders, with a strong selection on traits related to the ecological niche occupation, even if the high stochasticity of urban areas (Parris 2016) may act as a confounding effect on this selection process. In this work, we combined a taxonomic and functional analysis to discriminate the role of selective processes acting on the assemblages of foliage-dwelling spiders in the urban landscape. To achieve this aim, we tested the taxonomic and functional response of spider communities at two scales of analysis by: (i) comparing their

assemblages between the city of Torino (NW-Italy) and a control peri-urban natural park; and (ii) examining their response in urban parks distributed along an urbanization gradient within the city of Torino. Specifically, we expected that (i) urban foliage-dwelling spider assemblages represent a subset in respect to the ones found in the control area, and that (ii) functional and taxonomic diversity of foliage dwelling spiders progressively decrease within the city in relation to the level of urbanization.

Materials and methods

Sampling design

This study was conducted in the metropolitan area of Torino (NW-Italy, approximately 900,000 inhabitants), within 15 km of the city center. The altitude ranges between 220 and 280 m a.s.l. and, according to Köppen's classification of climates, Turin belongs to the Cfa band (humid temperate climate of the mid-latitudes with hot summers).

We selected a total of 32 sampling sites, among which 21 are located in 9 urban parks and 11 in the nearby control area of the Natural Park of La Mandria (Fig. 1; Table S1), a protected natural area extending in the outskirts of the city for approximately 3000 hectares (Tolve et al. 2024). All urban parks are managed by the same municipality, so we could reasonably assume that local management variations are negligible.

We adopted a hierarchically nested sampling design, as the study area comprehends different urban parks, each containing multiple sampling sites (roughly logarithmically proportional to the park area) and, at each sampling site, we performed three sampling replicates (Fig. 1). For each sampling site, we defined a buffer of radius 1 km centered on the sampling site. This radius was selected to allow us a better representation of the landscape characteristics around each sampling site. Within this buffer, we calculated a proxy of urbanization, defined as urban density, by extracting the percentage of built-up area (sensu Elvidge et al. 2007), which is highly representative of other variables, such as UHI (i.e. Piano et al. 2020a; Cabon et al. 2024) (Fig. 2) using the QGIS software (QGIS.org, 2023).

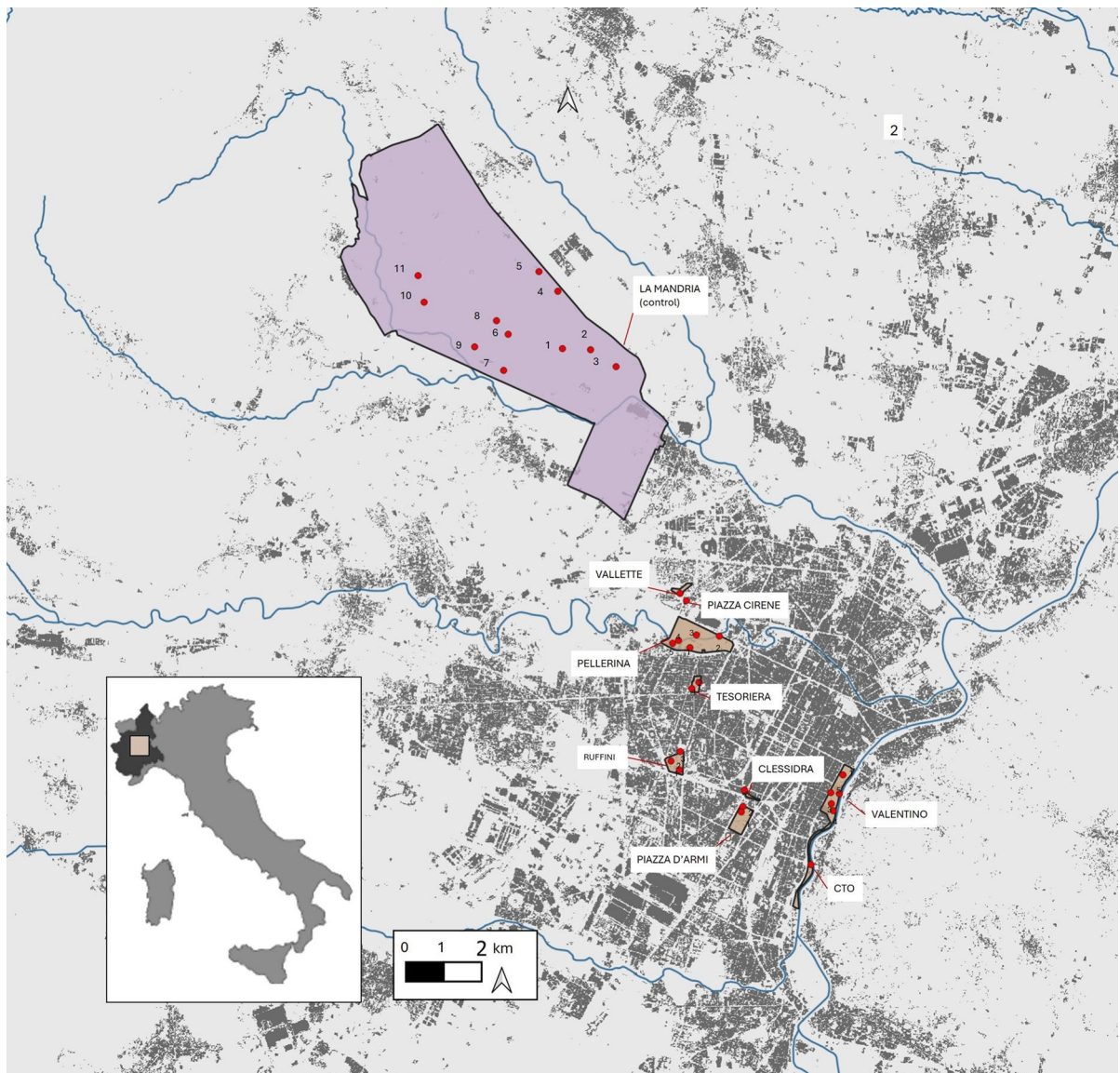


Fig. 1 Map representing the study area with sampling sites (red dots) within each urban park (within the city, in brown) and in the control natural Park of La Mandria (largest polygon upper-left, in violet)

To obtain this value, we used the layer for the reference year 2018, which shows the binary information of buildings (class 1) and no buildings (class 0) within the sealing outline derived from the Imperviousness Density layer for the period 2018 for the EEA38 countries and the United Kingdom (<https://doi.org/https://doi.org/10.2909/3e412def-a4e6-4413-98bb-42b571afd15e>). The level of urbanization (%Urb) ranged from 0.0 to 6.0% with an average value of 1.10% in the control area, and from 23.0

to 67.0% with an average of 43.3% within the city, therefore covering a wide gradient of urbanization. In parallel, within these buffers, we calculated six landscape fragmentation metrics reported in Jaeger (2000) by using the Fragscape plugin (INRAE 2021) in QGIS (QGIS.org, 2023) i.e. effective mesh size, degree of landscape division, splitting index, degree of coherence, splitting density, net product. Given that all urban parks are managed by the same municipality, we could reasonably assume that local management

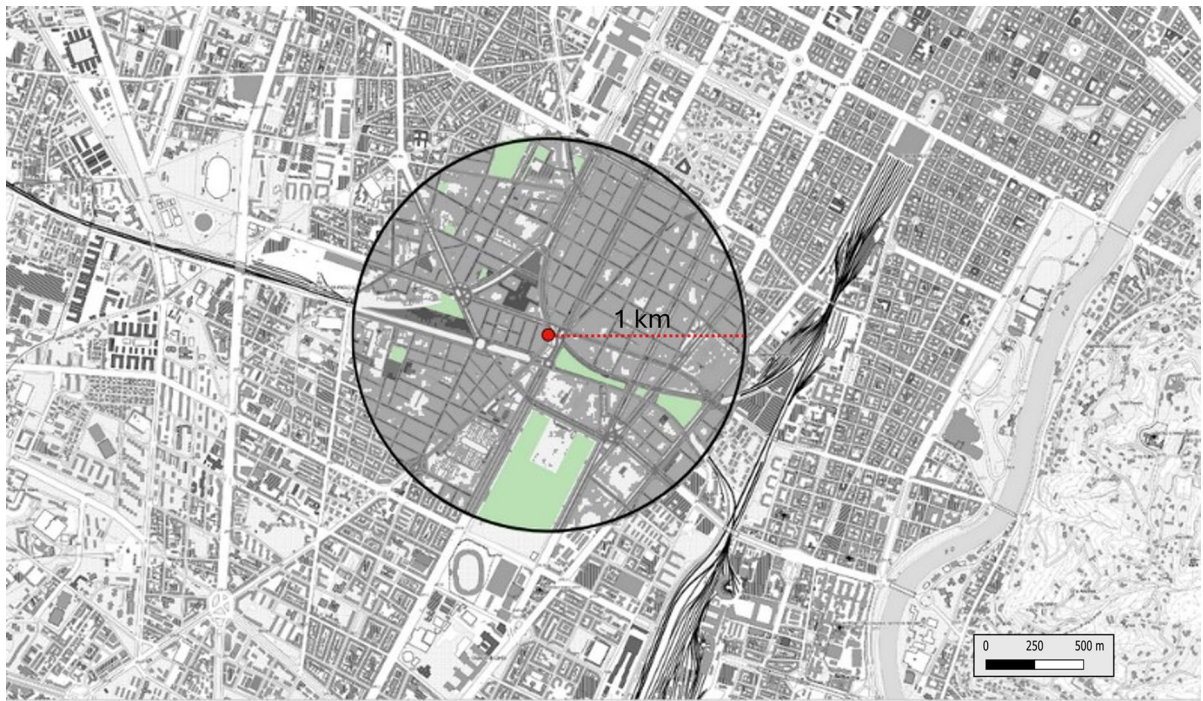


Fig. 2 Map showing one of the sampling plots (red dot) with a 1 km buffer. Inside the buffer, non-impervious surfaces are represented in green and the built up areas are represented in gray

variations are negligible and observed differences among sampling sites are due to landscape changes.

Data collection and species identification

Within each sampling site, we sampled spiders using a beating tray on shrubs and the low branches of trees. A beating tray consists of a white coloured cloth stretched out using a frame that is held under a tree or shrub while the foliage is shaken or beaten with a stick. Spiders were placed into vials containing 70% ethanol and carried to the laboratory for identification.

In each site we performed 3 replicates. The sampling was performed in two sampling seasons, namely autumn 2022, and spring 2023. Spiders were identified at species level using the online identification keys of Spiders of Europe (Nentwig et al. 2023). We built the spider database including both adult spiders and juveniles that could be morphologically identified at the species level. Although in studies on spider biodiversity juveniles are commonly excluded due to identification

challenges (e.g. Jerardino et al. 1991; Toti et al. 2000; Sørensen et al. 2002), as acknowledged by Coddington et al. (1996) and Dobyns (1997) the incorporation of juvenile specimens appears to be essential for obtaining accurate short-term sampling estimates of overall species richness and composition throughout the entire year (Urones and Puerto 1988; Scharff et al. 2003; Jiménez-Valverde and Lobo 2006). More in detail, we incorporated juveniles for those species displaying a species-specific distinguishable, characteristic pattern (e.g. species belonging to the genus *Theridion* sensu lato), and those species unique for their genus in the study area (e.g. *Dolomedes fimbriatus*). When the identification of juveniles to the species level was not possible, we aggregated all individuals, both juveniles and adults belonging to the same genus (e.g. *Brigittea* spp. that includes individuals belonging to both *B. civica* and *B. vicina*). All juveniles that could not be identified at least to the genus level were excluded from further analyses. Nomenclature follows World Spider Catalog (2024).

Taxonomic and functional diversity

The response of spider communities to urbanization was measured in terms of both taxonomic and functional diversity. Regarding taxonomic diversity, we calculated the species richness and total abundance for each replicate using the 'alpha.estimate' function of the 'BAT' package (Cardoso et al. 2015) in R software, version 4.3.1 (R Core Team 2023) applied to the site x species matrix.

Regarding functional diversity, we grouped spiders into foraging guilds defined on the basis of hunting strategy. More in detail, we distinguished weaving spiders based on their web type, while hunting spiders were classified according to their hunting strategy following the classification proposed by Isaia et al. (2007) for the regional fauna (weaving spiders: simple web weavers; orbicular web weavers; irregular web weavers; dome web weavers; tridimensional web weavers; hunting spiders: diurnal hunters; ambush hunters; nocturnal hunters; specialized hunters). Based on this classification, we calculated the number of hunting strategies, i.e. foraging guilds within each community as a proxy of functional diversity. To gain more insight into the functional response, we specifically analyzed the response of pollinator-feeding spiders. More in detail, we assigned a value ranging from 0 to 2 based on their preference for pollinators (0 = not feeding on pollinators, 1 = feeding on pollinators and other prey, 2 = strictly feeding on pollinators; Table S3). This categorization was obtained on the basis of expert opinion. For each sample we assigned the diet specialization score to each individual and summed all the scores, resulting in an integer value for each sample ranging from 0 to 10. Other functional traits, i.e. body size and dispersal capacity, were also examined but subsequently excluded from our analysis due to low representativeness. Despite body size being generally available in literature for adults, we lack data for juveniles and their body size can be greatly variable, not just between juvenile and adults, but even within the same species. We could not therefore assign body size values to juveniles, which represented more than a half of the individuals of our communities, jeopardizing the possibility of studying body size variation along the urbanization gradient. Regarding dispersal capacity, our spider community was composed almost exclusively by species that are able to reach the most suitable habitats

via highly efficient dispersion methods, i.e. ballooning (Bell 2005; Blandenier, 2009), compromising the usefulness of examining the variation of the community dispersal capacity across the urbanization gradient.

Data analysis

All analyses were conducted using R software, version 4.3.1 (R Core Team 2023).

Before proceeding with model fitting, we performed data exploration following the protocol proposed by Zuur et al. (2010) to identify possible outliers and collinearity among covariates. Specifically we performed a correlation analysis by means of Pearson correlation test among the landscape fragmentation metrics and the urban density (Fig. S1).

The response of each taxonomic and functional variable to urbanization was tested by means of generalized linear mixed models (GLMMs), using the 'glmmTMB' package (Brooks et al. 2017). Mixed models were adopted to keep into account the nested spatial aggregation of replicates within each sampling site and within each urban park. Given the low number of levels, in accordance with Zuur et al. (2009) the sampling season was included as a fixed factor. For each dependent variable, we performed two different models. To assess if foliage-dwelling spiders in the urban area represent either a subset of the species that can be found in a source habitat (semi-natural area) or a new set of species, we compared values of taxonomical and functional diversity in the urban and the control area.

The final model had the following structure:

$$y \sim \text{sampling_area} + \text{Sampling Season} + (1|\text{Site/Urban Park})$$

where 'y' is the response variable, 'Sampling Season' is autumn or spring, 'sampling_area' is either the urban area or the control area. The random factor includes the ID of the sampling site ('Site') nested within the urban park ('Urban Park').

To assess if increasing urbanization either filters out maladaptive species or incorporates new species displaying adaptive traits, we tested the response of spider assemblage against the gradient of urban density and the six landscape fragmentation metrics. Given that all considered metrics were highly correlated among each other and with

the urban density (Pearson's $r > 0.61$, see Fig. S1), we could not include them together in our models due to multicollinearity, in accordance with the protocol provided by Zuur et al. (2009). We thus performed seven different models, one for each covariate (the six landscape fragmentation metrics and the urban density), for each dependent variable, and compared them with the function 'AICc' of the package MuMIn (Bartoń, 2022) to identify the best urbanization proxy (Fig. S2). The final model had the following structure:

$$y \sim \text{covariate} + \text{Sampling Season} + (1|\text{Site/Urban Park})$$

where 'y' is the response variable, 'Sampling Season' is autumn or spring, and 'covariate' represents urban density or one of the landscape fragmentation metrics that were considered in our study. The random factor includes the ID of the sampling site ('Site') nested within the urban park ('Urban Park').

Given the nature of our response variables, i.e. count data without negative values, we adopted either a Poisson residual distribution with log-link function, or a negative binomial residual distribution when our response variable displayed a high dispersion of residuals. Specifically, we used the Poisson distribution for modeling the response of species richness, pollinator-feeders abundance, and number of foraging guilds and the negative binomial distribution for modeling spider abundance. Notably, due to the high abundance of zeros, we used a zero-inflated Poisson model for the pollinator-feeders abundance. Model validation was performed by plotting residuals versus fitted values and versus covariates and the residuals were assessed for spatial dependency following the protocol proposed by Zuur and Ieno (2016).

To assess the processes underlying the observed patterns in taxonomic and functional diversity, we measured the pairwise taxonomic and functional dissimilarity (hereafter taxonomic and functional β -diversity) among communities in the control area and among communities in the urban area. We used the beta function of the 'BAT' package, applying the Sørensen dissimilarity index, that allowed us to examine the contribution of species replacement (hereafter turnover) and species loss (hereafter nestedness) to the overall β -diversity.

Biodiversity projections

Based on the assumption that increasing the urban park size would enhance spider biodiversity—as demonstrated by the negative correlation between urban density and park size (Pearson's $r = -0.85$, P value < 0.001)—we developed a specific methodology employing a 1×1 km grid as a spatial framework in QGIS (QGIS.org, 2023) to pinpoint specific areas where management interventions should be implemented in this sense. This grid was designed to include the whole municipality of Torino and the control area for a total of 420 cells (Fig. 3a). We assessed the current urbanization level within each grid cell by calculating zonal statistics on the urbanization raster layer used to calculate the urban density within buffers (<https://doi.org/https://doi.org/10.2909/3e412def-a4e6-4413-98bb-42b571afd15e>). From this analysis, we obtained a shapefile reporting a mean urbanization cover value for each square of the grid (Fig. 3b). The statistical models developed were then used to project biodiversity values under the present urbanization scenario. Given the similar results obtained for the four biotic parameters, we applied the coefficients derived from the model examining the response of species richness, which was considered as representative of the spider biodiversity, to the urbanization value of each grid cell. For this analysis, we focused on the autumn season coefficients, as species richness was observed to be higher in autumn compared to spring. From this analysis, we obtained a shapefile reporting an expected mean value of spider biodiversity for each square of the grid in the current urbanization scenario.

Subsequently, we filtered the grid cells to include only those squares with urban density values ranging between 20 and 50%, based on the hypothesis that increasing the extension of urban parks would necessitate a substantial area of non-impervious surfaces. This selection was further refined by intersecting these cells with a shapefile of existing urban parks in the city of Torino. This approach enabled the identification of 50 grid cells with adequate non-impervious surface areas adjacent to existing parks, which could be expanded (hereafter 'management cells'). For each of these cells, we projected the biodiversity values under two future urbanization scenarios, namely by reducing the percentage of impervious cover by

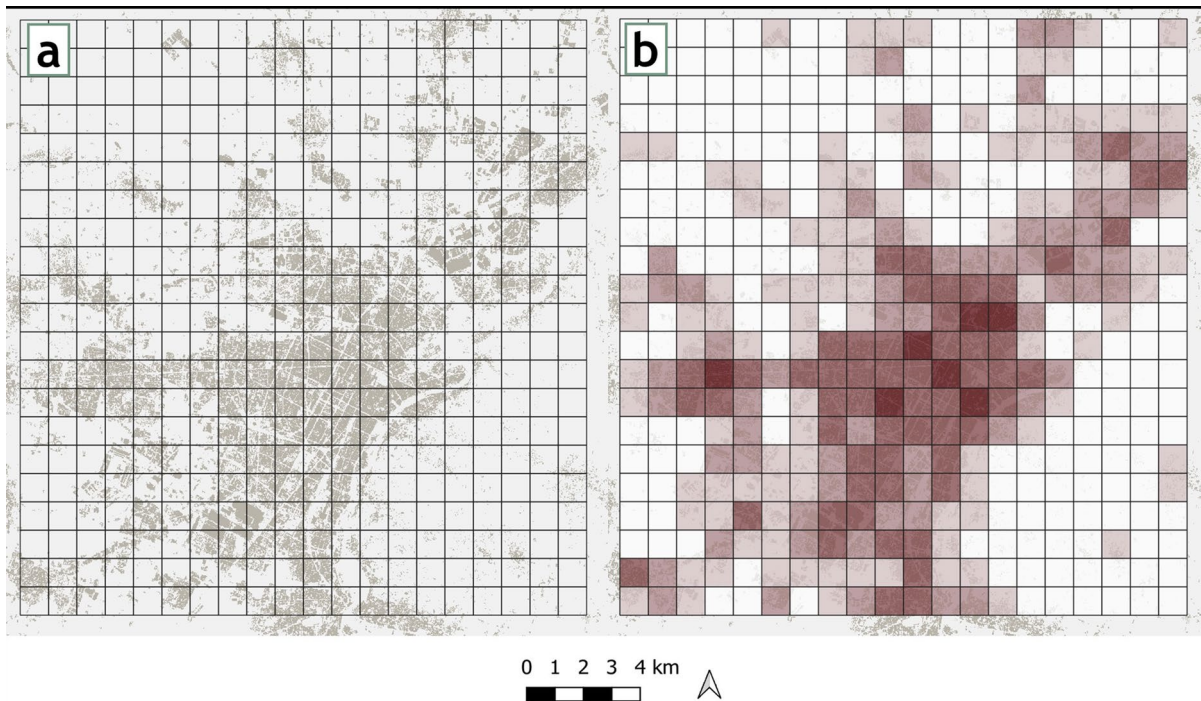


Fig. 3 Map showing the study area and the 420 cells grid cover (a); each cell is coloured according to its current urbanization level, with shades of red becoming darker at increasing urbanization density values (b)

3% (hereafter 3% scenario) and 5% (hereafter 5% scenario) in accordance with the indications of the European Biodiversity Strategy, which states an increase of urban green areas by 3% in 2040 and 5% in 2050. We then highlighted those cells where the biodiversity predicted values under the two urbanization scenarios were 2% higher than under the current scenario, which represent priority areas where management actions should be implemented (hereafter “priority cells”).

Results

We collected 2,564 spiders belonging to 101 species and to 18 families (Table S2). All families were present in the control area, while only 12 of them were collected within the city. Namely Gnaphosidae, Lycosidae, Oxyopidae, Pisauridae, Sparassidae, Uloboridae have not been found in urban context (Fig. 4).

Model results

Results of the model comparisons based on the AICc displayed that the urban density always performed better than the other landscape fragmentation metrics (Table S3; Fig. S2). We therefore report only the results obtained by testing the response of taxonomic and functional parameters against urban density.

Regarding the taxonomic response, model results displayed a significant decrease of spider abundance and species richness when comparing the urban with the control area and across the urbanization gradient within the city (Table 1; Fig. 5a, b). On average, we obtained 8.71 spiders/replicate and 4.14 species/replicate in the urban area and 14.82 spiders/replicate and 6.87 species/replicate in the control. Seasonality was never significant, except for the model comparing spider abundance in the urban vs. control (lower abundance in spring). Regarding the functional response, the number of foraging guilds and the abundance of pollinator feeding spiders significantly decreased both in the

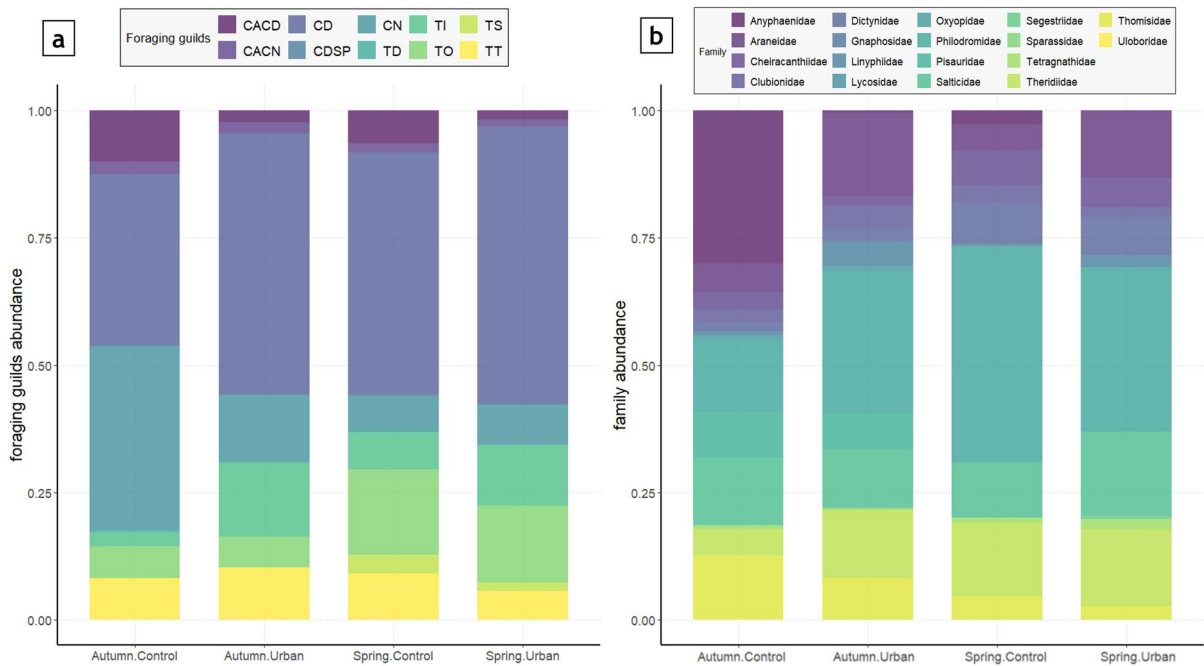


Fig. 4 Barplots representing the relative abundance of foraging guilds (a) and spider families (b) obtained from the urban and the control area in the two sampling seasons. Foraging guilds refer to the classification proposed by Isaia et al. (2007)

for the regional fauna (*TS* simple web weavers, *TO* orbicular web weavers, *TI* irregular web weavers, *TD* dome web weavers, *TT* tridimensional web weavers, *CD* diurnal hunters; *CA* ambush hunters; *CN* nocturnal hunters; *SP* specialized hunters)

contrast between urban and control areas and along the urbanization gradient (Table 1; Fig. 5c, d). The seasonality effect was not significant in both models for foraging guilds, while it was significant in both models for pollinators feeding species, with pollinator feeders being more present in autumn than spring.

The mean taxonomic β -diversity in the control area has a value of 0.761, of which 0.507 (67%) provided by the turnover component and 0.254 (33%) provided by the nestedness component. The mean taxonomic β -diversity in the urban area has a value of 0.768, of which 0.295 (38%) provided by the turnover component, and 0.473 (62%) provided by the nestedness component. When considering the functional β -diversity, we observed a mean value of 0.636 in the control area, with a value of 0.368 (58%) provided by the turnover component and a value of 0.267 (42%) provided by the nestedness component. The mean functional β -diversity in the urban area showed a value of 0.699, with a value of 0.218 (31%) provided by the turnover component, and a value of 0.482 (69%) provided by the nestedness component.

Biodiversity projections

The biodiversity projections under the current urbanization scenario (Fig. 6a) reported expected values of spider species richness ranging from 2 to 7, with 40% of the grid cells reporting the highest value, 19% with a diversity value of 6 species, 14% of cells reporting a value of 5 species, 11% of cells with a value of 4 species, 14% of cells with 3 species, and 2% of cells reporting the lowest value. When projecting biodiversity under the two future urbanization scenarios in the 50 cells where management actions should be implemented, we could highlight 8 priority cells under the 3% scenario (Fig. 6b), which become 42 priority cells under the 5% scenario (Fig. 6c).

Discussion

In this work we aimed at examining how urbanization affects the taxonomic and functional diversity of spiders by 1) comparing foliage dwelling assemblages in the urban and a control area and 2) testing variation

Table 1 Estimated parameters (Estimate), standard errors (Std. error) and *P* values referring to the effects of urban density in the comparison between the urban and the control area (left) and showing the response of each variable along the urbanization gradient (right)

Variables	Predictors	Estimate	Std. error	<i>z</i> value	<i>P</i> value
(A) Urban VS Control Area					
Abundance	sampling_area: Urban	− 0.585	0.112	− 5.23	< 0.001
	sampling_season: Spring	− 0.303	0.0778	− 3.90	< 0.001
Richness	sampling_area: Urban	− 0.471	0.0866	− 5.44	< 0.001
	sampling_season: Spring	− 0.0667	0.0659	− 1.01	0.312
Number of feeding guilds	sampling_area: Urban	− 0.291	0.0775	− 3.76	< 0.001
	sampling_season: Spring	− 0.0878	0.0792	− 1.11	0.267
Abundance of pollinator feeders	sampling_area: Urban	− 0.499	0.203	− 2.46	0.0141
	sampling_season: Spring	− 0.991	0.197	− 5.03	< 0.001
	Zero-infl model	− 1.31	0.438	− 2.99	0.00284
(B) Urbanization Gradient					
Abundance	%Urb	− 1.98	0.67	− 2.94	0.003
	sampling_season: Spring	− 0.30	0.12	− 2.44	0.015
Richness	%Urb	− 1.52	0.558	− 2.73	0.00641
	sampling_season: Spring	− 0.0205	0.0924	− 0.222	0.824
No. of feeding guilds	%Urb	− 1.30	0.471	− 2.76	0.00587
	sampling_season: Spring	− 0.096	0.112	− 0.853	0.393
Abundance of pollinator feeders	%Urb	− 3.32	1.12	− 2.95	0.00314
	sampling_season: Spring	− 1.34	0.368	− 3.64	< 0.001
	Zero-infl model	− 0.273	0.405	− 0.673	0.501

Significant values are highlighted in bold

along an urbanization gradient within the city of Torino.

Analysis on spider abundance revealed that urban samples host a lower number of individuals compared to the control area, and their abundance progressively declined along the urbanization gradient within the city. In parallel, our results showed that samples collected within the urban context are less species rich than those collected in the control, and species richness also significantly declined along the urbanization gradient. The significant decrease of species richness and abundance, observed here for the first time on foliage-dwelling spiders, confirms earlier findings obtained on ground-dwelling spiders in the same study area (Piano et al. 2020c), and is in line with what has been observed in other studies on spiders (Piano et al., 2020a, b; Bertellotti et al. 2023) and other arthropod groups (Christie et al. 2010; Norton et al. 2014; Philpott et al. 2014; Ootshi et al. 2015; Lagucki et al. 2017; Kyrö et al. 2018; Piano et al. 2020c; Fenoglio et al. 2021). Despite the current lack of agreement on how urbanization is expected

to affect the species richness and total abundance of individual organisms (see Magura et al. 2008, and Alarukka et al., 2002 for increase in individual abundance patterns), the harsh environmental conditions, along with the reduced connectivity and smaller size of semi-natural habitat patches, is expected to decrease spider abundance and richness in urban areas.

When analyzing the underlying processes determining this species decline, we demonstrated that this pattern is partially explained by the decrease of spider abundance (“More Individuals Hypothesis”, Srivastava and Lawton 1998) as demonstrated by the high correlation we observed among species richness and abundance (Pearson’s $r=0.75$; $p<0.001$). On the other hand, urbanization also acts as a species filter, such that only a limited set of species survives in the most urbanized settings (Niemelä and Kotze, 2009). This filtering action of urbanization clearly emerged when evaluating turnover and nestedness components of β -diversity between urban areas and the control: although the two sampling areas showed

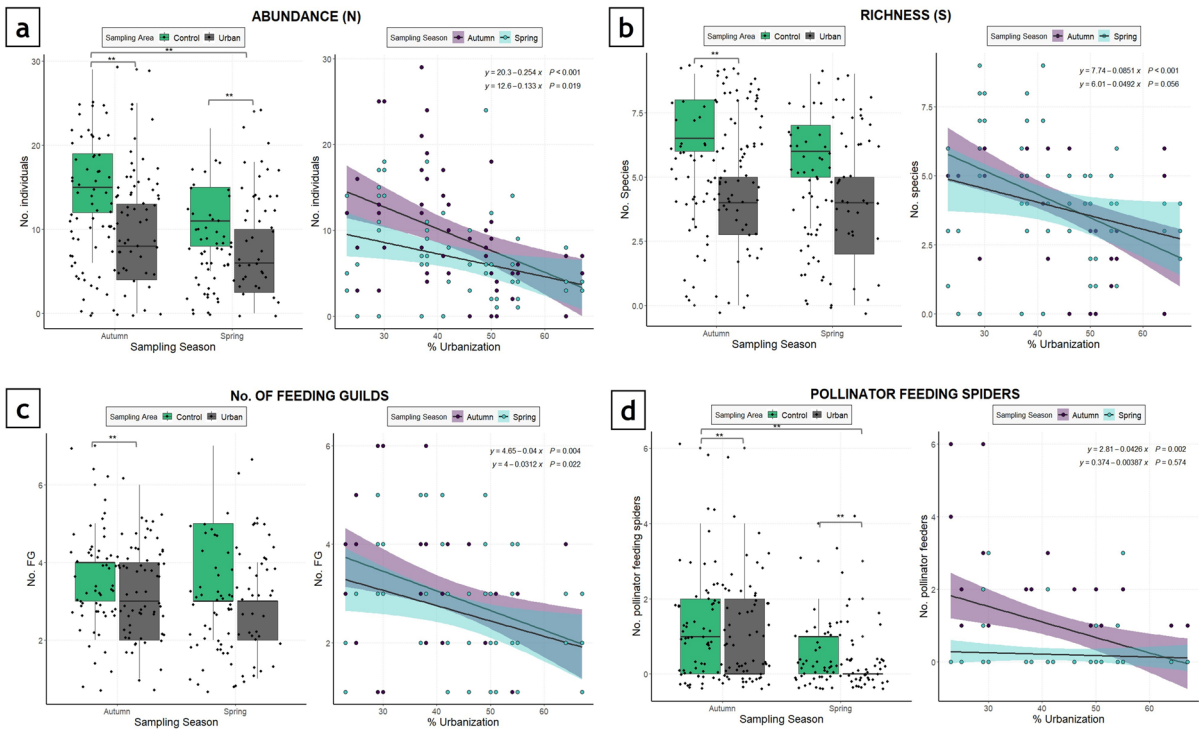


Fig. 5 Predicted values and distribution of spider abundance (a), spider richness (b), number of foraging guilds (c) and abundance of pollinator-feeding spiders (d). For each of these variables, the boxplots in the left panel represent the distribution of values in the control area (green) and in the urban area

(grey) in the two sampling seasons; the regression curves in the right panel represent the predicted values and their confidence intervals along the urbanization gradient (% Urbanization) inside the city only (control area excluded) in the two sampling seasons (purple = Autumn, blue = Spring)

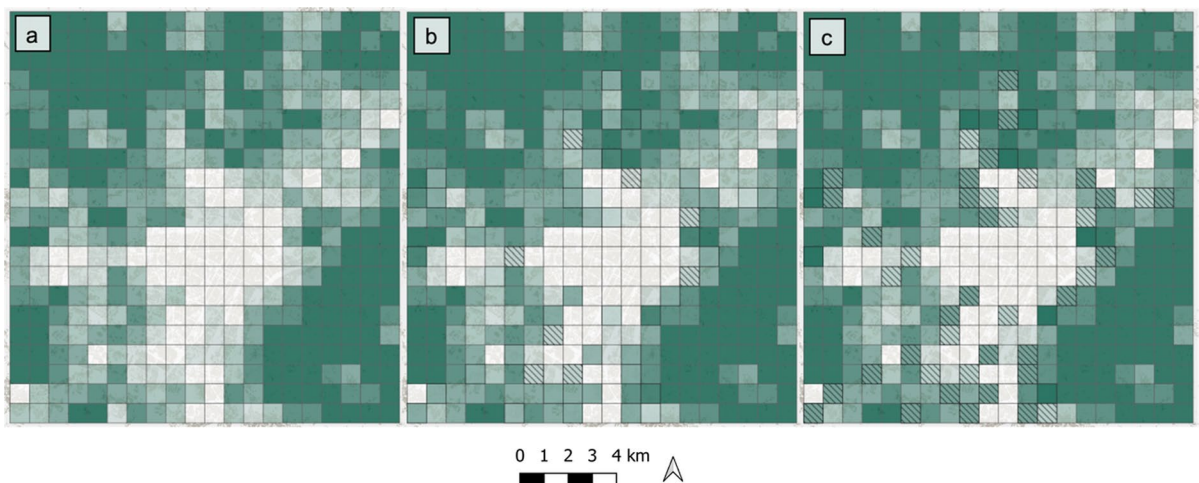


Fig. 6 Predicted values of biodiversity in Torino in 2024 (a), in 2040 (b) and in 2050 (c) according to European goals, with shades of green becoming darker at increasing biodiversity values. Priority cells are striped

similar levels of β -diversity, dissimilarity in urban samples was more explained by nestedness compared to control samples. This result suggests that the urban habitat contains a subset of the species found in the control. This biotic homogenization is likely due to homogeneous environmental conditions in the city, confirming the strong environmental filter exerted by urbanization (McKinney and Lockwood 1999; Knop 2016) that likely depletes species not preadapted to urban conditions, with a consequent decrease in diversity (Bates et al. 2011; Baldock et al. 2015; Piano et al. 2017; Fenoglio et al. 2020).

To verify whether this environmental filter effectively acts on species traits, we tested the response of two functional measures, namely the number of foraging guilds and the number of pollinator-feeding species. In accordance with results obtained for other arthropod taxa (Sattler et al. 2010a), the number of foraging guilds decreased in urban samples compared to control ones and declined along the urbanization gradient, revealing that urbanized sites are generally less functionally diverse than their semi-natural counterparts. This loss of functional feeding guilds is partially related to the decline of the most specialized groups, as confirmed by the significant reduction of pollinator-feeding species in the city in respect to control and along the urbanization gradient. When examining the role of functional turnover and nestedness in explaining functional β -diversity, we observed a similar pattern to what obtained for taxonomic β -diversity, confirming that urban foliage-dwelling spiders faced a functional homogenization, similarly to what observed for their ground counterpart (Piano et al. 2020a).

However, although the number of feeding guilds found in each site is significantly lower in the urban area than in the control, all feeding guilds found in the latter are also represented in the city. Therefore, we may assume that each site in the control area contains many different feeding guilds, while each city site is less diverse and contains only a few feeding guilds, randomly distributed across sampling sites. This result thus pinpoints the role of stochastic variability occurring in cities (Sattler et al. 2010b; Parris 2016) that may ultimately affect species composition and the functional structure of urban communities.

At the same time, the decreasing number of pollinator feeders along the urbanization gradient points out that the urbanization consistently favors

generalist species due to possible lower availability of resources and ecological niches (McKinney 2006; Knop 2016; Morelli et al. 2016; Callaghan et al. 2021, 2023). In addition, their abundance was consistently lower in Spring compared to Autumn, both in the control area and in the city, therefore being related to the phenology of the sampled spiders (but see Jiménez-Valverde and Lobo 2006, for contrasting patterns). Notably, the pollinator feeders resulted entirely absent from the urban area in Spring; this result underlies complex dynamics concerning the urban environment and possible source-sink processes that needs to be further investigated.

The prediction performed on future scenarios proved to be useful to identify areas where increasing the surface of urban parks may contribute most effectively to spider biodiversity. Specifically, in a preliminary step, we could demonstrate that the density of the built-up area is strictly correlated with the fragmentation process measured with specific landscape fragmentation metrics. Our results corroborate evidence in literature highlighting that urbanization and landscape fragmentation are highly correlated processes (e.g. Irwin and Bockstael 2007; Weng 2007; Li et al. 2019). Based on this assumption, our approach relying on the analysis of the biodiversity response along the urbanization gradient can provide novel insights to uncover the impacts of landscape fragmentation, offering valuable insights for land-use planning (Weng 2007), in light of the requirements of the European Biodiversity Strategy. Specifically, we identified 8 and 42 priority cells under the 3% and 5% scenarios respectively, where spider species richness is expected to show at least a 2% increase compared to current diversity values. Focusing management actions in these cells would therefore represent a good compromise between the efforts of increasing the surface of urban parks and the expected outcomes in terms of biodiversity. In light of this, integrating our priority cells in future urban plans should be considered as pivotal by urban planners to extend current urban parks.

Acknowledgements The authors are grateful to Nunzio Agostinacchio, Davide Giuva, Gianluca Gambatesa, Matteo Barbi, Alessandro Girodo for help in field sampling and to Marco Tagliabue for his help in sampling and identification of the specimens. We warmly thank Stano Pekár for providing his expert opinion on spider feeding specialization.

Author contributions A. P., E. P., M. T. and M. I. contributed to the study conception and design. Statistical analyses were performed by E. P. and A. P. M. T. and A.P. performed the field sampling. M.T and M.I. performed the identification of the specimens. M.I. obtained financial fundings. The first draft of the manuscript was written by A.P. and all authors reviewed and edited the first draft of the paper and provided important improvements to the original text. All authors read and approved the final manuscript.

Funding This work was realized within the framework of the “National Biodiversity Future Center—NBFC” funded under the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4—Call for tender No. 3138 of 16 December 2021, rectified by Decree n.3175 of 18 December 2021 of Italian Ministry of University and Research funded by the European Union – NextGenerationEU (Project code CN_00000033, Concession Decree No. 1034 of 17 June 2022 adopted by the Italian Ministry of University and Research, CUP D13C22001350001). The grant of EP is co-financed by the PON 30 “Research and Innovation” Programme (Axis IV “Education and Research for recovery” – Action IV.6 “Research contracts on Green themes”).

Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request. The list of the species and the coordinates of the sampling sites are provided within supplementary information files.

Declarations

Competing interests The authors declare no competing interests.

Consent to participate Not applicable.

Consent to publish Not applicable.

Ethical approval Not applicable.

Open Access This article is licensed under a Creative Commons Attribution-NonCommercial-NoDerivatives 4.0 International License, which permits any non-commercial use, sharing, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if you modified the licensed material. You do not have permission under this licence to share adapted material derived from this article or parts of it. The images or other third party material in this article are included in the article’s Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article’s Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by-nc-nd/4.0/>.

References

- Ancillotto L, Labadessa R (2023) Functional traits drive the fate of Orthoptera in urban areas. *Insect Conserv Divers* 17(2):304–311
- Argañaraz CI, Rubio GD, Gleiser RM (2018) Spider communities in urban green patches and their relation to local and landscape traits. *Biodivers Conserv* 27:981–1009
- Baldock KCR, Goddard MA, Hicks DM, Kunin WE, Mitschunas N et al (2015) Where is the UK’s pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proc R Soc B* 282(1803):20142849
- Bartoń K (2022) MuMIn: multi-model inference. R Package Version 1.46.6/r495. <https://cran.r-project.org/web/packages/MuMIn/index.html>. Accessed 10 Oct 2024
- Bates AJ, Sadler JP, Fairbrass AJ, Falk SJ, Hale JD, Matthews TJ (2011) Changing bee and hoverfly pollinator assemblages along an urban-rural gradient. *PLoS ONE* 6(8):e23459
- Bazzato E, Lallai E, Caria M et al (2022) Land-use intensification reduces multi-taxa diversity patterns of Small Woodlots Outside Forests in a Mediterranean area. *Agr Ecosyst Environ* 340:108149
- Beninde J, Veith M, Hochkirch A (2015) Biodiversity in cities needs space: a meta-analysis of factors determining intra-urban biodiversity variation. *Ecol Lett* 18(6):581–592. <https://doi.org/10.1111/ele.2015.18>
- Bell JR, Bohan DA, Shaw EM, Weyman GS (2005) Ballooning dispersal using silk: world fauna, phylogenies, genetics and models. *Bull Entomol Res* 95(2):69–114
- Bertellotti F, Sommer NR, Schmitz OJ, McCary MA (2023) Impacts of habitat connectivity on grassland arthropod metacommunity structure: a field-based experimental test of theory. *Ecol Evol* 13(11):e10686
- Blandenier G (2009) Ballooning of spiders (Araneae) in Switzerland: General Results from an Eleven-Year Survey. *Arachnology* 14(7):308–316. <https://doi.org/10.13156/araac.2009.14.7.308>
- Brice MH, Pellerin S, Poulin M (2016) Environmental filtering and spatial processes in urban riparian forests. *J Veg Sci* 27(5):1023–1035
- Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J* 9(2):378–400
- Bruggisser OT, Sandau N, Blandenier G, Fabian Y, Kehrli P et al (2012) Direct and indirect bottom-up and top-down forces shape the abundance of the orb-web spider *Argiope bruennichi*. *Basic Appl Ecol* 13(8):706–714
- Cabon V, Quénot H, Dubreuil V, Ridet A, Bergerot B (2024) Urban heat island and reduced habitat complexity explain spider community composition by excluding large and heat-sensitive species. *Land* 13(1):83
- Callaghan CT, Bowler DE, Pereira HM (2021) Thermal flexibility and a generalist life history promote urban affinity in butterflies. *Glob Change Biol* 27(15):3532–3546
- Callaghan CT, Palacio FX, Benedetti Y, Morelli F, Bowler DE (2023) Large-scale spatial variability in urban tolerance of birds. *J Anim Ecol* 92(2):403–416

- Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU, Perrings C, Venail P, Narwani A, Mace GM, Tilman D, Wardle DA, Kinzig AP, Daily GC, Loreau M, Grace JB, Larigauderie A, Srivastava DS, Naeem S (2012) Biodiversity loss and its impact on humanity. *Nature* 486 (7401):59–67 <https://doi.org/10.1038/nature11148>
- Cardoso P, Rigal F, Carvalho JC (2015) BAT—biodiversity assessment tools, an R package for the measurement and estimation of alpha and beta taxon, phylogenetic and functional diversity. *Methods Ecol Evol* 6:232–236
- Chase JM, McGill BJ, McGlenn DJ, May F, Blowes SA, Xiao X, Knight TM, Purschke O, Gotelli NJ (2018) Embracing scaledependence to achieve a deeper understanding of biodiversity and its change across communities. *Ecol Lett* 21(11):1737–1751. <https://doi.org/10.1111/ele.2018.21.10.1111/ele.13151>
- Chatelain M, Rüdiger J, Traugott M (2023) Urban-driven decrease in arthropod richness and diversity associated with group-specific changes in arthropod abundance. *Front Ecol Evol* 11:980387
- Christie FJ, Cassis G, Hochuli DF (2010) Urbanization affects the trophic structure of arboreal arthropod communities. *Urban Ecosyst* 13:169–180
- Coddington, J. A., Young, L. H., & Coyle, F. A. (1996). Estimating Spider Species Richness in a Southern Appalachian Cove Hardwood Forest. *J ARACHNOL*, 24(2): 111–128. <http://www.jstor.org/stable/3705945>
- Collins MK, Magle SB, Gallo T (2021) Global trends in urban wildlife ecology and conservation. *Biol Conserv* 261:109236. <https://doi.org/10.1016/j.biocon.2021.109236>
- Concepción ED, Moretti M, Altermatt F, Nobis MP, Obrist MK (2015) Impacts of urbanisation on biodiversity: the role of species mobility, degree of specialisation and spatial scale. *Oikos* 124(12):1571–1582
- Dahirel M, Dierick J, De Cock M, Bonte D (2017) Intraspecific variation shapes community-level behavioral responses to urbanization in spiders *Ecology* 98(9):2379–2390. <https://doi.org/10.1002/ecs.2017.98.10.1002/ecs.1915>
- Dampney FG, Opuni-Frinpong E, Collins AN, Addai J, Daniel KD, Schnerch B, Bentsi-Enchill F, Korjus H (2023) Taxonomic and community composition of epigeal arthropods in monoculture and mixed tree species plantations in a deciduous forest of Ghana. *J For Res* 34(3):641–653. <https://doi.org/10.1007/s11676-022-01508-y>
- De Souza ALT, Martins RP (2005) Foliage Density of Branches and Distribution of Plant-Dwelling Spiders. *Biotropica* 37(3):416–420. <https://doi.org/10.1111/btp.2005.37.10.1111/j.1744-7429.2005.00055.x>
- Dobyns JR (1997) Effects of Sampling Intensity on the Collection of Spider (Araneae) Species and the Estimation of Species Richness. *Environ Entomol* 26(2):150–162. <https://doi.org/10.1093/ee/26.2.150>
- Elvidge CD, Tuttle BT, Sutton PC, Baugh KE, Howard et al (2007) Global distribution and density of constructed impervious surfaces. *Sensors* 7(9):1962–1979
- Faeth SH, Bang C, Saari S (2011) Urban biodiversity: patterns and mechanisms. *Ann N Y Acad Sci* 1223(1):69–81
- Fattorini S (2014) Urban biodiversity hotspots are not related to the structure of green spaces: a case study of tenebrionid beetles from Rome. *Italy Urban Ecosyst* 17(4):1033–1045
- Fenoglio MS, Rossetti MR, Videla M (2020) Negative effects of urbanization on terrestrial arthropod communities: a meta-analysis. *Glob Ecol Biogeogr* 29(8):1412–1429
- Fenoglio MS, Calviño A, González E, Salvo A, Videla M (2021) Urbanisation drivers and underlying mechanisms of terrestrial insect diversity loss in cities. *Ecol Entomol* 46(4):757–771
- Hooper, DU, Chapin III FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75(1):3–35. <https://doi.org/10.1890/04-0922>
- INRAE (2021) Fragscape plugin for QGIS 3. Originally written by Mathieu Chailloux. Version 2.0.6. <https://github.com/HenrikSpa/GroupStats>. Accessed 30 September 2024
- Isaia M, Pantini P, Beikes S, Badino G (2007) Catalogo ragionato dei ragni (Arachnida, Araneae) del Piemonte e della Lombardia. Associazione Naturalistica Piemontese
- Irwin EG, Bockstael NE (2007) The evolution of urban sprawl: evidence of spatial heterogeneity and increasing land fragmentation. *Proc Natl Acad Sci* 104(52):20672–20677
- Jaeger JA (2000) Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. *Landsc Ecol* 15:115–130
- Jerardino M, Urones C, Fernández, JL (1991) Datos ecológicos de las arañas epigeas en dos bosques de la región mediterránea. *Orsis* 6:141–157
- Jiménez-Valverde A, Lobo JM (2006) Establishing reliable spider (Araneae, Araneidae and Thomisidae) assemblage sampling protocols: estimation of species richness, seasonal coverage and contribution of juvenile data to species richness and composition. *Acta Oecologica* 30(1):21–32
- Jones EL, Leather SR (2012) Invertebrates in urban areas: a review. *Eur J Entomol* 109(4):463–478
- Knop E (2016) Biotic homogenization of three insect groups due to urbanization. *Glob Change Biol* 22(1):228–236
- Kyrö K, Brenneisen S, Kotze DJ, Szallies A, Gerner M, Lehvävirta S (2018) Local habitat characteristics have a stronger effect than the surrounding urban landscape on beetle communities on green roofs. *Urban Forestry Urban Green* 29:122–130
- Lagucki E, Burdine JD, McCluney KE (2017) Urbanization alters communities of flying arthropods in parks and gardens of a medium-sized city. *PeerJ* 5:e3620
- Li F, Zheng W, Wang Y, Liang J, Xie S, Guo S et al (2019) Urban green space fragmentation and urbanization: a spatiotemporal perspective. *Forests* 10(4):333
- Magura T, Tóthmérész B, Molnár T (2008) A species-level comparison of occurrence patterns in carabids along an urbanisation gradient. *Land Urban Plan* 86(2):134–140. <https://doi.org/10.1016/j.landurbplan.2008.01.005>
- McGill BJ, Enquist B, Weiher E, Westoby M (2006) Rebuilding community ecology from functional traits. *TREE* 21(4):178–185. <https://doi.org/10.1016/j.tree.2006.02.002>
- McIntyre NE (2000) Ecology of Urban Arthropods: A Review and a Call to Action. *Ann Entomol* 93(4):825–835. [https://doi.org/10.1603/0013-8746\(2000\)093\[0825:EOUAAAR\]2.0.CO;2](https://doi.org/10.1603/0013-8746(2000)093[0825:EOUAAAR]2.0.CO;2)

- McKinney ML, Lockwood JL (1999) Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends Ecol Evol* 14(11):450–453
- McKinney ML (2006) Urbanization as a major cause of biotic homogenization. *Biol Conserv* 127:247–260
- McKinney ML (2008) Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosyst* 11:161–176
- Melliger RL, Rusterholz HP, Baur B (2017) Habitat-and matrix-related differences in species diversity and trait richness of vascular plants, Orthoptera and Lepidoptera in an urban landscape. *Urban Ecosyst* 20:1095–1107
- Menezes S, Baird DJ, Soares AMVM (2010) Beyond taxonomy: a review of macroinvertebrate trait-based community descriptors as tools for freshwater biomonitoring. *J Appl Ecol* 47(4):711–719. <https://doi.org/10.1111/jpe.2010.47.10.1111/j.1365-2664.2010.01819.x>
- Merckx T, Kaiser A, Van Dyck H (2018) Increased body size along urbanization gradients at both community and intraspecific level in macro-moths. *Glob Change Biol* 24(8):3837–3848
- Merckx T, Van Dyck H (2019) Urbanization-driven homogenization is more pronounced and happens at wider spatial scales in nocturnal and mobile flying insects. *Glob Ecol Biogeogr* 28(10):1440–1455
- Morelli F, Benedetti Y, Ibáñez-Álamo JD, Pape Moller A (2016) Evidence of evolutionary homogenization of bird communities in urban environments across Europe. *Glob Ecol Biogeogr* 25(11):1284–1293
- Nentwig W, Blick T, Bosmans R, Gloor D, Hänggi A, Kropf C (2023) Spiders of Europe. Version May 2021. <https://www.araneae.nmbe.ch>. Accessed 13 May 2024
- Niemelä J, Kotze JD (2009) Carabid beetle assemblages along urban to rural gradients: A review *Landscape Urban Plan* 92(2):65–71. <https://doi.org/10.1016/j.landurbplan.2009.05.016>
- Norton BA, Thomson LJ, Williams NSG, McDonnell MJ (2014) The effect of urban ground covers on arthropods: an experiment. *Urban Ecosyst* 17:77–99
- Otoshi MD, Bichier P, Philpott SM (2015) Local and landscape correlates of spider activity density and species richness in urban gardens. *Environ Entomol* 44:1043–1051
- Parris KM (2016) *Ecology of urban environments*. Wiley, Chichester
- Philpott SM, Cotton J, Bichier P, Friedrich RL, Moorhead LC, Uno S, Valdez M (2014) Local and landscape drivers of arthropod abundance, richness, and trophic composition in urban habitats. *Urban Ecosyst* 17:513–532
- Piano E, Bona F, Isaia M (2020a) Urbanization drivers differentially affect ground arthropod assemblages in the city of Turin (NW-Italy). *Urban Ecosyst* 23(3):617–629
- Piano E, Giuliano D, Isaia M (2020b) Islands in cities: urbanization and fragmentation drive taxonomic and functional variation in ground arthropods. *Basic Appl Ecol* 43:86–98
- Piano E, Souffreau C, Merckx T, Baardsen LF, Backeljau et al (2020c) Urbanization drives cross-taxon declines in abundance and diversity at multiple spatial scales. *Glob Change Biol* 26(3):1196–1211
- Piano E, De Wolf K, Bona F, Bonte et al (2017) Urbanization drives community shifts towards thermophilic and dispersive species at local and landscape scales. *Glob Change Biol* 23(7):2554–2564
- R Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>
- Saari S, Richter S, Higgins M, Oberhofer M, Jennings A, Faeth SH (2016) Urbanization is not associated with increased abundance or decreased richness of terrestrial animals—dissecting the literature through meta-analysis. *Urban Ecosyst* 19:1251–1264
- Sattler T, Borcard D, Arlettaz R, Bontadina F et al (2010a) Spider, bee, and bird communities in cities are shaped by environmental control and high stochasticity. *Ecology* 91(11):3343–3353
- Sattler T, Duelli P, Obrist MK et al (2010b) Response of arthropod species richness and functional groups to urban habitat structure and management. *Landscape Ecol* 25:941–954
- Scharff N, Coddington JA, Griswold CE, Hormiga G, de Place Bjørn P (2003) When to quit? Estimating spider species richness in a northern European deciduous forest. *J Arachnol* 31(2):246–273. [https://doi.org/10.1636/0161-8202\(2003\)031\[0246:WTQESS\]2.0.CO;2](https://doi.org/10.1636/0161-8202(2003)031[0246:WTQESS]2.0.CO;2)
- Sørensen, LL, Coddington JA, Scharff N (2002) Inventorying and Estimating Subcanopy Spider Diversity Using Semi-quantitative Sampling Methods in an Afrotropical Forest. *Environ Entomol* 31(2):319–330. <https://doi.org/10.1603/0046-225X-31.2.319>
- Southwood TRE (1977) Habitat the Templet for Ecological Strategies? *J Anim Ecol* 46(2):336–365. <https://doi.org/10.2307/3817>
- Southwood TRE (1988) Tactics, strategies and templets. *Oikos* 52(1):3–18. <https://doi.org/10.2307/3565974>
- Srivastava DS, Lawton JH (1998) Why more productive sites have more species: an experimental test of theory using tree-hole communities. *Am Nat* 152(4):510–529
- Svenningsen CS, Bowler DE, Hecker S, Bladt J et al (2022) Flying insect biomass is negatively associated with urban cover in surrounding landscapes. *Divers Distrib* 28(6):1242–1254
- Tolve et al (2024) An inventory of the spider species of the “LaMandria” Regional Natural Park (NW-Italy) (Arachnida:Araneae). *FragmentaEntomologica*
- Toti DS, Coyle FA, Miller JA (2000) A structured inventory of Appalachian grass bald and heath bald spider assemblages and a test of species richness estimator performance. *J Arachnol* 28(3):329–345. [https://doi.org/10.1636/0161-8202\(2000\)028\[0329:ASIOAG\]2.0.CO;2](https://doi.org/10.1636/0161-8202(2000)028[0329:ASIOAG]2.0.CO;2)
- Turrini T, Knop E (2015) A landscape ecology approach identifies important drivers of urban biodiversity. *Glob Change Biol* 21(4):1652–1667
- Urones C, Puerto A (1988) Ecological study of the clubinoidea and thomisoidea (araneae) in the spanish central system. *Revue Arachnologique* 8(1):1–32
- Violle C, Navas ML, Vile D, Kazakou E, Fortunel C et al (2007) Let the concept of trait be functional! *Oikos* 116(5):723–902
- Webb CT, Hoeting JA, Ames GM, Pyne MI, LeRoy Poff N (2010) A structured and dynamic framework to advance traits-based theory and prediction in ecology. *Ecol Lett* 13(3):267–283

- Weng YC (2007) Spatiotemporal changes of landscape pattern in response to urbanization. *Landsc Urban Plan* 81(4):341–353
- World Spider Catalog (2024) World Spider Catalog. Version 25.0. Natural History Museum Bern. <http://wsc.nmbe.ch>. Accessed March 2024
- Zeng H, Zhu Y, Zhang J, Li C, Zhang J, Liu H et al (2024) Butterfly taxonomic and functional diversity in the urban green spaces of Hefei city. *J for Res* 35(1):55
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects modelling for nested data. In: *Mixed effects models and extensions in ecology with R. Statistics for biology and health*. Springer, New York
- Zuur AF, Ieno EI, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol* 1(1):3–14
- Zuur AF, Ieno EN (2016) A protocol for conducting and presenting results of regression-type analyses. *Methods Ecol Evol* 7(6):636–645

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.